MAGILL'S ENCYCLOPEDIA OF SCIENCE

PLANT LIFE

Volume 1

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Acid Precipitation–DNA: Recombinant Technology

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PUBLISHER'S NOTE

Magill's Encyclopedia of Science: Plant Life is designed to meet the needs of college and high school students as well as nonspecialists seeking general information about botany and related sciences. The definition of "plant life" is quite broad, covering the range from molecular to macro topics: the basics of cell structure and function, genetic and photosynthetic processes, evolution, systematics and classification, ecology and environmental issues, and those forms of life—archaea, bacteria, algae, and fungi—that, in addition to plants, are traditionally studied in introductory botany courses. A number of practical and issue-oriented topics are covered as well, from agricultural, economic, medicinal, and cultural uses of plants to biomes, plant-related environmental issues, and the flora of major regions of the world. (Readers should note that, although cultural and medicinal uses of plants are occasionally addressed, this encyclopedia is intended for broad information and educational purposes. Those interested in the use of plants to achieve nutritive or medicinal benefits should consult a physician.)

Altogether, the four volumes of *Plant Life* survey 379 topics, alphabetically arranged from *Acid precipitation* to *Zygomycetes*. For this publication, 196 essays have been newly acquired, and 183 essays are previously published essays whose contents were reviewed and deemed important to include as core topics. The latter group originally appeared in the following Salem publications: *Magill's Survey of Science: Life Science* (1991), *Magill's Survey of Science: Life Science, Supplement* (1998), *Natural Resources* (1998), *Encyclopedia of Genetics* (1999), *Encyclopedia of Environmental Issues* (2000), *World Geography* (2001), and *Earth Science* (2001). All of these previously published essays have been thoroughly scrutinized and updated by the set's editors. In addition to updating the text, the editors have added new bibliographies at the ends of all articles.

New appendices, providing essential research tools for students, have been acquired as well:

- a "Biographical List of Botanists" with brief descriptions of the contributions of 134 famous naturalists, botanists, and other plant scientists
- a Plant Classification table
- a Plant Names appendix, alphabetized by common name with scientific equivalents
- another Plant Names appendix, alphabetized by scientific name with common equivalents
- a "Time Line" of advancements in plant science (a discursive textual history is also provided in the encyclopedia-proper)
- a Glossary of 1,160 terms
- a Bibliography, organized by category of research
- a list of authoritative Web sites with their sponsors, URLs, and descriptions

Every essay is signed by the botanist, biologist, or other expert who wrote it; where essays have been revised or updated, the name of the updater appears as well. In the tradition of Magill reference, each essay is offered in a standard format that allows readers to predict the location of core information and to skim for topics of interest: The title of each article lists the topic as it is most likely to be looked up by students; the "Category" line indicates pertinent scientific subdiscipline(s) or area(s) of research; and a capsule "Definition" of the topic follows. Numerous subheads guide the reader

through the text; moreover, key concepts are italicized throughout. These features are designed to help students navigate the text and identify passages of interest in context. At the end of each essay is an annotated list of "Sources for Further Study": print resources, accessible through most libraries, for additional information. (Web sites are reserved for their own appendix at the end of volume 4.) A "See also" section closes every essay and refers readers to related essays in the set, thereby linking topics that, together, form a larger picture. For example, since all components of the plant cell are covered in detail in separate entries (from the *Cell wall* through *Vacuoles*), the "See also" sections for these dozen or so essays list all other essays covering parts of the cell as well as any other topics of interest.

Approximately 150 charts, sidebars, maps, tables, diagrams, graphs, and labeled line drawings offer the essential visual content so important to students of the sciences, illustrating such core concepts as the parts of a plant cell, the replication of DNA, the phases of mitosis and meiosis, the world's most important crops by region, the parts of a flower, major types of inflorescence, or different classifications of fruits and their characteristics. In addition, nearly 200 black-and-white photographs appear throughout the text and are captioned to offer examples of the important phyla of plants, parts of plants, biomes of plants, and processes of plants: from bromeliads to horsetails to wheat; from Arctic tundra to rain forests; from anthers to stems to roots; from carnivorous plants to tropisms.

Reference aids are carefully designed to allow easy access to the information in a variety of modes: The front matter to each of the four volumes includes the volume's contents, followed by a full "Alphabetical List of Contents" (of all the volumes). All four volumes include a "List of Illustrations, Charts, and Tables," alphabetized by key term, to allow readers to locate pages with (for example) a picture of the apparatus used in the *Miller-Urey Experiment*, a chart demonstrating the genetic offspring of *Mendel's Pea Plants*, a map showing the world's major zones of *Desertification*, a cross-section of *Flower Parts*, or a sampling of the many types of *Leaf Margins*. At the end of volume 4 is a "Categorized Index" of the essays, organized by scientific subdiscipline; a "Biographical Index," which provides both a list of famous personages and access to discussions in which they figure prominently; and a comprehensive "Subject Index" including not only the personages but also the core concepts, topics, and terms discussed throughout these volumes.

Reference works such as *Magill's Encyclopedia of Science: Plant Life* would not be possible without the help of experts in botany, ecology, environmental, cellular, biological, and other life sciences; the names of these individuals, along with their academic affiliations, appear in the front matter to volume 1. We are particularly grateful to the project's editor, Bryan Ness, Ph.D., Professor of Biology at Pacific Union College in Angwin, California. Dr. Ness was tireless in helping to ensure thorough, accurate, and up-to-date coverage of the content, which reflects the most current scientific knowledge. He guided the use of commonly accepted terminology when describing plant life processes, helping to make *Magill's Encyclopedia of Science: Plant Life* easy for readers to use for reference to complement the standard biology texts.

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ACID PRECIPITATION

Categories: Environmental issues; pollution

Acid precipitation is rain, snow, or mist which has a pH lower than unpolluted precipitation. Increased levels of acid precipitation have significant effects on food chains and ecosystems.

Precipitation—rain, snow, hail, sleet, or mist—is naturally acidified by carbonic acid (H_2CO_3). Carbon dioxide (CO_2) in the atmosphere reacts with water molecules, lowering the pH of precipitation to 5.6. A pH scale is used to measure a solution's acidity or alkalinity; pH is defined as the negative logarithm of the concentration of hydrogen ions, H^+. A solution with a pH of 7.0 is neutral. A pH lower than 7 is acidic, and a pH greater than 7 is alkaline. Other acidic substances are also present in the atmosphere, causing "unpolluted" precipitation to have a pH approaching 5.0. Solutions with a pH of 5.0 or less have concentrations of hydroxyl ion, or OH^-, and carbonate ion, or CO_3^-, approaching zero.

Acid precipitation is the name given to rain or snow contaminated with oxides of sulfur (SO_x) and oxides of nitrogen (NO_x). These chemicals combine with water droplets to form sulfuric acid and nitric acid. SO_x is formed by combustion of materials containing sulfur, and NO_x is formed by oxidation of molecular nitrogen in the atmosphere during combustion. SO_x sometimes arises from natural sources such as volcanoes and geyser fields, and NO_x is formed by lightning. Downwind of smelting facilities, hydrochloric acid (HCl) and hydrofluoric acid (HF) may also contribute to acid precipitation. Acid precipitation may detrimentally change soil chemistry, either by stripping nutrients, especially magnesium and calcium, or mobilizing *phytotoxic trace elements* (elements toxic to plants).

Geographic Extent of Damage

Acid precipitation is a regional problem. SO_x and NO_x can travel many thousands of kilometers in the atmosphere after being emitted by large, stationary sources, especially those that have very high smokestacks. These pollutants are slowly transformed into sulfuric and nitric acid aerosols and are incorporated into precipitation, which eventually makes contact with the earth's surface. Acid precipitation in the eastern United States contains more SO_x than precipitation in the western United States, which contains more NO_x.

In North America, acid precipitation and *dry deposition* (of acid aerosol particles) are major environmental problems in New England and New York State and in Ontario and Quebec. These regions attribute much of their acid precipitation to emissions from large coal-burning plants in the American Ohio Valley. Scandinavian activists blame coal-burning power plants and factory emissions in the British Isles for that region's acid rain problems. Central Europe—including Poland, the Czech Republic, Slovakia, and eastern Germany—has many power plants and factories that burn high-sulfur coal. Acid-laden pollution plumes stretch thousands of kilometers downwind from smokestacks in that region.

Controlled Studies

Controlled experiments on individual plant species have revealed short-term damage to a limited number of those species. Experiments using *simulated acid rain* (SAR) are difficult to extrapolate to field conditions, where the specific pollutants and pH levels vary widely over time. In controlled conditions, studies showed no link between SAR and yield in Amsoy soybeans. However, field studies demonstrated that acid deposition does decrease yield in Amsoy soybeans.

Acid precipitation influences plant diseases by acting on both pathogens and host organisms. Seedlings of *Pinus rigida*, *Pinus echinata*, *Pinus taeda*, and *Pinus strobus* exposed to SAR of pH 3.0 had a 100 percent mortality rate because of fungal *damping-off*, a diseased condition of seedlings marked by wilting or rotting. Red spruce seedlings subjected to dilute sulfuric acid mist developed brown lesions on their needles, followed by needle drop. Studies showed a reduction in the growth of sugar maple seedlings following exposure to low-pH moisture, and that seedling survival decreased with increasing acidity.

Crop and Forest Decline

In field experiments, soybeans have shown reduced yields with decreasing pH (increasing acidity) of moisture applied. Yields of seed and seed protein are both reduced in soybeans exposed to high acidity. A lower number of seed pods were found in plants exposed to high acidity, compared to control plants.

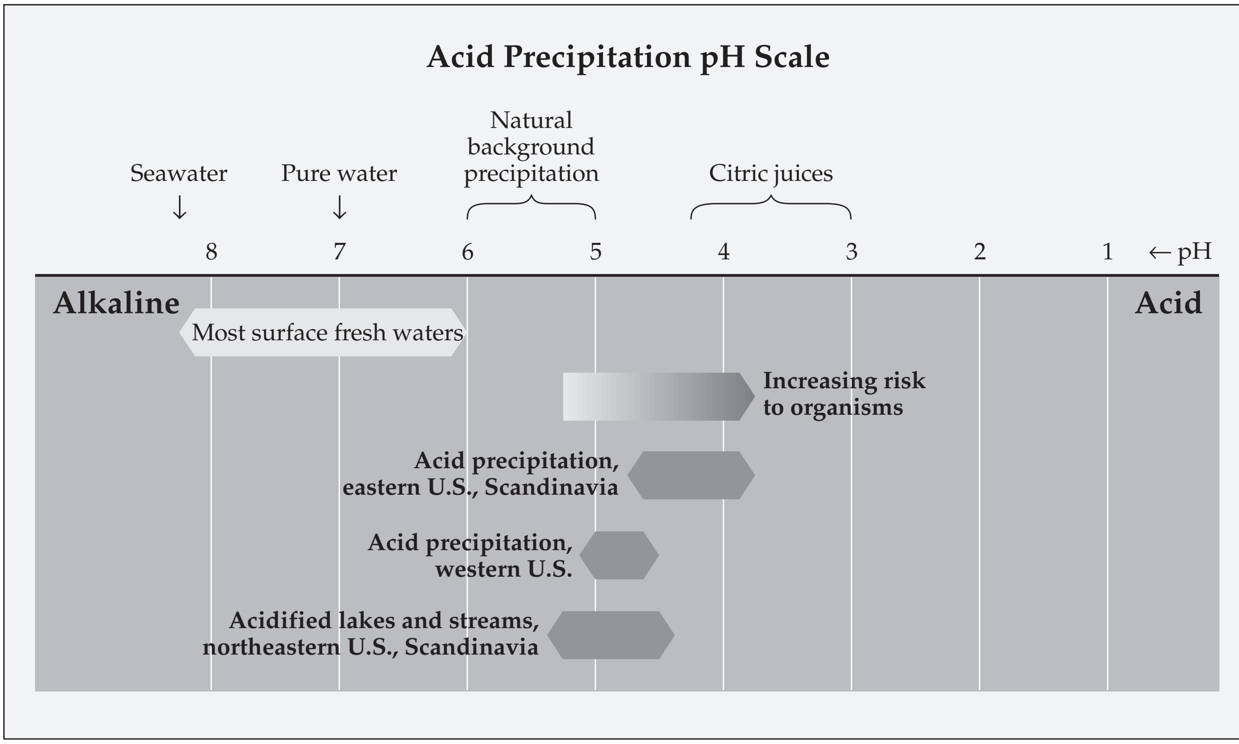
Acid precipitation causes detrimental long-term effects in most ecosystems, especially forests. Root systems under acidic stress show great variability in tolerance and injury. Acidic stress on roots decreases root growth, measured by a reduction in root length, and severely damaged trees have more fine roots with opaque tip zones than do slightly damaged trees. Some scientists have suggested that the radical growth rate in yellow pines in the southeastern United States may be reduced by acid precipitation.

PhotoDisc

Activists blame coal-burning power plants and factory emissions for acid rain problems. After being emitted by large, stationary sources, especially those that have very high smokestacks, pollutants can travel thousands of kilometers in the atmosphere. Those that are transformed into sulfuric and nitric acid aerosols are incorporated into precipitation, which eventually makes contact with the earth's surface.

Since the 1960's Central European soils have been progressively acidified, altering soil buffering capacities. Acid rain containing nitrates (which are not immobilized in soil) played an important role in this soil acidification. Acidification has reduced the magnesium, calcium, and potassium available for nutrient uptake by plants and has affected root growth. One-quarter of European forests are moderately or severely damaged by acid precipitation, with dry deposition believed (by scientists and politicians) to be largely responsible. This pattern of damage, first detected in the 1980's, has been called *neuartige Waldschäden* (literally, "new-type forest decline"). It has been detected throughout Central Europe at all elevations and on all soil types. *Waldschäden* is most pronounced downwind of major air pollution sources.

Abnormally high numbers of red spruce have died in the high-elevation northern Appalachian Mountains since the 1960's. This die-off has been attributed to high rates of acid deposition (up to 4 kiloequivalents of hydronium ions per hectare per year) and exposure to acid fog droplets for up to two thousand hours per year. Very high levels of trace metals (known to be phytotoxic) have accumulated in the region.



Note: The acid precipitation pH ranges given correspond to volume-weighted annual averages of weekly samples.
Source: Adapted from John Harte, "Acid Rain," in *The Energy-Environment Connection*, edited by Jack M. Hollander, 1992.

Aquatic Ecosystems

Most freshwater ecosystems range from pH 6.0 to pH 8.0. In limestone terrain, acid precipitation is neutralized by dissolution of calcium carbonate. As a freshwater environment becomes acidified, the number of species it supports declines. When conditions are more acidic than pH 5.5, dissolved inorganic carbon exists only as dissolved carbon dioxide. Planktonic algae, which can use low levels of dissolved inorganic carbon, are favored in these environments. Acid environments greatly reduce the numbers of herbivores that graze on aquatic plants; this is thought to explain why filamentous green algae are found in most acidified lakes. Scientists point out that it is difficult to separate the effects that acidification alone produces in an aquatic ecosystem.

Anita Baker-Blocker

See also: Air pollution; Old-growth forests; Root uptake systems.

Sources for Further Study

Adriano, D. C., and A. H. Johnson, eds. *Biological and Ecological Effects*. Vol. 2 in *Acidic Precipitation*. New York: Springer-Verlag, 1989. Extremely detailed volume contains individual chapters by different authors, devoted to the effects of acid precipitation on trees, crops, and freshwater biota. Reviews damage to North American and European forests. Each chapter offers an extensive bibliography of acid precipitation research relevant to the topic. Includes many charts and diagrams, fully indexed.

Ahrens, C. Donald. *Meteorology Today*. 6th ed. Pacific Grove, Calif.: Brooks/Cole, 2000. College meteorology text reviews the sources of acid precipitation and where its major effects occur. Includes illustrations, bibliography, index, and glossary.

Canter, Larry W. *Acid Rain and Dry Deposition*. Chelsea, Mich.: Lewis, 1989. About sixty pages of this book are devoted to geographic extent of acid rain and the chemical transformations and transport of pollutants in the atmosphere. Covers the effects of acid rain on vegetation, crops, and floral species. It is a guide to research done through the 1980's on acid rain. Comprehensive literature review and bibliography; index.

Lutgens, Frederick K., and Edward J. Tarbuck. *The Atmosphere*. 8th ed. Upper Saddle River, N.J.: Prentice Hall, 2001. Excellent introductory meteorology text with good description of acid precipitation and its effects, including a color photograph of trees in the Great Smokey Mountains severely damaged by acid precipitation. Color illustrations, bibliography, index, and glossary.

ACTIVE TRANSPORT

Categories: Cellular biology; physiology; transport mechanisms

Active transport is the process by which cells expend energy to move atoms or molecules across membranes, requiring the presence of a protein carrier, which is activated by ATP. Cotransport is active transport that uses a carrier that must simultaneously transport two substances in the same direction. Countertransport is active transport that employs a carrier that must transport two substances in opposite directions at the same time.

Biologists in nearly every field of study have discovered that one of the major methods by which organisms regulate their metabolisms is by controlling the movement of molecules into cells or into organelles such as the nucleus. This regulation is possible because of the semipermeable nature of *cellular membranes*. The membranes of all living cells are fluid mosaic structures composed primarily of lipids and proteins. The lipid molecules are *aliphatic*, which means that their molecular structure exhibits both a hydrophilic (water-attracted) and a hydrophobic (water-repelling) portion. These aliphatic molecules form a double layer: The hydrophilic heads are arranged opposite one another on the inner and outer surfaces, and the hydrophobic tails are aligned across from one another within the interior, sandwiched between the hydrophilic heads. The protein in the membrane is interspersed periodically throughout the lipid bilayer. Some of the protein, referred to as *peripheral protein*, penetrates only one of the lipid layers. The *integral protein*, as the remaining protein is called, extends through both layers of lipid to interface with the environment on both the internal and external surfaces of the membrane. These integral proteins can serve as transport channels and carriers.

Cellular Energy

Transport across the membrane is accomplished by three different mechanisms: *simple diffusion*, *facilitated diffusion*, and active transport. The first two mechanisms are referred to as passive processes because they do not require the direct input of cellular energy, and they involve transport down a *concentration gradient*, that is, from the side with a higher concentration to the side with a lower concentration of the substance being transported. In many instances, however, substances are transported across a membrane from the side with a low concentration to the side containing a greater concentration. This "uphill" movement across membranes is called active transport, and it requires the expenditure of cellular energy.

Cellular energy, produced by the biological oxidation of fuels such as carbohydrates, is stored as adenosine triphosphate (ATP). When this high-energy phosphate is hydrolyzed, the stored energy is released to drive cellular reactions such as active transport. The ATPase protein located in membranes belongs to one of the groups of enzymes which hydrolyze ATP. The mechanism has not been completely deciphered, but it appears as though a protein carrier molecule binds with the substance to be transported at the surface on one side of the membrane. This binding occurs at a specific activated region on the carrier protein called the *active site*. After combining with the carrier, the substance is moved across the membrane and released at the surface on the other side of the membrane. ATP is then hydrolyzed by an ATPase, and the energy released in this reaction prepares the protein carrier for attachment to another molecule to be transported by reactivating the active site. There is some question as to whether ATPase is a component of the carrier molecule or functions separately from it. Regardless of the spatial arrangement, the two molecules are intimately related in the active transport process.

Cotransport and Countertransport

There are two important modifications of the active transport process: *cotransport* and *countertransport*. Cotransport, or *symport*, involves a specialized protein molecule referred to as a symport carrier. A symport carrier has two attachment sites. One site is for the attachment of the molecule to be transported, and the other is for the attachment of a second molecule, which can be referred to as the *synergist*. Both the molecule to be transported and the synergist must be bound to the symport carrier before transport across the membrane can take place. The synergist is moved down a concentration gradient, and this downhill flow of the synergist drives the carrier to transport both molecules. In order to keep the synergist moving down a concentration gradient when attached to the symport carrier, the synergist must be pumped back across the membrane. This movement of the synergist in the opposite direction is mediated by a protein carrier activated by the energy released from the hydrolysis of ATP by an ATPase.

Countertransport, or *antiport*, also utilizes a specialized carrier with two attachment sites. This antiport carrier binds with the molecule to be transported at one of the attachment sites, and a second molecule, which can be called the *antagonist*, binds at the other. The carrier moves the molecule to be transported across the membrane while simultaneously moving the antagonist in the opposite direction. Again, both molecules must be attached to the antiport carrier before either can be transported, and the flow of the antagonist down a concentration gradient drives the transport by the carrier in both directions. The antagonist is pumped back across the membrane by a protein carrier activated by the energy released from the hydrolytic action of an ATPase on ATP. This action maintains a concentration gradient favorable for transport when the antagonist is attached to the antiport carrier.

Transport in Action

The presence of these three active transport mechanisms has been well documented. Calcium, for example, has been shown to be pumped from the cell by a carrier protein activated by the hydrolysis of ATP. Sugars for energy and carbohydrate structure must be cotransported into the cell by a symport carrier that utilizes the sodium ion as a synergist. At least two countertransport ion pumps have been identified. One pumps the potassium ion into the cell at the same time that it pumps the hydrogen ion out. The second pumps the potassium ion into the cell while the antagonist, sodium, is moved in the opposite direction. It is likely that numerous other active transport systems exist that have not yet been positively identified.

A protein carrier is one of the basic components of any active transport mechanism. Although no specific carrier molecule has yet been positively identified, there is ample indirect evidence to support the presence of such a protein. Much of this evidence comes from studies showing that active transport exhibits *saturation kinetics*. This means that the transport of a specific ion will increase as the concentration increases, up to a certain point. At this point, further increases in concentration will have no effect on transport. These results strongly suggest that the ion is binding with another molecule in the membrane, such as a carrier protein, which is limited in concentration and becomes saturated. Studies have also shown the transport of some substances to be competitively inhibited by the presence of another, very similar, substance. This indicates that both substances are competing for the same site on a membrane molecule, such as a protein carrier.

Role of Active Transport

The ability to accumulate substances against a concentration gradient is necessary for the normal function and survival of cells. There are numerous examples, however, of active transport being intimately involved in the regulation of some important biological processes. In the plant kingdom, sugar is produced by photosynthesis in the green leaves. This sugar must be transported out of the leaves and into nonphotosynthetic tissues, such as roots or fruit, through specialized transport cells in the *phloem*. The loading of sugars into the phloem is dependent on an active cotransport mechanism.

Almost every field of life science is concerned with *gene regulation*. Genes are continually being induced (activated) or repressed (deactivated) as organisms develop and change from the time of their conception until their death. Repression is usually caused by the presence of a protein molecule in the cell nucleus, but induction may very often be the result of metabolites being actively transported into the cell or nucleus. Hence, the active transport mechanisms may be a very important component of gene regulation.

D. R. Gossett

See also: Cells and diffusion; Osmosis, simple diffusion, and facilitated diffusion; Vesicle-mediated transport.

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ADAPTATIONS

Categories: Evolution; genetics

The results of natural selection in which succeeding generations of organisms become better able to live in their environments are called adaptations. Many of the features that are most interesting and beautiful in biology are adaptations. Specialized structures, physiological processes, and behaviors are all adaptations when they allow organisms to cope successfully with the special features of their environments.

Adaptations ensure that individuals in populations will reproduce and leave well-adapted offspring, thus ensuring the survival of the species. Adaptations arise through *mutations*—inheritable changes in an organism's genetic material. These rare events are usually harmful, but occasionally they give specific survival advantages to the mutated organism and its offspring. When certain individuals in a population possess advantageous mutations, they are better able to cope with their specific environmental conditions and, as a result, will contribute more offspring to future generations than those individuals that lack the mutation. Over time, the number of individuals that have the advantageous mutation will increase in the population at the expense of those that do not have it. Individuals with an advantageous mutation are said to have a higher *fitness* than those without it, because they tend to have comparatively higher survival and reproductive rates. This is *natural selection*.

Natural Selection

Over very long periods of time, evolution by natural selection results in increasingly better adaptations to environmental circumstances. Natural selection is the primary mechanism of evolutionary change, and it is the force that either favors or selects against mutations. Although natural selection acts on individuals, a population gradually changes as those with adaptations become better represented in the total population. Most flowering plants, for example, are unable to grow in soil containing high concentrations of certain elements (for example, heavy metals) commonly found in mine tailings. Therefore, an adaptation that conferred resistance to these elements would open up a whole new habitat where competition with other plants would be minimal. Natural selection would favor the mutations, which confer specific survival advantages to those that carry them and impose limitations on individuals lacking these advantages. Thus, plants with special adaptations for resistance to the poisonous effects of heavy metals would have a competitive advantage over those that find heavy metals toxic. These attributes would be passed to their more numerous offspring and, in evolutionary time, resistance to heavy metals would increase in the population.

Types of Adaptations

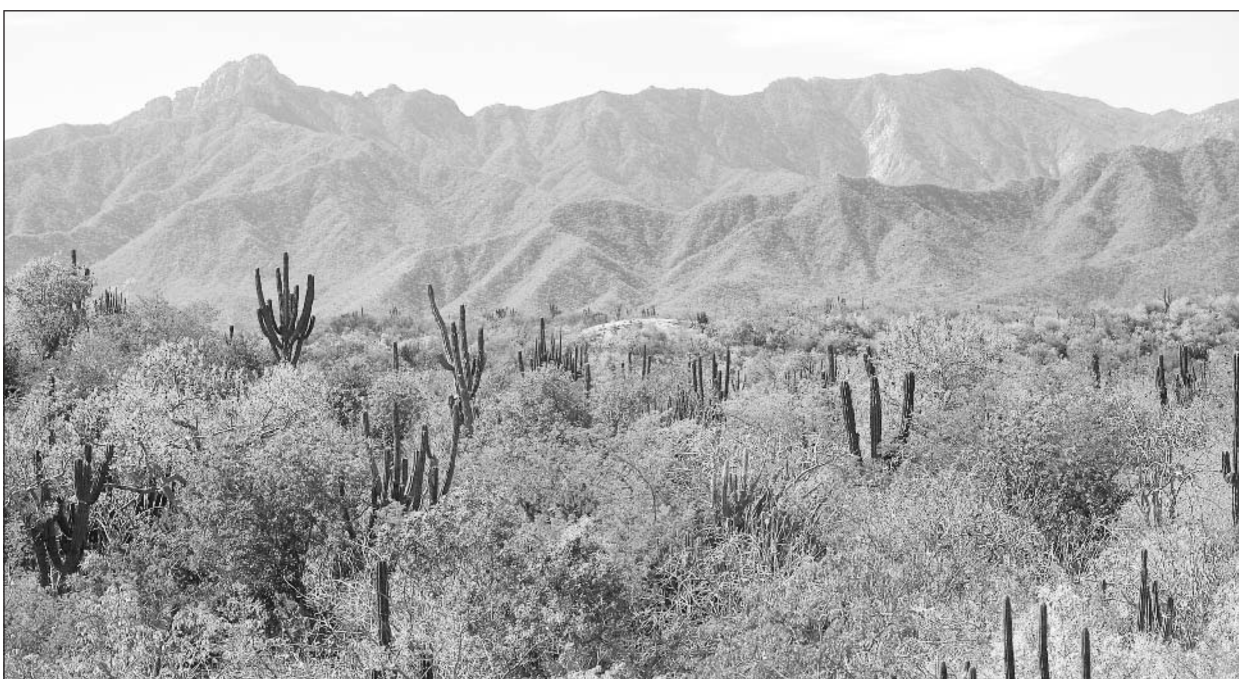
Although natural selection serves as the instrument of change in shaping organisms to very specific environmental features, highly specific adaptations may ultimately be a disadvantage. Adaptations that are specialized may not allow sufficient *flexibility* (generalization) for survival in changing environmental conditions. The degree of adaptative specialization is ultimately controlled by the nature of the environment. Environments, such as the tropics, that have predictable, uniform climates and have had long, uninterrupted periods of climatic stability are biologically complex and have high species *diversity*. Scientists generally believe that this diversity results, in part, from complex competition for resources and from intense predator-prey relationships. Because of these factors, many narrowly specialized adaptations have evolved when environmental stability and predictability prevail. By contrast, harsh physical environments with unpredictable or erratic climates seem to favor organisms with general adaptations, or adaptations that allow flexibility. Regardless of the environment type, organisms with both general and specific adaptations exist because both types of adaptation enhance survival under different environmental circumstances.

Structural adaptations are parts of organisms that enhance their survival ability. Camouflage that enables organisms to hide from predators or their prey; protective spines on cacti that inhibit organisms that might feed on them; color, scent, or shape of flowers that promotes seed production—these are all structural adaptations. These adaptations enhance survival because they assist individuals in dealing with the rigors of the physical environment, obtaining nourishment, competing with others, or attracting pollinators.

Metabolism is the sum of all chemical reactions taking place in an organism, whereas physiology consists of the processes involved in an organism carrying out its function. *Physiological adaptations* are changes in the metabolism or physiology of organisms, giving them specific advantages for a given set of environmental circumstances. Because organisms must cope with the rigors of their physical environments, physiological adaptations for temperature regulation, water conservation, varying metabolic rate, and dormancy allow organisms to adjust to the physical environment or respond to changing environmental conditions.

Adaptations and Environment

Desert environments, for example, pose a special set of problems for organisms. Hot, dry environments require physiological mechanisms that enable organisms to conserve water and resist prolonged periods of high temperature. Evolution has favored a specialized form of photosynthesis in cacti and other succulents inhabiting arid regions. Crassulacean acid metabolism (CAM) photosynthesis allows plants with this physiological adaptation to absorb carbon dioxide at night, when relative humidity is comparatively high and air temperatures relatively low. Taking in carbon dioxide during the day would dehydrate plants, because opening the pores through which gas exchange takes place al-



Corbis

Structural adaptations are parts of organisms that enhance their survival ability. For example, protective spines on cacti can inhibit organisms that might feed on them.

lows water to escape from the plant. CAM photosynthesis, therefore, allows these plants to exchange the atmospheric gases essential for their metabolism at night, when the danger of dehydration is minimized.

Because organisms must also respond and adapt to an environment filled with other organisms—including potential predators and competitors—adaptations that minimize the negative effects of biological interactions are favored by natural selection. Often the interaction among species is so close that each species strongly influences the others and serves as the selective force causing change. Under these circumstances, species evolve together in a process called *coevolution*. The adaptations resulting from coevolution have a common survival value to all the species involved in the interaction. The coevolution of flowers and their pollinators is a classic example of these tight associations and their resulting adaptations.

Speciation

Adaptations can be general or highly specific. General adaptations define broad groups of organisms whose lifestyles are similar. At the species level, however, adaptations are more specific and give narrow definition to those organisms that are more closely related to one another. Slight variations in a single characteristic, such as bill size in the seed-eating Galapágos finches, are adaptive in that they enhance the survival of several closely related species. An understanding of how adaptations function to make species distinct also furthers the knowledge of how species are related to one another.

Why so many species exist is one of the most intriguing questions of biology. The study of adaptations offers biologists an explanation. Because there are many ways to cope with the environment, and because natural selection has guided the course of evolutionary change for billions of years, the vast variety of species existing on the earth today is simply an extremely complicated variation on the theme of survival.

Robert W. Paul, updated by Bryan Ness

See also: Adaptive radiation; C_4 and CAM photosynthesis; Coevolution; Competition; Evolution: gradualism vs. punctuated equilibrium.

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ADAPTIVE RADIATION

Categories: Ecology; ecosystems; evolution; genetics

In adaptive radiation, numerous species evolve from a common ancestor introduced into an environment with diverse ecological niches. The progeny evolve genetically into customized variations of themselves, each adapting to survive in a particular niche.

In 1898 Henry F. Osborn identified and developed the evolutionary phenomenon known as adaptive radiation, whereby different forms of a species evolve, quickly in evolutionary terms, from a common ancestor. According to the principles of *natural selection*, organisms that are the best adapted (most fit) to compete will live to reproduce and pass their successful traits on to their offspring. The process of adaptive radiation illustrates one way in which natural selection can operate when members of one population of a species are cut off or migrate to a different environment that is isolated from the first. Such isolation can occur from one patch of plantings to another, from one mountaintop or hillside to another, from pond to pond, or from island to island. Faced with different environments, the group will diverge from the original population and in time become different enough to form a new species.

Genetic Changes

In a *divergent population*, the relative numbers of one form of *allele* (characteristic) decrease, while the relative numbers of a different allele increase. New environmental pressures will select for favorable alleles that may not have been favored in the old environment. Over successive generations, therefore, a new gene created by random *mutation* (change) may replace the original form of the gene if, for example, the trait encoded by that gene allows the divergent group to cope better with environmental factors, such as food sources, predators, or temperature. The result in the long term is that deoxyribonucleic acid (DNA) changes sufficiently through the growth of divergent populations to allow new generations to become significantly different from the original population. In time, they are unable to reproduce with members of the original species and become a new species.

Galápagos Islands Case Study

Adaptive radiation occurs dramatically when a species migrates from one landmass to another. This may occur between islands or between continents and islands. A classic example of adaptive radiation is the evolution of finches noted by Charles Darwin during his trips to the Galápagos Islands off the west coast of South America. Several species of plants and animals had migrated to these islands from the South American mainland by means of flight, wind, ocean debris, or other means of transport. Finches from the mainland—perhaps aided by winds—settled on fifteen of the islands in the Galápagos group and began to adapt to the various unoccupied *ecological niches* on those islands, which differed. Over several generations, natural selection favored a variety of finch species with beaks adapted for the different types of foods available on the different islands. As a result, several species of different finches evolved, roughly simultaneously, on these islands.

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Hawaiian Silversword Alliance

Although plants seem unable to "migrate" as birds and other animals do, adaptive radiation occurs in the plant world as well. In the Hawaiian Islands, for example, twenty-eight species of the *Asteraceae* family are known together as the Hawaiian silversword alliance. The entire group appears to be traceable to one ancestor, thought to have arrived on the island of Kauai from western North America. The silverswords—which compose three genera, *Argyroxiphium*, *Dubautia*, and *Wilkesia*—have since evolved into twenty-eight species, and this speciation came about due to major ecological shifts. These plants are therefore prime examples of adaptive radiation.

Within the silversword alliance, different species have adapted to widely varying ecosystems found throughout the islands. *Argyroxiphium sandwicense*, for example, is endemic to the island of Maui and grows at high elevations from 6,890 to 9,843 feet (2,100-3,000 meters) on the dry, alpine slopes of the volcano Haleakala. This species has succulent leaves covered with silver hairs. It is thought that the hairs lessen the pace of evaporative moisture loss and protect the leaves from the sun. In contrast, species of the genus *Dubautia* that grow in wet, shady forests have large leaves that lack hairs.

Despite their "customized" physiologies, the silverswords that have evolved in Hawaii are all closely related to one another, so much so that any two can hybridize. Studies of the silverswords have provided what geneticist Michael Purugganan called a "genetic snapshot of plant evolution." Adaptive radiation is one window into how new plant structures arise.

Jon P. Shoemaker, updated by Christina J. Moose

See also: Evolution: convergent and divergent; Hardy-Weinberg theorem; Species and speciation; Trophic levels and ecological niches.

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AFRICAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

Soil and climatic conditions throughout Africa determine not only agricultural practices, such as which crops can be grown, but also whether plant life is capable of sustaining livestock on the land and enabling fishing of the oceans.

Rainfall—the dominant influence on agricultural output—varies greatly among Africa's fifty-six countries. Without irrigation, agriculture requires a reliable annual rainfall of more than 30 inches (75 centimeters). Portions of Africa have serious problems from lack of rainfall, such as increasing desertification and periods of drought.

Food output has declined, with per capita food production 10 percent less in the 1990's than it was in the 1980's. In most African countries, however, more than 50 percent, and often 80 percent, of the population works in agriculture, mostly subsistence agriculture. Large portions of the continent, such as Mali and the Sudan, have the potential of becoming granaries to much of the continent and producing considerable food exports.

Traditional African Agriculture

Traditionally, agriculture in Africa has been subsistence farming in small plots. It has been labor-intensive, relying upon family members. New land for farming was obtained by the *slash-and-burn* method (*shifting cultivation*). The trees in a forested area would be cut down and burned where they fell. The ashes from the burned trees fertilized the soil. Both men and women worked at such farming. Slash-and-burn agriculture is common not only in Africa but also in tropical areas around the world. In areas of heavy rainfall, the rains wash out the nutrients from soil and burned trees in a period of two to three years.

The crops grown depend upon the region. In the very dry, yet habitable, parts of Africa—such as the Sudano-Sahelian region that stretches from Senegal and Mali in the west of Africa to the Sudan in the east—a key subsistence crop is green millet, a grain. Ground into a type of flour, it can be made into a bread-like substance. In moister areas, traditional crops are root and tuber crops, such as yams and cassava. Cassava has an outer surface or skin that is poisonous, but it can be treated to remove the poison. The tuber then can be ground and used to make a bread-like substance. Other important traditional crops are rice and corn, which were introduced by Europeans when they came to Africa.

Animal husbandry, or seminomadic herding, is another form of traditional agriculture. Problems that have arisen with this type of agriculture are the availability of water and grass or hay for cattle. Regions that are very moist, such as the Gulf of Guinea, which has rain forest, are not good for cattle because of the tsetse fly, which carries diseases such as sleeping sickness.

Crops

The most widely grown crop is rice, which is grown on more than one-third of the irrigated crop area in Africa. Cultivated mostly in wetlands and valley bottoms, rice is the most common crop in the humid areas of the Gulf of Guinea and Eastern Africa. It is also grown on the plateaus of Madagascar. In the northern and southern regions, rice represents only a small portion of the total crops under water management. Wheat and corn are cultivated and irrigated, mostly in Egypt, Morocco, South Africa, Sudan, and Somalia.

Vegetables, including root and tuber crops, are present in all regions and almost every country. Vegetables are grown on about 8 percent of the cultivated areas under water management. In Algeria, Mauritania, Kenya, Burundi, and Rwanda, they are the most widespread crops under water management. *Arboriculture* (growing of fruit trees), which represents 5 percent of the total irrigated crops, is concentrated in the northern region and consists mostly of citrus fruits. Commercial crops (for cash and export) are grown mostly in the Sudan and in the countries of the southern region and consist mostly of cotton and oilseeds. Other commercial crops in Africa are sugarcane, coffee, cocoa, oil and date palm, bananas, tobacco, and cut flowers. Sugarcane is grown in all countries except in the northern region. The other commercial crops are concentrated in a few countries.

North Africa

In Morocco, Algeria, Tunisia, Libya, and Egypt, the region's agricultural resources are limited by its dry climate. Its products are those typical of the Mediterranean, steppe, and desert regions: wheat, barley, olives, grapes, citrus fruits, some vegetables, dates, sheep, and goats.

Selected Agricultural Products of Africa

Agriculture employs less than 20 percent of the working population in Libya and as much as 55 percent in Egypt. From about the middle of the twentieth century, North Africa's production failed to keep pace with its population growth and remained susceptible to large annual fluctuations. Cropland occupies about 33 percent of Tunisia but less than 3 percent of Algeria, Egypt, and Libya. Some export crops, such as citrus fruits, tobacco, and cotton, have suffered from strong international competition. The northern region is not a major contributor to the continent's fish catch. Morocco, however, with its cool, plankton-rich Atlantic waters and access to the Mediterranean Sea, is one of the world's largest fish producers.

Sudano-Sahelian Region

This region comprises Mauritania, the western Sahara, Senegal, Gambia, Mali, Burkina-Faso, Niger, Chad, and the Sudan. Because of the region's extreme dryness, mostly subsistence farming and seminomadic herding are practiced. Millet is the primary crop. In the late twentieth century, this region was devastated by long droughts that caused famine and starvation. Mali and the Sudan have the Niger and Nile Rivers flowing through them. These great rivers provide plenty of water for irrigation of fields. During the rainy season in Mali—typically June through September—the Niger River widens into a great, extensive floodplain. This area is good for the growing of rice. Similarly, in the Sudan the Blue and White Niles meet at Khartoum to form the Nile River.

Gulf of Guinea

This region comprises Guinea-Bissau, Cape Verde, Guinea, Liberia, Sierra Leone, Côte d'Ivoire, Togo, Ghana, Benin, and Nigeria. With the exception of Nigeria, agriculture there is dominated by rice cultivation. The percentage of total land area that is under cultivation ranges from 60 percent in Liberia to just 9 percent in Sierra Leone.

The total cultivable area of Ghana is 39,000 square miles (100,000 square kilometers), or 42 percent of its total land area. Only 4.8 percent of the total land area was under cultivation at the end of the twentieth century. Much of the cultivation is subsistence farming of yams and other crops. Ghana's efforts in agriculture have been hampered by droughts. Additional problems are that organic matter has been leached out of the soils by heavy rainfall and that increasing deforestation has led to additional erosion. This is the situation in much of the Gulf of Guinea and the central regions.

About half of Nigeria's available land is under cultivation. Increasing rainfall from the semiarid north to the tropically forested south allows for great crop diversity. Principal food crops are corn, millet, yams, sorghum, cassava, rice, potatoes, and vegetables. Nigeria was the world's fourth-largest exporter of cocoa beans in 1990-1991, accounting for about 7.1 percent of world trade in this commodity. However, Nigeria's share of the world cocoa market has been substantially reduced because of aging trees, low prices, black pod disease, smuggling, and labor shortages.

Central Region

This region comprises the Central African Republic, Cameroon, Congo-Brazzaville, Congo-Kinshasa, Gabon, Equatorial Guinea, Burundi, Rwanda, and São Tomé and Príncipe. Cameroon has 14.7 million acres of arable land. In 1997, 55,000 tons of rice were produced, but the country imported 124,000 tons in 1995. In the central region, the percentage of arable land ranges from 0.4 percent for the Congo-Brazzaville to 47 percent for Rwanda. Cassava is harvested in Congo-Brazzaville, Congo-Kinshasa, Equatorial Guinea, and Gabon. Corn is harvested in Congo-Brazzaville, Congo-Kinshasa, and Burundi. In Rwanda, 17 percent of the harvested land is used to grow sweet potatoes. Agriculture is not important in the economy of São Tomé and Príncipe.

Eastern Region

This region comprises Eritrea, Djibouti, Ethiopia, Somalia, Kenya, Uganda, and Tanzania. Agriculture employs about 80 percent of the labor force in Uganda and Ethiopia. Approximately 2.5 million small farms dominate agriculture in both countries. About 84 percent of Uganda's land is suitable for agriculture—a high percentage compared to the majority of African countries, such as Ethiopia with only 12 percent. Food crops account for about 74 percent of agricultural production. Only one-third is marketed; the rest is for home consumption. In four years out of five, the minimum needed rainfall may be expected in 78 percent of Uganda but in only 15 percent of Kenya. Somalia and Ethiopia receive almost none of the needed minimum.

Tanzania has almost four million farms. Traditional export crops include coffee, cotton, cashew

Leading Agricultural Crops of African Countries with More than 15 Percent Arable Land

Country	*Products*	*Percent Arable Land*
Burundi	Coffee, cotton, tea, corn, sorghum, sweet potatoes, bananas, manioc	44
Comoros	Vanilla, cloves, perfume essences, copra, coconuts, bananas, cassava	35
Gambia	Peanuts, millet, sorghum, rice, corn, cassava, palm kernels	18
Malawi	Tobacco, sugarcane, cotton, tea, corn, potatoes, cassava, sorghum, pulses	18
Mauritius	Sugarcane, tea, corn, potatoes, bananas, pulses	49
Morocco	Barley, wheat, citrus, wine, vegetables, olives	21
Nigeria	Cocoa, peanuts, palm oil, corn, rice, sorghum, millet, cassava, yams, rubber	33
Rwanda	Coffee, tea, pyrethrum (insecticide made from chrysanthemums), bananas, beans, sorghum, potatoes	35
Togo	Coffee, cacao, cotton, yams, cassava, corn, beans, rice, millet, sorghum	38
Tunisia	Olives, dates, oranges, almonds, grain, sugar beets, grapes	19

Source: Data are from *The Time Almanac 2000*. Boston: Infoplease, 1999.

nuts, tobacco, and tea. Major staple foods (corn, rice, and wheat) are exported in times of surplus. Tanzania's climatic growing conditions are favorable for the production of a wide range of fruits, vegetables, and flowers. Drought-resistant crops (sorghum, millet, and cassava) and other substaples such as onions, Irish potatoes, sweet potatoes, bananas, and plantains are also produced.

Areas that have 20-30 inches (50-75 centimeters) of rainfall per year rely on a mixture of agriculture and livestock herding. Regions with a smaller annual rainfall or a long dry season can support only drought-resistant crops such as sorghum, millet, and cassava. Over large areas of eastern Africa, rainfall is inadequate for crop cultivation. The whole of Somalia and 70 percent of Kenya receive less than 20 inches (50 centimeters) of rain four years out of five. In these areas, the only feasible use of land is for raising livestock. Agriculture is not an important factor in the economies of Eritrea and Djibouti.

Southern Region

This region comprises Angola, Namibia, Zambia, Zimbabwe, Malawi, Mozambique, Botswana, Lesotho, Swaziland, and South Africa. The arable percentage of the total land area ranges from 14 percent in Malawi to just 1 percent in Namibia. With the exception of Mozambique, where cassava predominates, corn is the major crop in the countries in this region.

About 13 percent of South Africa's land area can be used for crop production. Rainfall varies across the country, and varied climatic zones and terrains enable the production of almost any kind of crop. The largest area of farmland is planted with corn, followed by wheat, then oats, sugarcane, and sunflowers. The nation is well known for the high quality of its fruits, such as apples and citrus.

Agriculture is the predominant economic activity in Zimbabwe, accounting for 40 percent of total export earnings—about 22 percent of the total economy—and employing more than 60 percent of the country's labor force. The main export crops are tobacco, cotton, and oilseeds. Zimbabwe is usually self-sufficient in food production. Its main food crops are corn, soybeans, oilseeds, fruits and vegetables, and sugar.

Mozambique's agriculture has been badly hindered by civil war. However, the country has considerable potential for irrigation due to the Zambezi and Limpopo Rivers. The irrigation potential is estimated to be 7.5 million acres. In the 1990's, only 110,000 acres were irrigated, growing rice, sugarcane, corn, and citrus.

Agriculture and livestock production employ about 62 percent of Botswana's labor force. Most of the country has semidesert conditions with erratic rainfall and poor soil conditions, making it more suitable to grazing than to crop production. The principal food crops are sorghum and corn. Namibia's cultivated area is only 506,000 acres—only 0.8 percent of the cultivable area. Agriculture makes up approximately 10 percent of the economy but employs more than 80 percent of the population. The major irrigated crops are corn, wheat, and cotton.

Indian Ocean Islands

This region comprises Madagascar, Mauritius, the Comoros, and the Seychelles. During the 1990's an estimated 8.7 million people lived in the rural areas, 65 percent of whom lived at the subsistence level. Only 5.2 percent of Madagascar's total land area (7.4 million acres) was under cultivation. Of the total land area, 50.7 percent supported livestock production, while 16 percent (1.2 million acres) of the land under cultivation was irrigated.

Cassava, planted almost everywhere on the island, is grown as well as corn and sweet potatoes, with smaller quantities of cotton, bananas, and cloves. The fisheries sector, especially the export of shrimp, has been the most rapidly growing area of the agricultural economy in the Indian Ocean Islands region.

Mauritius has 30,000 acres of sugarcane plantations that have had one of the highest sugarcane and sugar yields in the world. The Seychelles have a total land area of only 72 square miles (187 square kilometers), of which only 3,000 acres are cultivated. This 3 percent of the land area accounts for only 4 percent of the island nation's economy. The Comoros' agriculture is heavily weighted toward rice, the staple food of the populace.

Dana P. McDermott

See also: African flora; Agricultural revolution; Agriculture: history and overview; Agriculture: traditional; Agriculture: world food supplies; Alternative grains; Desertification; Drought.

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AFRICAN FLORA

Category: World regions

With few exceptions, Africa's flora (vegetation) is tropical or subtropical. This is primarily because none of the African continent extends far from the equator, and there are only a few high-elevation regions that support more temperate plants.

Listed in order of decreasing land area, the three main biomes of Africa are subtropical desert, tropical savanna, and tropical forest. The flora in southern Africa has been most studied. The flora of central and northern Africa is less known.

The subtropical desert biome is the driest of the biomes in Africa and includes some of the driest locations on earth. The largest desert region is the Sahara in northern Africa. It extends from near the west coast of Africa to the Arabian Peninsula and is part of the largest desert system in the world, which extends into south central Asia. A smaller desert region in southern Africa includes the Namib Desert, located along the western half of southern Africa, especially near the coast, and the Kalihari Desert, which is primarily inland and east of the Namib Desert.

Where more moisture is available, grasslands predominate, and as rainfall increases, grasslands gradually become tropical savanna. The difference between a grassland and a savanna is subjective but is in part determined by tree growth, with more trees characterizing a savanna. The grassland/tropical savanna biome forms a broad swath across much of central Africa and dominates much of eastern and southern Africa.

Tropical forests make up a much smaller area of Africa than the other two biomes. They are most abundant in the portions of central Africa not dominated by the grassland/tropical savanna biome and are not far from the coast of central West Africa. Scattered tropical forest regions also occur along major river systems of West Africa, from the equator almost to southern Africa.

Subtropical Desert

The subtropical deserts of Africa seem, at first, to be nearly devoid of plants. While this is true for some parts of the Sahara and Namib Deserts that are dominated by sand dunes or bare, rocky outcrops, much of the desert has a noticeable amount of plant cover. The Sahara is characterized by widely distributed species of plants that are found in similar habitats. The deserts of southern Africa have more distinctive flora, with many species endemic to specific local areas.

Succulents of the Subtropical Desert

To survive the harsh desert climate, plants use several adaptations. *Mesembryanthemum*, whose species include ice plant and sea figs, is a widespread genus, with species occurring in all of Africa's deserts. It typically has thick, succulent leaves. Such *succulents* store water in their leaves or stems, which they retain by using a specialized type of photosynthesis. Most plants open their stomata (small openings in the leaves) during the day to get carbon dioxide from the surrounding air. This would lead to high amounts of water loss in a desert environment, so succulents open their stomata at night. Through a biochemical process, they store carbon dioxide until the next day, when it is released inside the plant so photosynthesis can occur without opening the stomata.

To prevent water loss, many succulents have no leaves at all. *Anabasis articulata*, found in the Sahara desert, is a leafless succulent with jointed stems. Cacti are found only in North and South America, but a visitor to the Sahara would probably be fooled by certain species in the spurge family that resemble cacti. For example, *Euphorbia echinus*, another Saharan plant, has succulent, ridged stems with spines. The most extreme adaptation in succulents is found in the living stones of southern Africa. Their plant body is reduced to two plump, rounded leaves that are very succulent. They hug the ground, sometimes partially buried, and have camouflaged coloration so that they blend in with the surrounding rocks and sand, thus avoiding being eaten by grazing animals. Other succulents, such as the quiver tree, attain the size and appearance of trees.

Water-Dependent Plants of the Subtropical Desert

Water-dependent plants are confined to areas near a permanent water source, such as a spring. The most familiar of these plants is the date palm, which is a common sight at desert oases. Tamarind and acacia are also common where water is available. A variety of different sedges and rushes occur wherever there is abundant permanent freshwater, the most famous of these being the papyrus, or bulrush.

Ephemerals of the Subtropical Desert

Annuals whose seeds germinate when moisture becomes available and quickly mature, set seed, and die, are called *ephemerals*. These plants account for a significant portion of the African desert flora. A majority of the ephemerals are grasses. Ephemerals are entirely dependent on seasonal or sporadic rains. A few days after a significant rain the desert turns bright green, and after several more days flowers, often in profusion, appear. Some ephemerals germinate with amazing speed, such as the pillow cushion plant, which germinates and produces actively photosynthesizing seed leaves only ten hours after being wetted. Reproductive rates for ephemerals, and even for perennial plants, are rapid. Species of morning glory can complete an entire life cycle in three to six weeks.

Tropical Savanna

Tropical savanna ranges from savanna grassland, which is dominated by tall grasses lacking trees or shrubs, to thicket and scrub communities, which are composed primarily of trees and shrubs of a fairly uniform size. The most common type of savanna in Africa is the savanna woodland, which is composed of tall, moisture-loving grasses and tall, deciduous or semideciduous trees that are unevenly distributed and generally well spaced. The type of savanna familiar to viewers of African wildlife documentaries is the savanna parkland, which is primarily tall grass with widely spaced trees.

Savanna Grasses and Herbs

Grasses represent the majority of plant cover beneath and between the trees. In some types of savanna, the grass can be more than 6 feet (1.8 meters) high. Although much debated, two factors seem to perpetuate the dominance of grasses: seasonal moisture with long intervening dry spells and periodic fires. Given excess moisture and lack of fire, savannas seem inevitably to become forests. Activities by humans, such as grazing cattle or cutting trees, also perpetuate, or possibly promote, grass dominance.

A variety of herbs exist in the savanna, but they are easily overlooked, except during flowering periods. Many of them also do best just after a fire, when they are better exposed to the sun and to potential pollinators. Plants such as hibiscus and coleus are familiar garden and house plants popular the world over. Vines related to the sweet potato are also common. Many species from the legume or pea and sunflower families are present. Wild ginger often displays its showy blossoms after a fire.

Savanna Trees and Shrubs

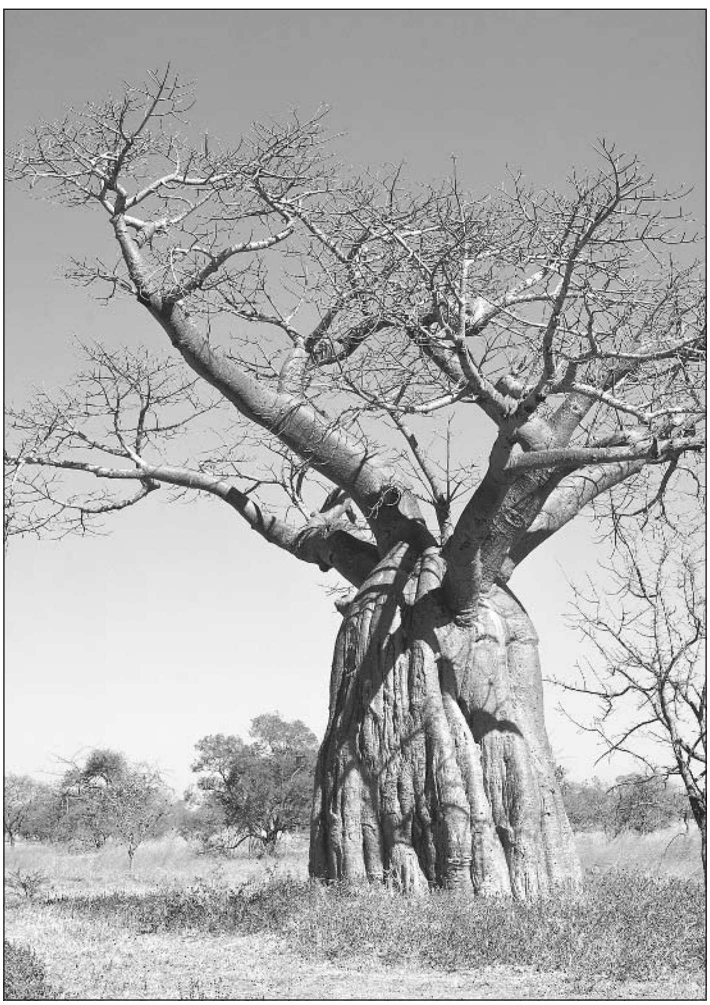
Trees of the African savanna often have relatively wide-spreading branches that all terminate at about the same height, giving the trees a flat-topped appearance. Many are from the legume family, most notably species of *Acacia*, *Brachystegia*, *Julbernardia*, and *Isoberlinia*. With the exception of acacias, these are not well known outside Africa. There is an especially large number of *Acacia* species ranging from shrubs to trees, many with spines. A few also have a symbiotic relationship with ants that protect them from herbivores. The hashab tree, a type of acacia that grows in more arid regions, is the source of gum arabic.

Although not as prominent, the baobab tree is renowned for its large size and odd appearance and occurs in many savanna regions. It has an extremely thick trunk with smooth, gray bark and can live for up to two thousand years. Many savanna trees also have showy flowers, such as the flame tree and the African tulip tree.

Tropical Forest

The primary characteristics of African tropical forests are their extremely lush growth, high species diversity, and complex structure. The diversity is often so great that a single tree species cannot be identified as dominant in an area. Relatively large trees, such as ironwood, iroko, and sapele, predominate. Forest trees grow so close together that their crowns overlap, forming a *canopy* that limits the amount of light that falls beneath them. A few larger trees, called emergent trees, break out above the thick canopy.

A layer of smaller trees live beneath the main canopy. A few smaller shrubs and herbs grow near the ground level, but the majority of the herbs and other perennials are *epiphytes*, that is, plants that grow on other plants. On almost every available space on the trunks and branches of the canopy trees there are epiphytes that support an entire, unique community. All this dense plant growth is supported by a monsoon climate in which 60 inches (150 centimeters) or more of rain often falls annually, most of it in the summer.



Corbis

Baobab tree in Zambia.

Lianas and Epiphytes

Lianas are large, woody vines that cling to trees, many of them hanging down near to the ground. They were made famous by Tarzan movies. Many lianas belong to families with well-known temperate vine species, such as the grape family, morning glory family, and cucumber family. Other, related plants remain intimately connected to the trunks of trees. One of these, the strangler fig, is a strong climber that begins life in the canopy.

The fruits are eaten by birds or monkeys, and the seeds are deposited in their feces on branches high in the canopy. The seeds germinate and send a stem downward to the ground. Once the stem reaches the ground, it roots; additional stems then develop and grow upward along the trunk of the tree. After many years, a strangler fig can so thoroughly surround a tree that it prevents water and nutrients from flowing up the trunk. Eventually, the host tree dies and rots away, leaving a hollow tube of mostly strangler fig. Other climbers include members of the *Araceae* family, the most familiar being the ornamental philodendron.

The most common epiphytes are bryophytes, lower plants related to mosses, and lichens, a symbiotic combination of algae (or cyanobacteria) and fungus. The most abundant higher plants are ferns and orchids. As these plants colonize the branches of trees, they gradually trap dust and decaying materials, eventually leading to a thin soil layer that other plants can use. Accumulations of epiphytes can be so great in some cases that tree branches break from their weight. Epiphytes are not parasites (although there are some parasitic plants that grow on tree branches); they simply use the host tree for support.

Tropical Forest Floor Plants

Grasses are almost entirely absent from the forest floor; those that grow there have much broader leaves than usual. Some forest-floor herbs are able to grow in the deep shade beneath the canopy, occasionally being so highly adapted to the low light that they can be damaged if exposed to full sunlight. Some popular house plants have come from among these plants, because they do not need direct sunlight to survive. Still, the greatest numbers of plants occur beneath breaks in the canopy, where more light is available.

Bryan Ness

See also: African agriculture; Biomes: types; C_4 and CAM photosynthesis; Cacti and succulents; Deserts; Forests; Grasslands; Rain-forest biomes; Savannas and deciduous tropical forests.

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AGRICULTURAL CROPS: EXPERIMENTAL

Categories: Agriculture; economic botany and plant uses; food

Experimental crops are foodstuffs with the potential to be grown in a sustainable manner, produce large yields, and reduce people's reliance on the traditional crops wheat, rice, and corn.

Shifting from a hunter-gatherer society to an agrarian society led to increasingly larger-scale agricultural production that involved selecting local crops for domestication. In recent history there has been a reduction in the number of agricultural crops grown for human consumption. There are estimated to be at least 20,000 species of edible plants on earth, out of more than 350,000 known species of higher plants. However, only a handful of crops feed most of the world's people. These include wheat, rice, corn, potatoes, sugar beets, sugarcane, cassava, barley, soybeans, tomatoes, and sorghum. Rice, wheat, and corn together account for a majority of calories consumed. In the effort to develop experimental crops, agricultural goals include expanding the diversity of plant food in the human diet.

Image Not Available

Recent Successes

Soybeans (*Glycine max*) are a relatively new crop that gained worldwide acceptance and widespread cultivation in the second half of the twentieth century. Originally cultivated in China, soybeans gradually spread throughout Asia and became a staple food there. High in protein, soybeans were first grown in the Western world as animal feed. Concerted breeding efforts have resulted in many locally adapted varieties. Today, soybeans as both meal and oil are commonplace. Worldwide soybean production is now the greatest of any legume.

Triticale (*x Triticosecale*) is a hybrid created to combine the ruggedness and high protein content of rye (*Secale cereale*) with the high yield of wheat (*Triticum aestivum*). Triticale has not replaced wheat or rye in bread-making due to its rather low gluten content but is used to supplement bread flours. Triticale is also adaptable to marginal agricultural soils.

Kiwifruit (*Actinidia deliciosa*) is another recent success story. A previously little-known fruit originally called Chinese gooseberry, it was introduced to New Zealand at the turn of the twentieth century and renamed kiwifruit. The name change was a marketing strategy that led to worldwide popularity. Today kiwifruit cultivation and consumption are increasing worldwide. Kiwifruit grows on a deciduous vine, much like grapes. It can be harvested and then stored for several months without loss of quality.

Grains and Cereals

Quinoa (*Chenopodium quinoa*) is a grain native to the Andes Mountains of South America. It has been a staple in the diets of people living in that region for centuries. Although the leaves are edible, it is principally the tiny seed which is consumed. The seeds contain high amounts of protein, calcium, phosphorus, and the essential amino acid lysine, which is typically lacking in other cereals such as wheat, rye, and barley. Quinoa seeds must be washed or otherwise processed to remove the bitter saponins contained in the pericarp and can then be cooked and eaten much like rice. Quinoa can also be ground into flour as a supplement for bread making. Cultivation and use of quinoa have increased steadily since the 1980's.

Grain amaranths (*Amaranth*) are being rediscovered and developed as a potential new source of grain. Amaranth was a staple crop for centuries in Mexico, Central America, and South America. Amaranth is grown as an annual and yields thick, heavy seed heads containing numerous tiny seeds. The hard seed coat is removed by heating or boiling and can be prepared much like corn. Amaranth is comparable to other grains in protein, contains high amounts of lysine, and can be consumed by those allergic to typical grains. Breeding efforts over the last few decades involving *A. hypochondriacus*, *A. cruentus*, and *A. hybridus* have greatly increased seed yield as well as desirable plant growth habit. Another important characteristic is amaranth's drought resistance.

Legumes

Members of the *Leguminosae* family are particularly valuable as food sources because they contain high levels of protein. This is in part due to their ability to fix atmospheric nitrogen in *root nodules* that contain *nitrogen-fixing bacteria*. This symbiotic relationship with the bacteria means relatively little nitrogenous fertilizer is required for agricultural production of legumes. Tarwi (*Lupinus mutabilis*) is a legume native to the South American Andes that has a high protein and oil content, similar to the soybean. Tarwi is also high in the essential amino acid lysine. It grows well in poor soils and is drought-resistant. Current breeding efforts focus on reducing the bitter alkaloids, which can be removed by rinsing in water.

The winged bean (*Psophocarpus tetragonolobus*), native of tropical Asia, is entirely edible—leaves, flowers, seeds, pods, and tuberous roots. Like most legumes, the winged bean has a high protein content. This species could have tremendous potential in many tropical regions of the world, rivaling the success of the soybean.

A native of North America, the groundnut (*Apios americana*) was a major food source of many American Indian tribes. It is purported to have been offered to the Pilgrims to avert starvation. The numerous underground tubers can be prepared (cooking is necessary) like potatoes yet have a much higher protein content.

Several other legumes whose use and acceptance are likely to increase include the tepary bean (*Phaseolus acutiflius*), the pigeon pea (*Cajanus cajan*), and the bambara groundnut (*Voandzeia subterranea*).

Other Crops

There are many other potential food crops. Most have been cultivated on a small scale for years and are being rediscovered and researched for commercial production. Some of these include potato-like oca tubers (*Oxalis tuberosa*), fruits such as cherimoya (*Annona cherimola*), pepino (*Solanum muricatum*), and feijo (*Acca sellowiana*), and nuts such as egg nut (*Couepia longipendula*).

Thomas J. Montagno

See also: Agriculture: world food supplies; Alternative grains; Culturally significant plants; Fruit crops; Grains; Legumes; Nitrogen fixation; Nutrition in agriculture; Plants with potential; Vegetable crops.

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AGRICULTURAL REVOLUTION

Categories: Agriculture; economic botany and plant uses; history of plant science

The agricultural revolution marked the transition by humans from hunting and gathering all their food to domesticating plants for food.

People first obtained their food by scavenging kills made by other animals, by hunting animals, and by gathering wild food plants. Between ten thousand and twelve thousand years ago, people began to use plants in new ways. Some scientists and historians call this period of time the "agricultural revolution."

Agricultural Beginnings

Before the 1960's, many scientists and historians believed that hunter-gatherers abruptly switched from foraging to farming. Those who thought that agriculture arose quickly coined the term "agricultural revolution." They suggested that this revolution spread rapidly because it was a tremendous improvement over the old foraging lifestyle, with the availability of cultivated food sources far more dependable than those of wild sources.

Since the 1960's, scientists and historians have challenged this view of agricultural beginnings. Later studies have shown that modern hunting-gathering societies have a remarkably sophisticated knowledge about native plants and plants' life cycles. Gatherers use a large number of plant species for food. Hunting and gathering cultures today do not have to plant seeds intentionally to keep from starving and most likely did not have to do so in the past.

Domesticated and Wild Plants

Domesticated plants are genetically distinct from their wild ancestors. *Domestication* involves processes by which a wild plant adapts to the needs of the farmer. The traits that make a plant desirable as a human food plant may not be ones that confer survival value on plants in their natural habitats and may actually be detrimental to the plant's survival in the wild.

People who gathered wild plants looked for traits that made gathering easier and more profitable. They would have gathered grasses, for example, that had bigger seeds or plants, had more seeds or fruits or edible parts, or had seed heads that did not shatter easily. If seeds from such plants are the ones that were planted, accidentally or on purpose, their useful traits would be reinforced in successive generations. The appearance of a domesticated plant in the archaeological record is the end result of generations of cumulative genetic transformations that might have taken hundreds or even thousands of years. Therefore, it becomes difficult to pick a single point in the past for any continent or geographic region that signals the beginning of an agricultural economy.

Geography of Agricultural Origins

The area of the Middle East called the Fertile Crescent (between the Tigris and Euphrates Rivers in what is now Iraq) seems to be the first area where formal agriculture began. The native grasses were highly productive. Wild wheat and barley grew in dense stands and were valuable food sources before cultivation began. It was this use of gathered wild grasses for food that probably led to their early domestication. Along with the grasses, complementary sources of protein were adopted, namely leguminous crops such as pea and lentil, and animals were domesticated. The plants that were domesticated in the Middle East include einkorn wheat, emmer wheat, bread wheat, barley, lentil, pea, vetch, the fava (or broad) bean, chickpea, lupine, and flax.

Agriculture originated in northeast China with the Yang Shao culture around six thousand years ago and spread quickly into Korea and Japan. Some of the plants brought under cultivation include barley, barnyard millet, common or broomcorn millet, foxtail millet (or foxtail grass), soybean, adzuki and mung beans, hemp, buckwheat, bottle gourd, Chinese cabbage, great burdock, lacquer tree, paper mulberry, and a number of fruit trees, including apricot, pear, peach, and plum.

In Southeast Asia, as well as the Pacific Islands and India, cultivated plants included sesame, the pigeon pea, eggplant, rice, sugarcane, bananas, plantains, coconuts, oranges, mango, Asian yam, betel nut, pepper, taro, bitter gourd, winter melon, snake gourd, luffa, mangosteen, durian, rambutan, breadfruit, and bamboo.

In Africa, plant domestication took place south of the Sahara Desert and north of the equator. Many crops were grown, including various kinds of millet, sorghum, okra, coffee, watermelon, several species of yam, African rice, cowpea, African oil palm, and cola nut. In Ethiopia, Ethiopian oats, coffee, enset, tef, noog, and chat were cultivated.

In Central America, archaeological evidence suggests that squash and pumpkins may have been cultivated before corn, especially in the Oaxaca region. In Oaxaca and Tamaulipas, along with squash and pumpkins, people were cultivating beans and bottle gourds, followed later by corn. In the Tehuacán Valley of Central Mexico, corn, chile peppers, avocado, beans, amaranth, and foxtail grass were among the very earliest cultivated plants. Cultivated plants either originating or cultivated early in South America include quinoa, white potato, peanut, cacao, jicama, lima bean, common bean, pineapple, chile pepper, papaya, sweet potato, yucca, and avocado. Tomatoes were cultivated in both Central and South America.

In North America, prior to the diffusion of the corn-squash-beans complex from the southwest after 1000 C.E., Indians of Eastern North America were cultivating a number of plants, including bottle gourd, erect knotweed, sumpweed, goosefoot, maygrass, little barley, and sunflower.

Carol S. Radford

See also: African agriculture; Agriculture: traditional; Asian agriculture; Central American agriculture; Fruit crops; Grains; Plant domestication and breeding; South American agriculture; Vegetable crops.

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AGRICULTURE: HISTORY AND OVERVIEW

Categories: Agriculture; disciplines; economic botany and plant uses

Agriculture is the ability to produce sufficient food and fiber to feed and shelter the population, the most important natural resource a nation can have. In modern urban societies, it is also the natural resource that is most often taken for granted.

The beginnings of agriculture predate written history. No one knows when the first crop was cultivated, but at some time in the distant past humans discovered that seeds from certain wild grasses could be collected and planted in land that could be controlled and the grasses later gathered for food. Most scholars believe this occurred at about the same time in both the Eastern and Western Hemispheres, some eight thousand to ten thousand years ago.

Ephemeral Archives

The earliest agricultural centers were located near large rivers that helped maintain soil fertility with the deposition of new topsoil during each annual flooding cycle.

Early Agriculture

The earliest attempts to grow crops were primarily to supplement the food supply provided by hunting and gathering. However, as the ability to produce crops increased, people began to *domesticate* plants and animals, and their reliance on hunting and gathering decreased, allowing the development of permanent settlements in which humans could live. As far back as six thousand years ago, agriculture was firmly established in Asia, India, Mesopotamia, Egypt, Mexico, Central America, and South America.

The earliest agricultural centers were located near large rivers that helped maintain soil fertility by the deposition of new *topsoil* with each annual flooding cycle. As agriculture moved into regions that lacked the annual flooding of the large rivers, people began to utilize a technique known as *slash-and-burn agriculture*. In this type of agriculture, a farmer clears a field, burns the tress and brush, and farms the field. After a few years soil nutrients become depleted, so the farmer must repeat the process at a new location. This type of agriculture is still practiced in some developing countries and is one reason tropical rain forests are disappearing at a fast rate.

Until the nineteenth century, most farms and ranches were family-owned, and most farmers practiced *sustenance agriculture*: Each farmer produced a variety of crops sufficient to feed his or her family as well as a small excess which was sold for cash or bartered for other goods or services. Agricultural tools such as plows were made of wood, and almost all agricultural activities required human or animal labor. This situation placed a premium on large families to provide the help needed in the fields.

The arrival of the Industrial Revolution changed agriculture, just as it did almost all other industries. Eli Whitney invented the cotton gin in 1793. The mechanical reaper was invented by Cyrus McCormick, and John Lane and John Deere began the commercial manufacture of the steel plow in 1833 and 1837, respectively. These inventions led the way to the development of the many different types of agricultural machinery that resulted in the *mechanization* of most farms and ranches. By the early part of the twentieth century, most agricultural enterprises in the United States were mechanized. American society was transformed from an agrarian society into an urban society. People involved in agricultural production left farms to go to cities to work in factories. At the same time, there was no longer a need for large numbers of people to produce crops. As a result, fewer people were required to produce the growing amounts of agricultural products that supplied an increasing number of consumers.

Modern Agriculture

As populations continued to grow, there was a need to select and produce crops with higher yields. The *Green Revolution* of the twentieth century helped to make these higher yields possible. Basic information supplied by biological scientists allowed agricultural scientists to develop new, higher-yielding varieties of numerous crops, particularly the *seed grains* which supply most of the calories necessary for maintenance of the world's population. These higher-yielding crop varieties, along with improved farming methods, resulted in tremendous increases in the world's food supply.

The new crop varieties also led to an increased reliance on *monoculture*. While the practice of growing only one crop over a vast number of acres has resulted in much higher yields, it has also decreased the genetic variability of many agricultural plants, increased the need for commercial fertilizers, and produced an increased susceptibility to damage from a host of biotic and abiotic factors. These latter two developments have resulted in a tremendous growth in the *agricultural chemical in-*

Major Crops and Places of Original Cultivation

Crop	*Region*	*Crop*	*Region*
Apples	Central Asia and the Middle East	Olives	Mediterranean
Apricots	China	Onions	Mediterranean
Asparagus	Mediterranean	Oranges	China, India, and Southeast Asia
Avocados	Central and South America	Papayas	Central and South America
Bananas	India and Southeast Asia	Parsnips	Mediterranean
Beans	Ethiopia	Peaches	China
Bell peppers	Central and South America	Peanuts	Central and South America
Cantaloupes	Central Asia and the Middle East	Pears	Central Asia and the Middle East
Carrots	Central Asia and the Middle East	Peas	Ethiopia
Cashews	Central and South America	Pineapples	Central and South America
Celery	Mediterranean	Potatoes	Central and South America
Cherries	China	Pumpkins	Central and South America
Coconuts	India and Southeast Asia	Radishes	India and Southeast Asia
Coffee	Ethiopia	Rhubarb	Mediterranean
Corn	Central and South America	Rice	India and Southeast Asia
Cotton	Central Asia and the Middle East	Rye	Central Asia and the Middle East
Cucumbers	China	Soybeans	China
Eggplant	China	Spinach	Central Asia and the Middle East
Figs	Central Asia and the Middle East	Sugarcane	China
Garlic	Central Asia and the Middle East	Sweet potatoes	Central and South America
Ginger	India and Southeast Asia	Tangerines	India and Southeast Asia
Grapes	Central Asia and the Middle East	Tea	China
Leeks	Central Asia and the Middle East	Tomatoes	Central and South America
Lettuce	Mediterranean	Turnips	Central Asia, the Mediterranean, and the Middle East
Lima beans	Central and South America	Walnuts	China
Mangoes	India and Southeast Asia	Wheat	Central Asia and the Middle East
Mustard	India and Southeast Asia	Yams	India and Southeast Asia
Oats	Central Asia and the Middle East		
Okra	Ethiopia		

Source: Data are from Brian Capon, *Botany for Gardeners: An Introduction and Guide* (Portland, Oreg.: Timber Press, 1990), p. 81.

dustry. Today's modern agricultural unit requires relatively few employees, is highly mechanized, devotes large amounts of land to the production of only one crop, and is highly reliant on agricultural chemicals such as fertilizers and pesticides.

Agricultural Diversity

Modern agriculture is subdivided into many different specialties. Those agricultural industries that deal with plants include *agronomy*, the production of field crops; *forestry*, the growth and production of trees; and *horticulture*. Horticulture is subdivided into *pomology*, the growth and production of fruit crops such as oranges and apples; *olericulture*, the growth and production of vegetable crops (tomatoes, lettuce); *landscape horticulture*, the growth and production of trees and plants that are used in landscape design; and *floriculture*, the growth and production of flowering plants used in the floral industry.

The various agriculture industries produce a tremendous number of agricultural products. Agricultural products that are derived from plants can be subdivided into timber products (lumber, furniture), grain products (wheat, oats), fiber products (cotton, flax), fruit products (grapes, peaches), nut crops (pecans, hazelnuts), vegetable products (lettuce, cabbage), beverage products (tea, coffee), spice and drug crops (garlic, mustard, opium, quinine), ornamental crops (carnations, chrysanthemums), forage crops (alfalfa, clover), and other cash crops such as sugarcane, tobacco, artichokes, and rubber.

Impact on Soil Resources

While there have been tremendous increases in agricultural productivity through the use of modern agricultural practices, these practices have had a significant impact on some other natural resources. *Soil* is one of the most overlooked and misunderstood resources. Most people think of soil as an inert medium from which plants grow. In reality, *topsoil*—that upper 15 to 25 centimeters (6 to 10 inches) of the earth's terrestrial surface in which nearly all plants grow—is a complex mixture of weathered mineral materials from rocks, partially decomposed organic molecules, and a large number of living organisms.

The process of soil formation is very slow. Under ideal conditions, enough topsoil can form in one year to produce a layer of about 1 millimeter (0.04 inch) thick when spread over 1 hectare (2.5 acres). With proper management, topsoil can be kept fertile and productive indefinitely. Unfortunately, many agricultural techniques lead to the removal of trees and shrubs, which provide windbreaks, or to the depletion of soil fertility, which reduces the plant cover over the field. These practices expose the soil to increased erosion from wind and moving water. As a result, as much as one-third of the world's current croplands are losing topsoil faster than it can be replaced.

Water and Irrigation

Because plants require water in order to grow, agriculture represents the largest single use of global water. About 73 percent of all fresh water withdrawn from groundwater supplies, rivers, and lakes is used in the irrigation of crops. Almost 15 percent of the world's croplands are irrigated. Water use varies among countries. Some countries have abundant water supplies and irrigate liberally, while water is very scarce in other countries and must be used very carefully. Because as much as 80 percent of the water intended for irrigation is lost to evaporation before reaching the plants, the efficiency of water use in some countries can be very low.

There is no doubt that irrigation has dramatically increased crop production in many areas, but some irrigation practices have been detrimental. Overwatering can lead to a *waterlogging* of the soil. Waterlogging cuts off the supply of oxygen to the roots, and the plants die. Irrigation of crops in dry climates can often result in *salinization* of the soil. In these climates, the irrigation water rapidly evaporates from the soil, leaving behind mineral salts that were dissolved in the water. As the salts accumulate, they become lethal to most plants. Some experts estimate that as much as one-third of the world's agricultural soil has been damaged by salinization. There is also an argument as to whether the increased usage of water for agriculture has decreased the supply of potable water fit for other uses.

Fertilizers

Plants require sunshine, water either from rainfall or irrigation, carbon dioxide from the atmosphere, and thirteen mineral nutrients from the soil. Of these, calcium, magnesium, nitrogen, phosphorus, and potassium are required in the greatest amounts. Calcium and magnesium are plentiful in soils located in dry climates, but in wetter climates these nutrients are often *leached* through the soil. In these regions, calcium and magnesium are returned to the soil in the form of lime, which is also sometimes added to soil to raise its pH (increase its alkalinity). Nitrogen, phosphorus, and potassium are the nutrients which are most often depleted from agricultural soils, and these nutrients are often referred to as the *fertilizer elements*. Because these nutrients stimulate plant growth and can greatly increase crop yields, it is necessary to apply them to the soil regularly in order to maintain fertility.

The amount of fertilizer applied to the soil increased more than 450 percent in the second half of the twentieth century. While this increase in the use of fertilizers has more than doubled worldwide crop production, it has also caused some problems. The increased production of fertilizers has required the use of energy and mineral resources that could have been used elsewhere. In many cases, farmers tend to overfertilize. Overfertilization not only wastes money but also contributes to environmental degradation. Fertilizer elements, particularly nitrogen and phosphorus, are carried away by water runoff and are eventually deposited in the rivers and lakes, where they contribute to pollution of aquatic ecosystems. In addition, nitrates can accumulate in underground water supplies. These nitrates can be harmful if ingested by newborns.

Other Resources

Modern agriculture, as it is practiced in the United States, consumes large amounts of energy. Farm machinery used in planting, cultivating, harvesting, and transporting crops to processing plants or to market consumes large supplies of liquid fossil fuels such as gasoline or diesel. The energy required to produce fertilizers, pesticides, and other agricultural chemicals is the second largest energy cost associated with agriculture. The use of fuel required by pumps to irrigate crops is also a major energy consumer. Additional energy is used in food processing, distribution, storage, and cooking after the crop leaves the farm. The energy used for these activities may be five times as much as that used to produce the crop.

About 16 percent of the total energy used in the United States is consumed by systems devoted to feeding people, and most of the foods consumed in the United States require more calories of energy to produce, process, and distribute to the market than they provide when they are eaten. The next major development in agriculture will be the *biotechnical revolution*, in which scientists will be able to use molecular biological techniques to produce new crop varieties. In the future, agricultural scientists may be able to develop crop plants that can be produced, processed, and distributed with less impact on other resources.

Commercial Impact

While fewer than 1 percent of Americans are directly involved in agricultural production, agriculture in the United States employs about seventeen million people in some phase of the industry, from production to retail sales. This includes workers hired by agricultural chemical companies which produce or sell agricultural implements and machinery, processing and canning plants, and wholesale and retail marketing firms such as grocery stores. In 1997 there were six thousand to eight thousand different agricultural products on the market. Agriculture is also big business, with assets of about one hundred billion dollars. This figure equals 88 percent of the combined capital assets of all the major U.S. corporations. American farmers now produce 76 percent more crops than the previous generation did on the same amount of land, and one-third of all American agricultural products are exported. This makes the United States the world's most agriculturally productive country and the largest exporter of agricultural products.

D. R. Gossett

See also: Agricultural crops: experimental; Agricultural revolution; Agriculture: marine; Agriculture: modern problems; Agriculture: traditional; Agriculture: world food supplies; Agronomy; Alternative grains; Asian agriculture; Australian agriculture; Biofertilizers; Biopesticides; Biotechnology; Caribbean agriculture; Central American agriculture; Composting; Corn; Drought; European agriculture; Farmland; Fertilizers; Grains; Green Revolution; Herbicides; High-yield crops; Horticulture; Hybridization; Hydroponics; Integrated pest management; North American agriculture; Organic gardening and farming; Pesticides; Plant biotechnology; Plants with potential; Rice; Slash-and-burn agriculture; Soil; South American agriculture; Sustainable agriculture; Vegetable crops.

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AGRICULTURE: MARINE

Categories: Agriculture; economic botany and plant uses; food; water-related life

Marine agriculture uses techniques of artificial cultivation, such as growing, managing, and harvesting, and applies them to marine plants and animals. The products are then used for human consumption.

Marine agriculture is also known as *mariculture* or *aquaculture*, although aquaculture is a more general term referring to both freshwater and marine farming of organisms. The world's oceans cover approximately three-fourths of the globe, including vast regions of unexplored life and landforms. The potential for exploiting the oceans agriculturally is great but currently meets significant obstacles. Because of the expense of equipment and personnel involved, most marine species are not cultivated. Coastal pollution, habitat destruction, competition for land use, and economics all limit mariculture programs. Nevertheless, mariculture does offer several food, medical, and other products that are currently being marketed.

Food

Seaweeds are edible, especially the red and brown algae. The three most common types of seaweeds are known by their Japanese names: *nori* (*Porphyra*), a red seaweed high in vitamin C and digestible protein; *kombu* (*Laminaria*); and *wakame* (*Undaria*), high in calcium. They are eaten raw, cooked, or dried and have several vitamins and minerals as well as protein. Seaweeds are low in fats, and 35 to 50 percent of the dry weight of red seaweeds is protein. Seaweeds can be used to add taste and variety to foods. They are used as a hot vegetable, boiled and formed into cakes and fried, in salads, and in preparing desserts, breads, soups, casseroles, sandwiches, teas, and candy.

The world's yearly harvest of seaweeds is approximately 8.4 million tons of green seaweed, 2.8 million tons of brown seaweed, and 1.2 million tons of red seaweed. The total seaweed market in 1998 was worth more than $5 billion, with $600 million deriving from food additives alone. China is the leading harvester and the world's biggest seaweed consumer. Japan is the leading seaweed importer and, at the end of the twentieth century, employed more than thirty-five thousand people in the industry. Harvesting and marketing edible seaweed is a growing business in the United States, especially on the West Coast.

Seaweeds produce several types of *phycocolloids*, starchlike chemicals used in food processing and manufacturing. An important type called *algin*, which makes up alginic acid and alginates, is used in manufacturing dairy products such as ice cream, cheese, and toppings as well as to prevent frostings and pies from desiccation. Another extract is *agar*, used to form jellies and protect fish and meats during canning. Agar is also used in low-calorie foods and as a thickener. Red algae is a source of the agglutinant *carrageenan*, which is used in many food products as an emulsifier to give body to dairy products and other processed foods, including instant puddings. Additionally, seaweed-based food additives are common in prepared and fast foods, including hamburgers and yogurt.

Kelp farming is a major livelihood in the eastern Pacific, with approximately 140,000 tons harvested each year for the extraction of alginates used in food and food additives. Kelp is a good source of calcium, potassium, iron, iodine, bromine, and zinc. It is also low-fat, has some protein, and is a natural tenderizer. Kelp flakes are used as a low-sodium salt substitute.

Medicine

The use of marine plants in medicine is still in the early stages of exploration and faces many challenges, including identification of useful chemicals and the cultivation of significant quantities. Dinoflagellates and other microalgae are being investigated for compounds that might fight cancerous tumors. Diluted algae toxins from red tides can be used to inhibit the growth of most bacteria. Green algae has halosphaerin, a strong antibiotic. Seaweed is used in wound dressings in hospitals and as a source of iodine, A, B, D, and E vitamins, calcium, magnesium, potassium, sodium, sulfur, and trace antioxidants such as selenium and zinc. The seaweed extract agar is used in laxatives and as a medium to grow bacteria and molds.

Kelp is rich in *chlorophyll*, which can help detoxify the body, fight inflammations, and increase the formation of oxygen-carrying red blood cells. Chlorophyll is also used to fight bad breath and as an ingredient in deodorants. Kelp is used to reduce cholesterol, treat gastrointestinal, respiratory, and genitourinary disorders, and lower blood pressure. The alginic acid produced by kelp can rid the body of radioactive strontium, the most dangerous to humans of all components in the fallout from atomic explosions.

Other Uses

Marine plants are used for a variety of other purposes. Seaweed is used as a component of many fertilizers, as a food additive in animal feed, and to reduce soil acidity. Research on cattle and swine has revealed that the addition of seaweed to animal feed can enhance the immune system and makes the meat a more desirable color. It can also save cattle from the effects of fungus-infected grass.

Seaweed is used as an ingredient in cosmetics as well as to nourish, revitalize, condition, and improve the skin, hair, and body. It is used in cleansers, toners, moisturizers, scrubs, body lotions, and hair and bath products. The giant kelp (*Macrocystis*) is a major source of algin for commercial uses, as is the brown algae *Laminaria*, which is harvested in the north Atlantic. Algin is used in shampoos, shaving cream, plastics, pesticides, rubber products, paper, paints, and cosmetics. Additionally, kelp is used in emulsifiers for toothpastes and printing inks. Kelp has even been used to make fishing lines. Some research has been done on using kelp as a fuel to produce a clean-burning methane gas. Kelp can be used to ferment human waste and garbage, which can then be sold as fertilizers.

Virginia L. Hodges

See also: Agricultural crops: experimental; Agriculture: world food supplies; Algae; Brown algae; Carbohydrates; Green algae; Marine plants; Medicinal plants; Red algae.

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AGRICULTURE: MODERN PROBLEMS

Categories: Agriculture; economic botany and plant uses; environmental issues

Many current problems in agriculture are not new. Erosion and pollution, for example, have been around as long as agriculture. However, agriculture has changed drastically within its ten-thousand-year history, especially since the dawn of the Industrial Revolution in the seventeenth century. Erosion and pollution are now bigger problems than before and have been joined by a host of other issues that are equally critical—not all related to physical deterioration.

Monoculture

Modern agriculture emphasizes *crop specialization*, also known as *monoculture*. Farmers, especially in industrialized regions, often grow a single crop on much of their land. Problems associated with this practice are exacerbated when a single variety or cultivar of a species is grown. Such a strategy allows the farmer to reduce costs, but it also makes the crop, and thus the farm and community, susceptible to widespread crop failure. The corn blight of 1970 devastated more than 15 percent of the North American corn crop. The corn was particularly susceptible to the harmful organisms because 70 percent of the crop being grown was of the same high-yield variety. Chemical antidotes can fight pests, but they increase pollution. Maintaining species diversity or varietal diversity—growing several different crops instead of one or two—allows for crop failures without jeopardizing the entire economy of a farm or region that specializes in a particular monoculture, such as tobacco, coffee, or bananas.

Genetic Engineering

Growing *genetically modified* (GM) crops is one attempt to replace post-infestation chemical treatments. Recombinant technologies used to splice genes into varieties of rice or potatoes from other organisms are becoming increasingly common. The benefits of such GM crops include more pest-resistant plants and higher crop yields. However, environmentalists fear new genes could trigger unknown side effects with more serious, long-term environmental and economic consequences than the problems they were used to solve. GM plants designed to resist herbicide applications could potentially pass the resistant gene to closely related wild weed species that would then become "super weeds." Also, pests, just as they can develop resistance to pesticides, may also become resistant to defenses engineered into GM plants. The high cost of recombinant technologies calls into question the feasibility of continuing development of GM plants.

Erosion

An age-old problem, soil loss from *erosion* occurs all over the world. As soil becomes unproductive or erodes away, more land is plowed. The newly plowed lands usually are considered *marginal*, meaning they are too steep, nonporous or too sandy, or deficient in some other way. When natural vegetative cover blankets these soils, it protects them from erosive agents: water, wind, ice, or gravity. Plant cover "catches" rainwater that seeps downward into the soil rather than running off into rivers. As marginal land is plowed or cleared to grow crops, erosion increases.

Expansion of land under cultivation is not the only factor contributing to erosion. Fragile grasslands in dry areas also are being used more intensively. Grazing more livestock than these pastures can handle decreases the amount of grass in the pasture and exposes more of the soil to wind, the primary erosive agent in dry regions. *Overgrazing* can affect pastureland in tropical regions too. Thousands of acres of tropical forest have been cleared to establish cattle-grazing ranges in Latin America. Tropical soils, although thick, are not very fertile. After one or two growing seasons, crops grown in these soils will yield substantially less than before.

Tropical fields require *fallow periods* of about ten years to restore the soil after it is depleted. That is why tropical farmers using *slash-and-burn agriculture* move to new fields every few years in a cycle that returns them to the same place years later, after their particular lands have regenerated. Where there is heavy forest cover, soils are protected from exposure to the massive amounts of rainfall. Organic material for crops is present as long as the forest remains in place. When the forest is cleared, however, the resulting grassland cannot provide the adequate protection, and erosion accelerates. Lands that are heavily grazed provide even less protection from heavy rains, and erosion accelerates even more.

The use of machines also promotes erosion, and modern agriculture relies on machinery such as tractors, harvesters, trucks, balers, and ditchers. In industrialized nations, machinery is used intensely. Machinery use is on the rise in developing countries such as India, China, Mexico, and Indonesia, where traditional, nonmechanized farming methods are the norm. Farming machines, in gaining traction, loosen topsoil and inhibit vegetative cover growth, especially when farm implements designed to rid the soil of weeds are attached. The soil is then more prone to erode.

Eco-fallow farming has become more popular in the United States and Europe as a way to reduce erosion. This method of agriculture, which leaves the crop residue in place over the fallow (nongrowing) season, does not root the soil in place as well as living plants do. As a result, some erosion

Image Not Available

continues. Additionally, eco-fallow methods require heavy use of chemicals, such as herbicides, to "burn down" weed growth at the start of the growing season. This contributes to increased erosion and pollution.

Pollution and Silt

Besides causing resistance among harmful bacteria, insects, and weeds, pesticides inevitably wash into, and contaminate, surface and groundwater supplies. Chemicals, although problematic, are not as difficult to contend with as the increasingly heavy silt load choking the life out of streams and rivers. Accelerated erosion from water runoff carries silt particles into streams, where they remain suspended and inhibit the growth of many forms of plant and animal life.

The silt load in American streams has become so heavy that the Mississippi River Delta is growing faster than it once did. Heavy silt loads, combined with chemical residues, are creating an expanded dead zone. By taxing the capabilities of ecosystems around the Delta, sediments are filtered out slowly, plant absorption of nutrients is decreased, and salinity levels for aquatic life cannot be stabilized. Most of the world's population lives in coastal zones, and 80 percent of the world's fish catch comes from coastal waters over continental shelves that are most susceptible to this form of pollution.

Pesticide Resistance

With the onset of the *Green Revolution*, the use of herbicides, insecticides, and other *pesticides* increased dramatically all over the world. An increasing awareness of problems caused by overuse of pesticides extends even to household antibacterial cleaning agents and other products. Mutations among the genes of bacteria and plants have allowed these organisms to resist the effects of chemicals that were toxic to their ancestors. Use of pesticides leads to a cycle wherein more, or different combinations of, chemicals are used, and more pests develop resistance to these toxins. Additionally, the development of herbicide-resistant crop plants enables greater use of herbicides to kill undesirable weeds on croplands.

Increasing interest in *biopesticides* may slow the cycle of pesticide resistance. Types of biopesticides include beneficial microbes, fungi, and insects such as ladybugs that can be released in infested areas to prey upon specific pests. Biopesticides used today include naturally occurring and genetically modified organisms. Their use also avoids excessive reliance on chemical pesticides.

Fertilizers and Eutrophication

Increased use of *fertilizers* was another result of the Green Revolution. Particulate amounts of most fertilizers enter the hydrologic cycle through runoff. As a result, bodies of water become enriched in dissolved nutrients, such as nitrates and phosphates. The growth of aquatic plants in rivers and lakes is overstimulated, and this results in the depletion of dissolved oxygen. This process of *eutrophication* can harm all aquatic life in these ecosystems.

Water Depletion

With an increasing reliance on irrigation, groundwater resources are mismanaged and overtapped. The rate of groundwater recharge is slow, usually between 0.1 and 0.3 percent per year. When the amount of water pumped out of the ground exceeds the recharge rate, it is referred to as *aquifer overdraft*. An aquifer is a water-bearing stratum of permeable rock, sand, or gravel.

In Tamil Nadu, India, groundwater levels dropped 25 to 30 meters during the 1970's due to excessive pumping for irrigation. In Tianjin, China, the groundwater level declines 4.4 meters per year. In the United States, aquifer overdraft averages 25 percent over the replacement rate. The Ogallala aquifer under Kansas, Nebraska, and Texas represents an extreme example of overdraft: Depletion is 130 to 160 percent above the replacement rate annually. At this rate, this aquifer, which supplies water to countless communities and farms, has been projected to become nonproductive by 2030.

Soil Salinization

In addition, continued irrigation of arid regions can lead to soil problems. *Soil salinization* is widespread in the small-grained soils of these regions, which have a high water absorption capacity and a low infiltration rate. Some irrigation practices add large amounts of salts into the soil, increasing its natural rate of salinization. This can also occur at the base of a hill slope. Soil salinization has been recognized as a major process of land degradation.

Although surface and groundwater resources cannot be enriched by technology, conservation and improved environmental management can make the use of precious freshwater more efficient.

In agriculture, for example, drip irrigation can reduce water use by nearly 50 percent. In developing countries, though, equipment and installation costs often limit the availability of these more efficient technologies.

Urban Sprawl

As more farms become mechanized, the need for farmers and farm workers is being drastically reduced. From a peak in 1935 of about 6.8 million farmers farming 1.1 billion acres, the United States at the end of the twentieth century counted fewer than 2 million farmers farming 950 million acres.

Urban sprawl converts a tremendous amount of cropland into parking lots, malls, industrial parks, and suburban neighborhoods. If cities were located in marginal areas, then concern about the loss of farmland to commercial development would be nominal. However, the cities attracting the greatest numbers of people have too often replaced the best cropland. Taking the best cropland out of primary production imposes a severe economic penalty.

James Knotwell and Denise Knotwell, updated by Bryan Ness and Elizabeth Slocum

See also: Biopesticides; Drought; Erosion and erosion control; Fertilizers; Forest management; Pesticides.

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AGRICULTURE: TRADITIONAL

Categories: Agriculture; economic botany and plant uses

Two agricultural practices that are widespread among the world's traditional cultures, slash-and-burn agriculture and nomadism, share several features. Both are ancient forms of agriculture, both involve farmers not remaining in a fixed location, and both can pose serious environmental threats if practiced in a nonsustainable fashion. The most significant difference between the two is that slash-and-burn is associated with raising field crops, while nomadism usually involves herding livestock.

Slash-and-Burn Agriculture

Farmers have practiced *slash-and-burn agriculture*, which is also referred to as *shifting cultivation* or *swidden agriculture*, in almost every region of the world where farming is possible. Although at the end of the twentieth century slash-and-burn agriculture was most commonly found in tropical areas such as the Amazon River basin in South America, swidden agriculture once dominated agriculture in more temperate regions, such as northern Europe. Swidden agriculture was, in fact, common in Finland and northern Russia well into the early decades of the twentieth century.

Slash-and-burn acquired its name from the practice of farmers who cleared land for planting crops by cutting down the trees or brush on the land and then burning the fallen timber on the site. The farmers literally slash and burn. The ashes of the burnt wood add minerals to the soil, which temporarily improves its fertility. Crops the first year following clearing and burning are generally the best crops the site will provide. Each year after that, the yield diminishes slightly as the fertility of the soil is depleted.

Farmers who practice slash-and-burn do not attempt to improve fertility by adding fertilizers such as animal manure to the soil. They instead rely on the soil to replenish itself over time. When the yield from one site drops below acceptable levels, farmers then clear another piece of land, burn the brush and other vegetation, and cultivate that site while leaving their previous field to lie fallow and its natural vegetation to return. This cycle will be repeated over and over, with some sites being allowed to lie fallow indefinitely, while others may be revisited and farmed again in five, ten, or twenty years.


PhotoDisc

Farm workers in China harvest tea.

Farmers who practice slash-and-burn do not always move their dwelling places as they cultivate different fields. In some geographic regions, farmers live in a central village and farm cooperatively, with fields being alternately allowed to remain fallow and farmed, making a gradual circuit around the central village. In other cases, the village itself may move as new fields are cultivated. Anthropologists studying indigenous peoples in Amazonia, for example, discovered that village garden sites were on a hundred-year cycle. Villagers farmed cooperatively to clear a garden site. That garden would be used for about five years; then a new site was cleared. When the fields in use became an inconvenient distance from the village—about once every twenty years—the entire village would move to be closer to the new fields. Over a period of approximately one hundred years, a village would make a circle through the forest, eventually ending up close to where it had been located long before any of the present villagers had been born.

In more temperate climates, farmers often owned and lived on the land on which they practiced swidden agriculture. Farmers in Finland, for example, would clear a portion of their land, burn the covering vegetation, grow grains for several years, and then allow that land to remain fallow for five to twenty years. The individual farmer rotated cultivation around the land in a fashion similar to that practiced by whole villages in other areas but did so as an individual rather than as part of a communal society.

Although slash-and-burn is frequently denounced as a cause of environmental degradation in tropical areas, the problem with it is not the practice itself but the length of the cycle. If the cycle of shifting cultivation is long enough, forests will grow back, the soil will regain its fertility, and minimal adverse effects will occur. In some regions, a piece of land may require as little as five years to regain its maximum fertility; in others, it may take one hundred years. Problems arise when growing populations put pressure on traditional farmers to return to fallow land too soon. Crops are smaller than needed, leading to a vicious cycle in which the next strip of land is also farmed too soon, and each site yields less and less. As a result, more and more land must be cleared.

Nomadism

Nomadic peoples have no permanent homes. They earn their living by raising herd animals, such as sheep, horses, or other cattle, and they spend their lives following their herds from pasture to pasture with the seasons, going wherever there is sufficient food for their animals. Most nomadic animals tend to be hardy breeds of goats, sheep, or cattle that can withstand hardship and live on marginal lands. Traditional nomads rely on natural pasturage to support their herds and grow no grains or hay for themselves. If a drought occurs or a traditional pasturing site is unavailable, they can lose most of their herds to starvation.

In many nomadic societies, the herd animal is almost the entire basis for sustaining the people. The animals are slaughtered for food, clothing is woven from the fibers of their hair, and cheese and yogurt may be made from milk. The animals may also be used for sustenance without being slaughtered. Nomads in Mongolia, for example, occasionally drink horses' blood, removing only a cup or two at a time from the animal.

In mountainous regions, nomads often spend the summers high up on mountain meadows, returning to lower altitudes in the autumn when snow begins to fall. In desert regions, they move from oasis to oasis, going to the places where sufficient natural water exists to allow brush and grass to grow, allowing their animals to graze for a few days, weeks, or months, then moving on. In some cases, the pressure to move on comes not from the depletion of food for the animals but from the depletion of a water source, such as a spring or well. At many desert oases, a natural water seep or spring provides only enough water to support a nomadic group for a few days at a time.

In addition to true nomads—people who never live in one place permanently—a number of cultures have practiced *seminomadic farming*: The temperate months of the year, spring through fall, are spent following the herds on a long loop, sometimes hundreds of miles long, through traditional grazing areas, then the winter is spent in a permanent village.

Nomadism has been practiced for millennia, but there is strong pressure from several sources to eliminate it. Pressures generated by industrialized society are increasingly threatening the traditional cultures of nomadic societies, such as the Bedouin of the Arabian Peninsula. Traditional grazing areas are being fenced off or developed for other purposes.

Environmentalists are also concerned about the ecological damage caused by nomadism. Nomads generally measure their wealth by the number of animals they own and will try to develop their herds to as large a size as possible, well beyond the numbers required for simple sustainability. The herd animals eat increasingly large amounts of vegetation, which then has no opportunity to regenerate. Desertification may occur as a result. Nomadism based on herding goats and sheep, for example, has been blamed for the expansion of the Sahara Desert in Africa. For this reason, many environmental policymakers have been attempting to persuade nomads to give up their traditional lifestyle and become sedentary farmers.

Nancy Farm Männikkö

See also: Forest management.

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AGRICULTURE: WORLD FOOD SUPPLIES

Categories: Agriculture; food

Soil types, topography, climate, socioeconomics, dietary preferences, stages in agricultural development, and governmental policies combine to give a distinctive personality to regional agricultural characteristics and, hence, food supplies in various areas of the world.

All living things need food to live, grow, work, and survive. Almost all foods that humans consume come from plants and animals. Not all of earth's people eat the same foods, however. The types, combinations, and amounts of food consumed by different peoples depend upon historic, socioeconomic, and environmental factors.

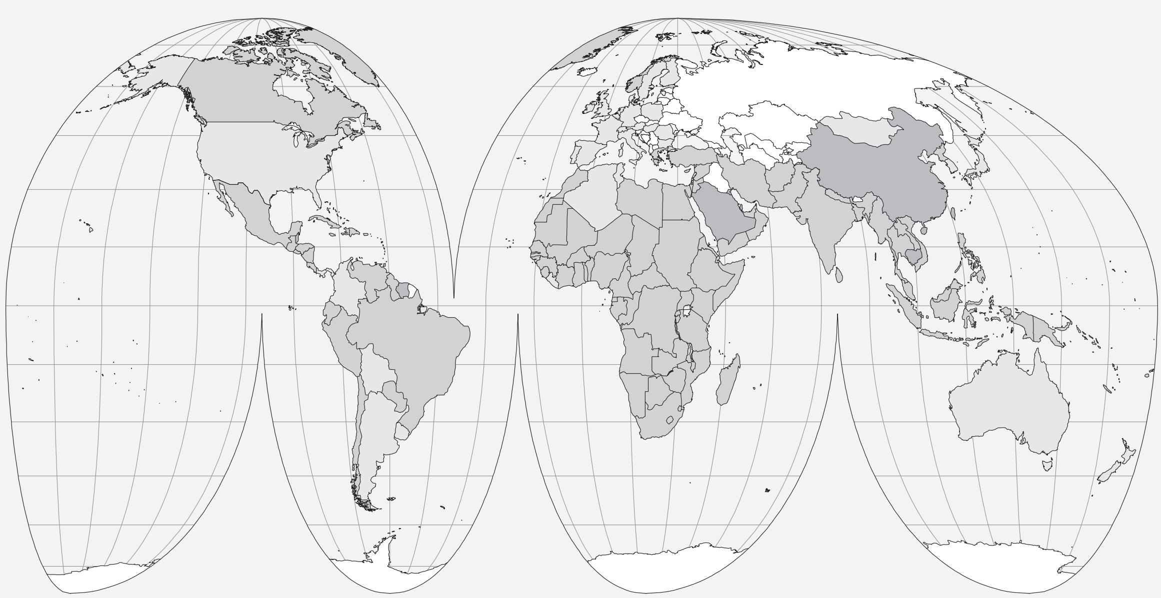
History of Food Consumption

Early in human history, people ate what they could gather or scavenge. Later, people ate what they could plant and harvest and the products of animals they could domesticate. Modern people eat what they can grow, raise, or purchase. Their diets or food composition is determined by income, local customs, religion or food biases, and advertising. There is a global food market, and many people can select what they want to eat and when they eat it according to the prices they can pay and what is available.

Historically, in places where food was plentiful, accessible, and inexpensive, humans devoted less time to basic survival needs and more time to activities that led to human progress and enjoyment of leisure. Despite a modern global food system, instant telecommunications, the United Nations, and food surpluses in some places, however, the problem of providing food for everyone on earth has not been solved.

In 1996 leaders from 186 countries gathered in Rome and agreed to reduce by half the number of hungry people in the world by the year 2015. United Nations data for 1998 revealed that more than 790 million people in the developing parts of

Increases in Land Used for Agriculture by Country, 1980-1994



the world did not have enough food to eat. This is more people than the total population of North America and Europe at that time. The number of undernourished people has been decreasing since 1990. Still, at the current pace of hunger reduction in the world, 600 million people will suffer from "acute food insecurity" and go to sleep hungry in 2015. Despite efforts being made to feed the world, outbreaks of food deficiencies, mass starvation, and famine are a certainty in the twenty-first century.

World Food Source Regions

Agriculture and related primary food production activities, such as fishing, hunting, and gathering, continue to employ more than one-third of the world's labor force. Agriculture's relative importance in the world economic system has declined with urbanization and industrialization, but it still plays a vital role in human survival and general economic growth. Demands on agriculture in the twenty-first century include supplying food to an increasing world population of nonfood producers as well as producing food and nonfood crude materials for industry.

Soil types, topography, weather, climate, socioeconomic history, location, population pressures, dietary preferences, stages in modern agricultural development, and governmental policies combine to give a distinctive personality to regional agricultural characteristics. Two of the most productive food-producing regions of the world are North America and Europe. Countries in these regions export large amounts of food to other parts of the world.

North America is one of the primary food-producing and food-exporting continents. After 1940 food output generally increased as cultivated zacreage declined. Progress in improving the quantity and quality of food production is related to mechanization, chemicalization, improved breeding, and hybridization. Food output is limited more by market demands than by production obstacles. Western Europe, although a basic food-deficit area, is a major producer and exporter of high-quality foodstuffs. After 1946 its agriculture became more profit-driven. Europe's agricultural labor force grew smaller, its agriculture became more mechanized, its farm sizes increased, and capital investment per acre increased.

Foods from Plants

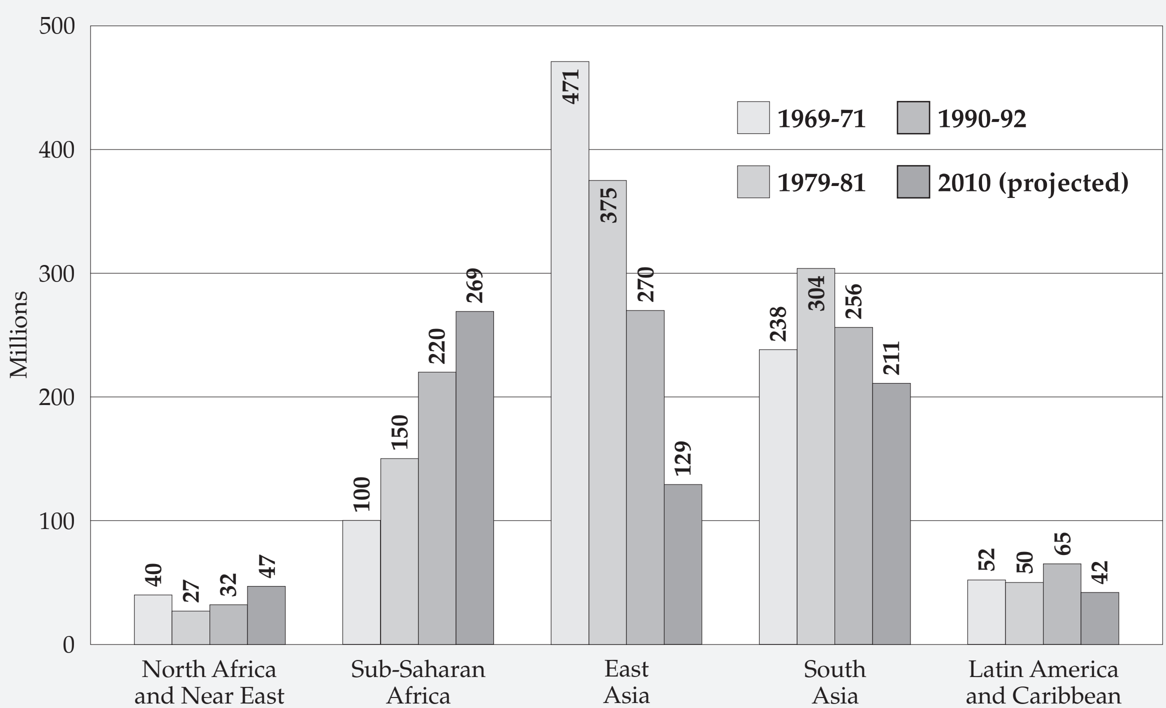
Most basic staple foods come from a small number of plants and animals. Ranked by tonnage produced, the most important food plants throughout the world are wheats, corn, rice, potatoes, cassava, barley, soybeans, sorghums and millets, beans, peas and chickpeas, and peanuts. Wheat and rice are the most important plant foods. More than one-third of the world's cultivated land is planted with these two crops. Wheat is the dominant food staple in North America, Western and Eastern Europe, northern China, the Middle East, and North Africa. Rice is the dominant food staple in southern and eastern Asia.

Corn, used primarily as animal food in developed nations, is a staple food in Latin America and southeast Africa. Potatoes are a basic food in the highlands of South America and in Central and Eastern Europe. Cassava is a tropical starch-producing root crop of special dietary importance in portions of lowland South America, the west coast countries of Africa, and sections of South Asia. Barley is an important component of diets in North African, Middle Eastern, and Eastern European countries. Soybeans are an integral part of the diets of those who live in eastern, southeastern, and southern Asia. Sorghums and millets are staple subsistence foods in the savanna regions of Africa and South Asia, while peanuts are a facet of dietary mixes in tropical Africa, Southeast Asia, and South America.

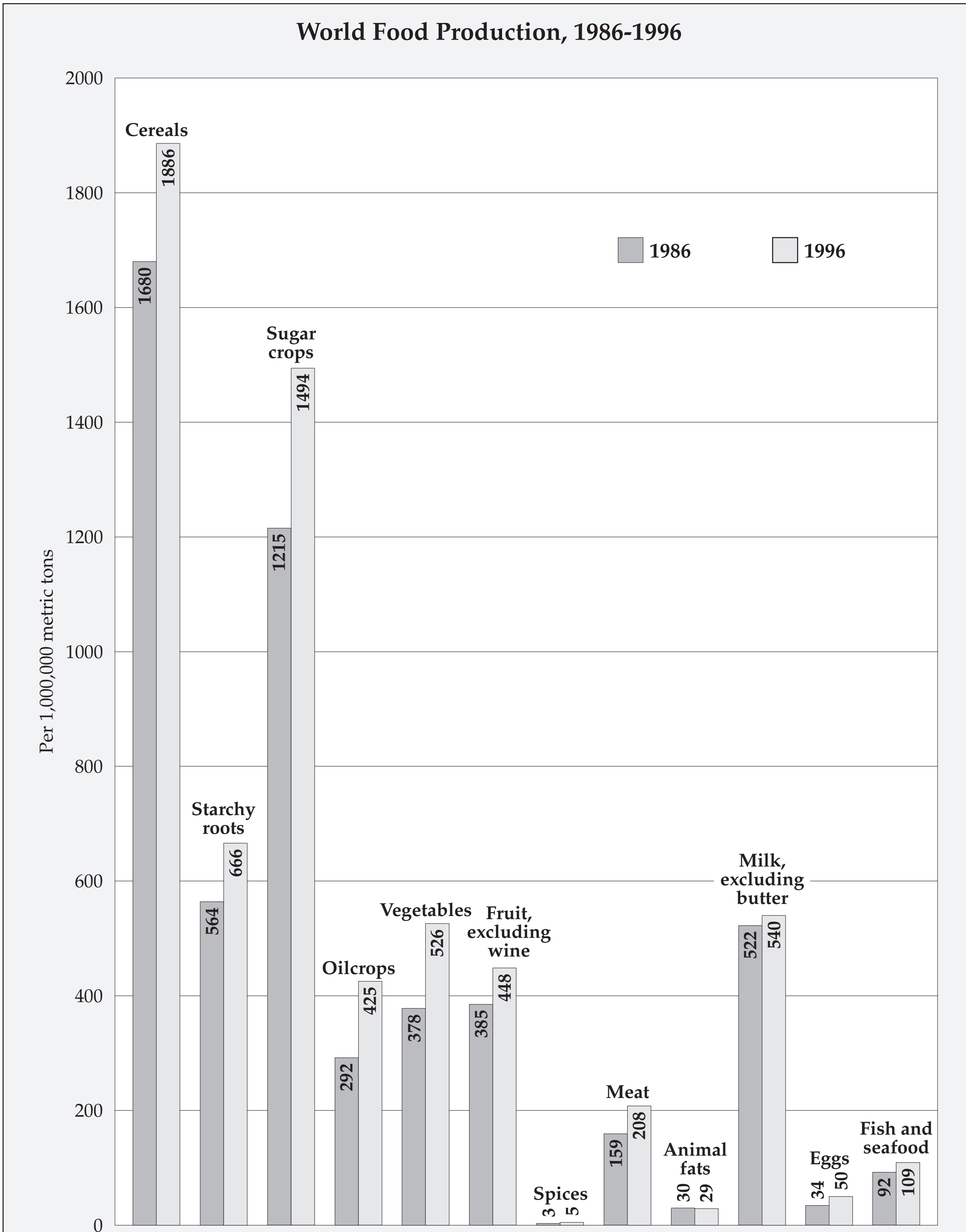
The World's Growing Population

The problem of feeding the world is compounded by the fact that population was increasing at a rate of nearly 80 million persons per year at the end of the twentieth century. That rate of increase is roughly equivalent to adding a country the size of Germany to the world every year. Compounding the problem of feeding the world are population redistribution patterns and changing food consump-

Number of Persons Chronically Undernourished in Developing Countries by Region



Source: United Nations Food and Agriculture Organization (FAOSTAT Database, 2000).



Source: Data are from United Nations Food and Agriculture Organization (FAOSTAT Database, 2000).

tion standards. By 2001, the world had exceeded the six billion mark, and the world population was projected to reach approximately ten billion people by 2050—four billion people more than were on the earth in 2000. Most of the increase in world population was expected to occur within the developing nations.

Urbanization

Along with an increase in population in developing nations is massive urbanization. City dwellers are food consumers, not food producers. The exodus of young men and women from rural areas has given rise to a new series of megacities, most of which are in developing countries. By the year 2015, twenty-six cities in the world are expected to have populations of ten million people or more.

When rural dwellers move to cities, they tend to change their dietary composition and food-consumption patterns. Qualitative changes in dietary consumption standards are positive, for the most part, and are a result of educational efforts of modern nutritional scientists working in developing countries. During the last four decades of the twentieth century, a tremendous shift took place in overall dietary habits. Dietary changes and consumption trends have contributed to a decrease in child mortality, an increase in longevity, and a greater resistance to disease. This globalization of people's diets has resulted in increased demands for higher quality, greater quantity, and more nutritious basic foods.

Perspectives

Humanity is entering a time of volatility in food production and distribution. The world will produce enough food to meet the demands of those who can afford to buy food. In many countries, however, food production is unlikely to keep pace with increases in the demand for food by growing populations. The food gap—the difference between production and demand—could more than double in the first three decades of the twenty-first century. Such a development would increase the dependence of developing countries on food imports. About 90 percent of the rate of increase in aggregate food demand in the early twenty-first century is expected to be the result of population increases. Factors that could lead to larger fluctuations in food availability include weather variations, such as those induced by El Niño and climatic change, the growing scarcity of water, civil strife and political instability, and declining food aid.

William A. Dando

See also: Agricultural crops: experimental; Agricultural revolution; Agriculture: history and overview; Agriculture: marine; Agriculture: modern problems; Agriculture: traditional; Agronomy; Biotechnology; Genetically modified foods; Green Revolution; Horticulture; Human population growth; Hydroponics; Plant biotechnology; Plants with potential.

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AGRONOMY

Categories: Agriculture; disciplines; economic botany and plant uses; soil

Agronomy is a group of applied science disciplines concerned with land and soil management and crop production. Agronomists' areas of interest range from soil chemistry to soil-plant relationships to land reclamation.

The word "agronomy" derives from the ancient Greek *agros* (field) and *nemein* (manage) and therefore literally means "field management." The American Society of Agronomy defines agronomy as "the theory and practice of crop production and soil management." There are many specialties within the study of agronomy.

PhotoDisc

Agronomy is a family of disciplines, including soil management; a component of soil management is tilling and plowing techniques. This field has been plowed by tractor.

Agronomic Specialties

Agronomy is the family of disciplines investigating the production of crops supplying food, forage, and fiber for human and animal use. It studies the stewardship of the soil upon which those crops are grown. Agronomy covers all aspects of the agricultural environment, from agroclimatology to soil-plant relationships. It includes crop science, soil science, weed science, and biometry (the statistics of living things) as well as crop, soil, pasture, and range management; turfgrass; agronomic modeling; and crop, forage, and pasture production and utilization.

Within each area are subdisciplines. For example, within soil science are traditional disciplines such as soil fertility, soil chemistry, soil physics, soil microbiology, soil taxonomy and classification, and *pedogenesis*, the science of how soils form. Newer disciplines within soil science include such studies as *bioremediation*, or the study of how living organisms can be used to clean up toxic wastes in the environment, and land reclamation, the study of how to reconstruct landscapes disturbed by human activities, such as surface mining.

Scientific Goals

Chief among detrimental human activities is poor field management, which leads to reduced productivity and reduced environmental quality. Historical examples abound; one is that of the 1930's Dust Bowl in the United States. In the early 1900's much of the American Southern Plains, which had been natural grassland, was converted to wheatland. Planting and plowing methods of the time did not enable wheat to protect the ground against winds. Additionally, *overgrazing* of livestock had destroyed what grassland remained by the 1930's. The soil eroded, drought conditions which would last for most of the decade set in, and a series of wind and dust storms whipped through the region.

An estimated 50 million acres of land were destroyed before soil conservation measures, implemented under the administration of Franklin Roosevelt, began to improve the situation.

It is the role of agronomy to manage soil and crop resources as effectively as possible so that the twin goals of productivity and environmental quality are preserved. Agronomy treats the agricultural environment as humankind's greatest natural resource: It is the source of food, clothing, and building materials. The agricultural environment purifies the air humans and other animals breathe and the water they drink.

Agronomists, whatever their specific field, seek to utilize soil and plant resources to benefit society. Crop breeders, for example, use the genetic diversity of wild varieties of domesticated plants to obtain the information needed to breed plants for greater productivity or pest resistance. Soil scientists study landscapes to determine how best to manage soil resources. Integrating agricultural practices with the environment maintains soil fertility and keeps soil in place so that erosion does not reduce the quality of the surrounding environment.

Mark S. Coyne, updated by Elizabeth Slocum

See also: Agriculture: history and overview; Soil; Soil conservation; Soil management.

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AIR POLLUTION

Categories: Environmental issues; pollution

Air pollution results from the contamination of air with naturally occurring or synthesized gases and particulates that reach levels that are harmful to biological systems. Air pollution damages plants in both natural and agricultural systems.

D*ry air* is a mixture of gases composed of approximately 78.08 percent nitrogen, 20.95 percent oxygen, 0.93 percent argon, and 0.036 percent carbon dioxide. The remainder is composed of trace amounts of gases, such as helium, hydrogen, neon, methane, nitrogen oxides, sulfur oxides, and others. *Environmental air* contains additional quantities of water vapor and other components related to natural geological and biological activities and human activities. The composition of environmental air is variable by time of day, season, geographic location, and altitude. Those components added by human activity are often linked to air pollution.

Types of Pollutants

Air pollutants may be classified as primary or secondary. *Primary pollutants* are classified as gaseous or particulate. *Gaseous pollutants* include compounds such as sulfur oxides, nitrogen oxides, and various types of hydrocarbons, such as methane, benzene, and chlorofluorocarbons (CFCs). Gaseous pollutants may impact plant health by directly damaging plant structure or by altering physiological processes. *Particulates* are irritants, such as soot and dust that clog plant stomata (pores). In addition, particulates may serve as carriers for harmful chemicals that adhere to the particulates' surfaces.

Secondary pollutants are produced as a result of the interactions of primary gaseous pollutants with one another or with other atmospheric components. For example, sulfur dioxide and nitrogen dioxide react with water to form sulfuric and nitric acids, respectively, which are important components of *acid precipitation*. Production of some secondary pollutants requires the presence of ultraviolet radiation. In the presence of ultraviolet light, nitrogen dioxide loses an oxygen atom, which then reacts with molecular oxygen to form the secondary pollutant, ozone. Ozone in the upper atmosphere protects the earth from harmful ultraviolet radiation but is, itself, harmful to organisms in the lower atmosphere. Peroxyacetyl nitrates (PAN) are secondary pollutants that result from the reaction of nitrogen oxides and hydrocarbons with ozone in the presence of ultraviolet light. Ozone and PAN are major components of *photochemical smog*.

Sources of Air Pollution

Anthropogenic air pollution is a result of human activities. Burning fossil fuels, such as coal and petro-

Image Not Available

Air Pollutant Emissions by Pollutant and Source, 1998

Source	*Particulates*[1]	*Sulfur Dioxide*	*Nitrogen Oxides*	*Volatile Organic Compounds*	*Carbon Monoxide*	*Lead (tons)*
Fuel combustion (stationary sources)						
Electric utilities	302	13,217	6,103	54	417	68
Industrial	245	2,895	2,969	161	1,114	19
Other fuel combustion	544	609	1,117	678	3,843	416
Residential	432	127	742	654	3,699	6
Subtotal	1,091	16,721	10,189	893	5,374	503
Industrial processes						
Chemical and allied product manufacturing	65	299	152	396	1,129	175
Metals processing	171	444	88	75	1,495	2,098
Petroleum and related industries	32	345	138	496	368	NA
Other	339	370	408	450	632	54
Subtotal	607	1,458	786	1,417	3,624	2,327
Solvent utilization	6	1	2	5,278	2	NA
Storage and transport	94	3	7	1,324	80	NA
Waste disposal and recycling	310	42	97	433	1,154	620
Highway vehicles						
Light-duty gas vehicles and motorcycles	56	130	2,849	2,832	27,039	12
Light-duty trucks	40	99	1,917	2,015	18,726	7
Heavy-duty gas vehicles	8	11	323	257	3,067	—
Diesels	152	86	2,676	222	1,554	NA
Subtotal	257	326	7,765	5,325	50,386	19
Off highway[2]	461	1,084	5,280	2,461	19,914	503
Miscellaneous[3]	31,916	12	328	786	8,920	NA
Total emissions	34,742	19,647	24,454	17,917	89,454	3,972

Note: In thousands of tons, except as indicated.
— Represents or rounds to zero.
NA Not available.
1. Represents both particulates of less than 10 microns and particulate dust from sources such as agricultural tilling, construction, mining and quarrying, paved roads, unpaved roads, and wind erosion.
2. Includes emissions from farm tractors and other farm machinery, construction equipment, industrial machinery, recreational marine vessels, and small general utility engines such as lawn mowers.
3. Includes emissions such as from forest fires and other kinds of burning, various agricultural activities, fugitive dust from paved and unpaved roads, and other construction and mining activities, and natural sources.
Source: Adapted from U.S. Environmental Protection Agency, *National Air Pollutant Emission Trends*, 1900-1998, EPA-454/R-00-002. From *Statistical Abstract of the United States: 2001* (Washington, D.C.: U.S. Bureau of the Census, 2001).

leum products (including natural gas, gasoline, and fuel oil), leads to the release of large quantities of carbon dioxide. Atmospheric carbon dioxide levels have increased approximately 25 percent since the beginning of the Industrial Revolution as a result of fossil fuel burning. Carbon dioxide, as a result of the *greenhouse effect*, increases the atmosphere's heat-trapping capacity and is therefore a major factor in *global warming*. Sulfur oxides are released in the burning of fossil fuels and in mineral ore processing. Nitrogen oxides are produced in side reactions during fossil fuel combustion, in which high heat induces the oxidation of atmospheric nitrogen into nitrogen oxides. Hydrocarbons are released from industrial processes such as petroleum distillation and from incomplete fuel combustion. Particulates are products of farming, industrial processes, construction, demolition, and mining. Governments of many, but not all, countries continually monitor air quality and impose regulations to control anthropogenic pollution.

Some pollutants are released from natural sources. Bacterial decomposition of organic materials in oxygen-depleted swamps leads to methane production. Methane, an important greenhouse gas, is also a product of organic decomposition in landfills and is a waste gas associated with cattle feeding operations. The haze above some forests is caused by the release of volatile organic compounds, called *terpenes*, from trees. Ultraviolet light degrades some of the terpenes and induces synthetic reactions among various molecules, leading to the production of larger secondary compounds. Sulfur oxides and particulates are released during volcanic eruptions.

Plant Damage from Air Pollution

Air pollution damages plant life in both natural and agricultural ecosystems. Pollution effects on plants depend on several factors, including pollutant concentration, duration of exposure, and life stage of the plant, along with physical factors, such as temperature, light density, humidity, and season. Resistance to pollution stress is highly variable within and among plant species. Damage usually occurs after a specific threshold is reached. Although individual compounds are often studied, pollutants do not occur independently. Thus, harmful pollutant effects may be amplified or decreased by pollutant interactions.

High atmospheric carbon dioxide levels increase biomass production in most plants and improve water-use efficiency, while sometimes reducing overall plant protein and nitrogen contents. Increased growth at the expense of nutritional quality for the ecosystem's herbivores and for livestock may be a costly exchange, leading to reduced ecosystem stability and reduced nutritional value for consumers.

Nitrogen oxides enter plants through the stomata or by diffusion through the epidermis. Low levels of nitrogen oxides may have a fertilizing effect on nitrogen-limited plants, while higher levels may lead to direct toxicity through the production of nitric acid in the cytoplasm. Reduced cytoplasmic pH (greater acidity) may influence the movement and availability of nutrients in cells. Nitrogen oxides may cause chloroplasts to swell, thus affecting photosynthesis. Visible symptoms of plant damage from nitrogen oxides include *chlorosis* (yellowing) of the leaf tips and margins, which may progress into *necrosis* (tissue death).

Ozone causes direct *oxidation damage* to cuticles and enters plants through the stomata. Inside cells, ozone acts as a strong oxidant, reacting with many cellular components. Cell walls may become thickened and pigmented, leading to a characteristic *stippling*. White to red necrotic lesions may form, as well as chlorotic flecks and general leaf chlorosis.

Sulfur oxides enter plants through the stomata. In cells, sulfur oxides enter chloroplasts and cause acidification of the stroma, which contains enzymes responsible for photosynthetic carbohydrate production. Stroma pH (alkalinity versus acidity, where a measure of 7 is considered neutral) needs to be around 9 for proper enzyme function. Acidification by only 0.5 pH units may reduce net photosynthesis by 50 percent. Long-term effects of sulfur oxide damage include decreased growth and early leaf fall. Visible signs of injury include a characteristic chlorosis of leaf margins and interveinal spaces, while tissues next to veins remain green. Leaf undersurfaces may become silver or bronze in color. Necrotic areas may be ivory, brown, black, or red, or they may fall out completely.

Darrell L. Ray

See also: Acid precipitation; Eutrophication; Greenhouse effect; Ozone layer and ozone hole debate; Rain forests and the atmosphere.

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ALGAE

Categories: Algae; microorganisms; *Protista*; water-related life

Algae comprise a diverse group of (with few exceptions) photosynthetic oxygen-producing organisms, ranging in size from microscopic single cells to gigantic seaweeds.

The study of algae is known as *phycology* (in Greek, *phycos* means "algae"). Currently, most authors place eukaryotic algae in the kingdom *Protista* (domain *Eukarya*) and prokaryotic algae in the domain *Bacteria*. In the past algae were considered to be lower plants because some forms look like plants. As in plants, the primary photosynthetic pigment in algae is chlorophyll *a*, and oxygen is produced during photosynthesis.

What Are Algae?

Algae can be found nearly everywhere on earth: oceans, rivers, lakes, in the snow of mountaintops, on forest and desert soils, on rocks, on plants and animals (such as within the hollow hair of the polar bear), or even on other algae. They are involved in diverse interactions with other organisms, including symbiosis, parasitism, and epiphytism. *Lichens* are symbiotic associations between algae (blue-green algae, or *cyanobacteria*) and fungi. Atmospheric nitrogen-fixing cyanobacteria occur in symbiotic associations with plants such as bryophytes, water ferns, gymnosperms (such as cycads), and the angiosperms. The aquatic fern *Azolla*, commonly used as a biofertilizer in rice fields in Asian countries, harbors the symbiotic cyanobacterium *Anabaena azollae*. *Gunnera*, the only flowering plant to house symbiotic cyanobacterium *Nostoc*, is widely distributed in the tropics.

Symbiotic dinoflagellates known as *zooxanthellae* live within the tissues of corals. Corals get their colors and obtain energy from their photosynthetic symbionts. About 15 percent of red algae occur as parasites of other red algae. Parasitic algae may even transfer nuclei into host cells and transform them. After transformation, the reproductive cells of the host algae carry the parasite's genes. Various algae live on the surfaces of plants and other algae as epiphytes. Sometimes algae can be found in strange places—the pink color of flamingos originates, for example, comes from a pigment in the algae consumed by these birds.

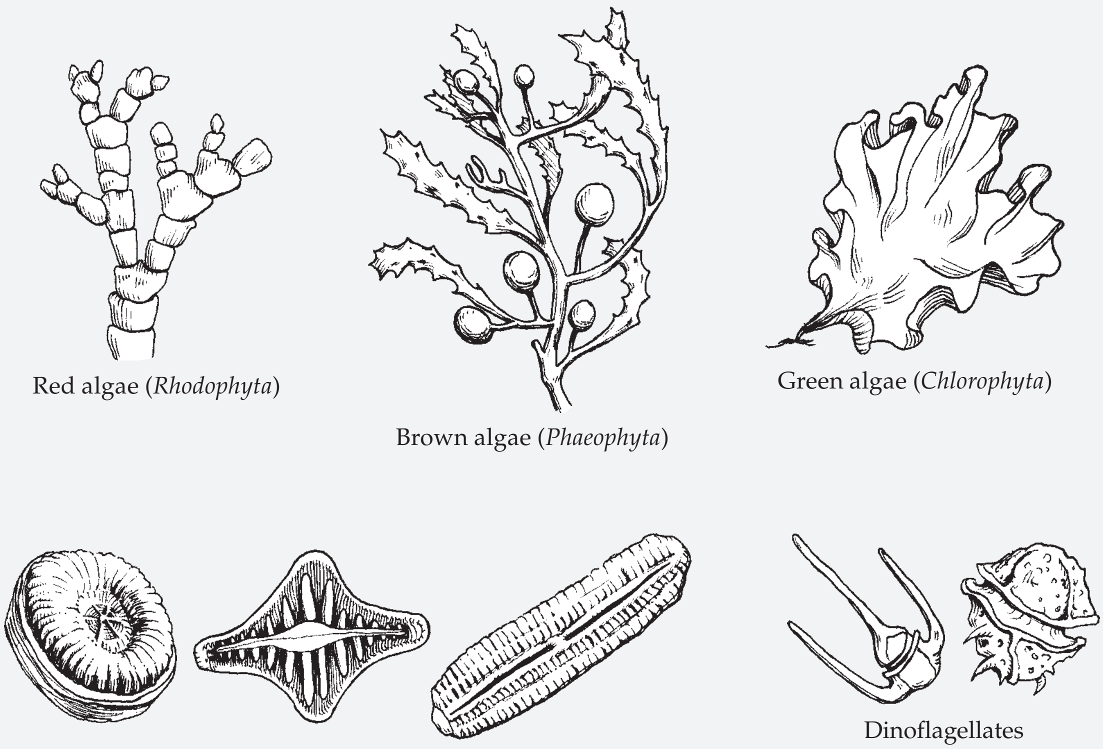
Algal Structure and Properties

Algal cells are bounded by a cell wall. Algal cells are either prokaryotic or eukaryotic. All prokaryotic algae belong to *Cyanophyta* (cyanobacteria) and lack both a nucleus and complex membrane-bound organelles, such as chloroplasts and mitochondria. Photosynthesis occurs in cyanobacteria in thylakoid membranes similar to those of plants. However, there is no double membrane surrounding the thylakoids of cyanobacteria.

All other algal groups are eukaryotic. Eukaryotic algae differ from cyanobacteria in that they possess chloroplasts and flagella with associated structures and in their cell wall composition. According to the *endosymbiont hypothesis*, some eukaryotic algae (red and green algae) obtained their chloroplasts by acquiring symbiotic prokaryotic cyanobacteria. This is known as primary endosymbiosis. Other eukaryotic algae probably obtained their chloroplasts by taking up eukaryotic endosymbiotic algae, a process known as secondary *endosymbiosis*. The existence of secondary endosymbiosis is indicated by the occurrence of more than two membranes around the chloroplasts of some algae, such as haptophytes, euglenophytes, dinoflagellates, and cryptomonads.

Pigments found in algae include chlorophylls, phycobilins, and carotenoids. All algae contain chlorophyll *a*. Accessory pigments vary among different algal groups.

Types of Algae



Kimberly L. Dawson Kurnizki

Photoautotrophy is the principal mode of nutrition in algae; in other words, they are "self-feeders," using light energy and a photosynthetic apparatus to produce their own food (organic carbon) from carbon dioxide and water. The majority of algal groups contain *heterotrophic* species, which obtain their organic food molecules by consuming other organisms. Numerous algae are *mixotrophs*; that is, they use different modes of nutrition (such as autotrophy and heterotrophy), depending on the availability of resources. The molecules used as food reserves differ among and are characteristic for algal groups. Food reserve molecules are polymers of glucose with different links between monomers.

Many algae are capable of movement. Movement is accomplished by means of flagellar action and by extrusion of mucilage. There are also peristaltic and amoeba-like algal movement. Within algal cells, movement of the cytoplasm, plastids, and nucleus also occurs. Advantages conferred by mobility include achieving optimal light conditions for photosynthesis, avoiding damage caused by excess light, and obtaining inorganic nutrients.

Algal Reproduction and Life Cycles

Algae may reproduce either asexually or sexually. Asexual reproduction among algae includes production of unicellular spores that germinate without fusing with other cells, fragmentation of filamentous forms, and cell division by splitting. In sexual reproduction, parent cells release gametes, which then fuse to form a zygote. Zygotes may either develop into new filaments or produce haploid spores by meiotic division.

Algae exhibit different types of life cycles. Some algal life cycles are characterized by an alteration of generations similar to that of plants. Two phases occur: sporophyte (usually diploid) and gametophyte (usually haploid). The sporophyte produces haploid spores through meiosis, and the haploid gametophyte produces male or female gametes by mitosis. Gametophyte and sporophyte may be structurally identical or dissimilar, depending on the algal group.

Roles of Algae

Algae have played significant roles in the earth's ecosystems since the origin of cyanobacteria (also known as blue-green algae) more than three billion years ago. Early cyanobacteria were responsible for the development of significant amounts of free oxygen in the atmosphere, which then made aerobic respiration possible. More than 70 percent of all photosynthetic activity on earth is carried out by *phytoplankton*—floating microscopic algae—rather than plants. Phytoplankton recharge the atmosphere with oxygen and simultaneously absorb carbon dioxide, helping to support the complex web of aquatic biota.

Algae are also very important in the global cycling of other elements, such as carbon, nitrogen, phosphorus, and silicon. Several algal groups—such as cyanobacteria, green algae, red algae, and the haptophyte algae—are able to generate calcium carbonate. Sedimented algae are the major contributors to deep-sea carbonate deposits (sand), which cover about half of the world's ocean floor. Calcified coralline red algae contribute to coral reefs in tropical waters. Silica sediments in oceans (sand) are based on abundant growth of another algal group, the diatoms, which contain silica in their cell walls.

Some algae (cyanobacteria) are able to fix atmospheric nitrogen and convert it to ammonia. Ammonia, in turn, can be a nitrogen source for plants and animals. On the other hand, high levels of nitrogen and phosphorus in rivers and lakes owing to pollution can cause the rapid and uncontrollable growth of algae, known as *algal blooms*. A bloom of algae is a threat to human and marine health, both directly and indirectly. It clogs fishes' gills, interferes with water filters, and ruins recreation sites. More than 50 percent of algal blooms produce toxins. Cases of human respiratory, skin, and gastrointestinal disorders associated with algal toxins have been reported. Certain blooms of algae are called *red tides*. The water appears to be red or brown because of the color of algal bodies, mainly dinoflagellates that contain the pigment xanthophyll.

Classification of Algae

Phylum	*Common Name*	*Species*
Bacillariophyta	Diatoms	100,000 or more
Chlorophyta	Green algae	17,000
Chrystophyta	Chrysophytes	1,000
Cryptophyta	Cryptomonads	200
Dinophyta	Dinoflagellates	4,000
Euglenophyta	Euglenoids	1,000
Haptophyta	Haptophytes	300
Phaeophyta	Brown algae	1,500
Rhodophyta	Red algae	6,000

Source: Data on species adapted from Peter H. Raven et al., *Biology of Plants*, 6th ed. (New York: W. H. Freeman/Worth, 1999).

Technological Applications

Algae have been used as food, medicine, and fertilizer for centuries. The earliest known reference to the use of algae as food occurs in Chinese poetic literature dated about 600 B.C.E. More recently, algae have begun to play important roles in certain biotechnological processes.

Several algae, including reds, browns, greens, and cyanobacteria, are used for food in Pacific and Asian countries, especially Japan. The annual harvest of the red alga *Porphyra* worldwide is worth several billion dollars. *Porphyra* (Japanese *nori*, Chinese *zicai*) is used as a wrapper for sushi or may be eaten alone. Another edible alga with a high iodine content is the brown alga *Laminaria* (Japanese *kombu*). The cyanobacterium *Spirulina*, with a protein level of 50 to 70 percent, was cultivated for centuries by indigenous Central Americans at Lake Texcoco near modern-day Mexico City for use as human food.

Several gelling agents are produced from red and brown algae. Agar from red algae is used as a medium for culturing microorganisms including algae, as a food gel, and in pharmaceutical capsules. Red algal carrageenan is used in toothpaste, cosmetics, and food such as ice cream and chocolate milk. Alginates from brown algae have extensive applications in the cosmetics, soap, and detergent industries. Sources of alginates are *Laminaria*, some *Fucus* species, and the giant kelp *Macrocystis*, which can grow to more than 60 meters long. Algae are also used as feed in the culture of commercially important fish and shrimp.

Mass cultivation of algae (microalgae)—in open ponds and photobioreactors for production of fuels (such as biomass) and biochemicals (such as carotenoids, amino acids, and carbohydrates) and for water purification—is a rapidly developing area based on the use of solar energy as energy source. The green alga *Dunaliella* is used in the industrial production of carotene. In wastewater treatment plants, algae are used to remove nutrients and heavy metals and to add oxygen to the water.

Algae are used worldwide as indicators (biomonitors) of water quality, helping to detect the presence of toxic compounds in water samples. Several fast-growing algae are used, including the green alga *Selenastrum capricornutum*. Many algae are widely employed as research tools because they are easy to culture and manipulate. Danish biologist Joachim Hammerling's experiments with the green alga *Acetabularia* identified the nucleus as the likely storage site of hereditary information.

Diversity

Taxonomists believe that there are between thirty-six thousand and ten million species of algae. Molecular comparisons using nucleotide sequences in ribosomal RNA (ribonucleic acid) suggest that algae do not fall within a single group linked by a common ancestor but that they evolved independently. The algae are divided into nine major phyla, which differ in their photosynthetic pigments, food reserves, cell structure, and reproduction. These groups include euglenoids, cryptomonads, dinoflagellates, haptophytes, and red algae.

Phylum *Euglenophyta* contains mostly unicellular forms with one or two flagella. Only one-third of this group possess chlorophyll-containing chloroplasts. Other euglenoids are strictly heterotrophic. The phylum contains more than nine hundred, mostly freshwater, species. The food reserve is the carbohydrate paramylon, a polymer of glucose. Euglenophytes have chlorophyll *a* and *b* as well as carotenoids as their photosynthetic pigments. There is no cell wall. Cells have several small chloroplasts; each is surrounded by three membranes. A close relative of euglenophytes is the protozoan *Trypanosoma*, which causes the human disease African sleeping sickness. Reproduction in the euglenophytes occurs by division of cells. Sexual reproduction is unknown.

Phylum *Cryptophyta* includes unicellular biflagellates. In addition to chlorophyll *a*, chloroplasts can contain chlorophyll *c*, carotenoids, and phycobilins. The carotenoid pigment alloxanthin is unique to *Cryptophyta*. Four membranes surround each chloroplast. Chloroplast endoplasmic reticulum borders the chloroplasts. The principal food reserve is starch. Instead of a typical cell wall, a periplast composed of protein plates occurs beneath the cell membrane. There are about two hundred freshwater and marine species. Reproduction is primarily asexual.

Members of the phylum *Dinophyta*, or dinoflagellates, have unicellular forms with two different flagella. There are between two thousand and four thousand marine species and about two hundred freshwater forms. Many have chlorophylls *a* and *c* as well as the unique carotenoid peridinin. Some members of *Dinophyta* have fucoxanthin. Chloroplasts have three closely associated membranes. The primary food reserve is starch, but lipids are also important storage molecules. A dinoflagellate cell is not surrounded by a cell wall but has a theca (a sort of armor) made of cellulose. Dinoflagellates can reproduce asexually and sexually.

Phylum *Haptophyta* includes primarily marine unicellular biflagellated algae. A haptophyte cell also has a flagellum-like haptonema, used to capture food. There are about three hundred species. The photosynthetic pigments include chlorophyll *a* and accessory pigments chlorophyll *c* and the carotenoid fucoxanthin. Each chloroplast has four membranes. The food reserve is chrysolaminarin, which is a polymer of glucose. Several layers of scales, or coccoliths, composed primarily of calcium carbonate may cover the haptophyte cell. Asexual and sexual reproduction is widespread.

Phylum *Rhodophyta*, or the red algae, has between four thousand and six thousand species. Red algae lack any flagellated stages. The photosynthetic pigments include chlorophyll *a* as well as accessory phycobilins and carotenoids. Two membranes surround each chloroplast. The food reserve is a floridean starch. A red algal cell is encircled by a wall composed of cellulose. Asexual and sexual reproduction, as well as alteration of generations, are widespread among *Rhodophyta*. A triphasic life cycle is unique for this group of algae.

Sergei A. Markov

See also: Bacteria; Biofertilizers; Biotechnology; Brown algae; *Charophyceae*; *Chlorophyceae*; Cryptomonads; Diatoms; Dinoflagellates; Eutrophication; Evolution of plants; Green algae; Haptophytes; Heterokonts; Lichens; Nitrogen cycle; Nitrogen fixation; Phosphorus cycle; Photosynthesis; Phytoplankton; *Protista*; Red algae; *Ulvophyceae*.

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ALLELOPATHY

Categories: Physiology; poisonous, toxic, and invasive plants

Allelopathy refers to all the biochemical interactions, both beneficial and harmful, among all types of plants, including microorganisms.

For an allelopathic interaction to occur, chemicals must be released into the environment by one plant that will affect the growth of another. In this way allelopathy differs from *competition*, which involves removal of some factor from the environment that is shared with other plants. Allelopathy was recognized as early as Theophrastus (300 B.C.E.), who pointed out that chick pea plants destroy weeds growing around them.

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Methods of Action

A variety of different allelochemicals are produced by plants, usually as secondary metabolites that do not have a specific function in the growth and development of the host plant but that do affect the growth of other plants. Originally plant physiologists thought these secondary products were simply metabolic wastes which plants had to store because they do not have an excretory system as animals do. Their various functions are now beginning to be understood.

One class of allelochemicals, *coumarins*, block or slow cell division in the affected plant, particularly in root cells. In this way growth of competing plants is inhibited, and seed germination can be prevented. Several kinds of allelochemicals, including *flavonoids*, *phenolics*, and *tannins*, suppress or alter hormone production or activity in competing plants. Other chemicals, including *terpenes* and certain antibiotics, alter membrane permeability of host cells, making them either leaky or impermeable. In some cases, membrane uptake can be enhanced, particularly for micronutrients in low concentration in the soil. Finally, a variety of allelochemicals have both positive and negative effects on metabolic activity of the affected plant.

Allelopathy in Agriculture

Most of the negative effects of weeds on crop plants have been attributed to competition; however, experiments using weed extracts have demonstrated that many weeds produce allelochemicals. Similarly, some crop plants are allelopathic to others and themselves, including wheat, corn, and rice. In these cases the residues of one year's crop can interfere with crop growth in subsequent years. This is increasingly important for farmers to consider who are incorporating low-tillage methods to reduce soil erosion. To minimize these effects, some of the traditional techniques of cover cropping, companion cropping, and crop rotation must be employed. Known allelopaths are also beginning to be used as biological control agents to manage invasive and weedy plant species.

Allelopathy in Nature

Several tree species, including black walnut, black locust, and various pines, are known to produce allelochemicals that inhibit the growth of understory species. In some cases this is a result of drip from the foliage or leachate from fallen leaves and fruit. In other cases, roots secrete allelochemicals that kill seedlings of other plants. Bracken fern (*Pteridium aquilinum*) is known to affect the growth of many other plants.

Marshall D. Sundberg

See also: Agriculture: traditional; Biochemical coevolution in angiosperms; Biofertilizers; Coevolution; Community-ecosystem interactions; Competition; Hormones; Invasive plants; Metabolites: primary vs. secondary; Organic gardening and farming; Pheromones; Soil degradation; Succession.

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ALTERNATIVE GRAINS

Categories: Agriculture; economic botany and plant uses; food

Alternative grains refers to alternatives to high-yield grain crops, the harvest of which has led to severe soil erosion and increased use of fertilizers and pesticides.

More than one-half of the calories consumed daily by humans comes from grains. Most of these grains are produced by plants of the *grass* family, *Poaceae*. Major *cereal* plants domesticated centuries ago include rice (*Oryza sativa*), wheat (*Triticum aestivum*), and corn (*Zea mays*). Other important grain crops, also plants of the grass family, include barley (originating in Asia), millet and sorghum (originating in Africa), and oats and rye (originating in Europe).

Grain Genetics

Since the early twentieth century, the scientific principles of genetics have been applied to improvements of crop plants. Some notable improvements occurred between 1940 and 1970. As a result of irrigation, improved genetic varieties, and the use of large amounts of fertilizers and pesticides, yields of major crops greatly increased. Norman Borlaug received a Nobel Prize in 1970 for his contributions to these developments, which came to be called the *Green Revolution*. However, it soon became apparent that the Green Revolution was not the boon first envisioned. For maximum yield, large-scale farming involving huge capital investment is required. Also, environmentalists became concerned over the erosion and other environmental damage caused by the use of large amounts of fertilizers and pesticides.

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Minor Cereals

Various alternatives have been proposed. For grain crops, several approaches offer promise, including more widespread use of minor cereals, especially those tolerant of unfavorable growing conditions; development of new cereal plants by hybridization or other genetic manipulation; and use of pseudocereals, nongrass crop plants that produce fruits (grains) similar to those of cereal plants.

Most *sorghum* (*Sorghum bicolor*) grown in the United States is used for silage or molasses. In Africa and India, various grain sorghums are grown in regions where rainfall is too low for most other grain crops. Well adapted to hot, dry climates, their grains are used to make a pancakelike bread. *Millet* refers to several grasses that are also useful cereal plants because they tolerate drought well. In Africa the most important are pearl millet (*Pennisetum glaucum*) and finger millet (*Eleusine coracana*). Grains of both species can be stored for long periods and are used to make bread and other foods. Other, perhaps less important, grain plants also called millet include foxtail millet (*Setaria italica*), native to India but now grown in China; proso millet (*Panicum milaeceum*), native to China but grown in Russia and central Asia; sanwa millet (*Echinochloa frumentacea*), cultivated in East Asia; and teff (*Eragrostis teff*), an important food and forage plant of Ethiopia. Such grain sorghums and millets have the potential to grow in areas with hot, dry climates far beyond the regions where they are now being utilized.

In a distinct category is *wild rice* (*Zizania aquatica*). Native to the Great Lakes region of the United States and Canada, it has been, and still is, harvested by American Indians. Like the common but unrelated rice (*Oryza sativa*), wild rice grows in flooded fields. Attempts to cultivate it since the 1950's have been somewhat successful as the result of the development of nonshattering varieties. However, it remains an expensive, gourmet item. Two cereal plants have promise because of the high-protein content of their grains. Wild oat (*Avena sterilis*) is a disease-resistant plant with large grains. Job's tears (*Coix lachryma-jobi*), native to Asia, is now planted throughout the tropics. Research on these and related species continues.

Although all important cereal plants have been improved by genetic techniques, the most notable new alternative grain plant is triticale (*Triticosecale*). The first human-made cereal, it is the result of crossing wheat with rye. The sterile hybrid from such a cross was made fertile by doubling its chromosomes. Thus, triticale varieties produce viable seeds. Triticale combines the superior traits of each of its parents: the cold tolerance of rye and the higher yield of wheat. The protein content of triticale compares favorably with that of wheat, and its quality, as measured by lysine content, is higher. However, flour made from triticale is not suitable for making bread unless mixed with wheat flour.

Pseudocereals

Pseudocereals are plants that are not of the grass family but produce nutritious, hard, grainlike fruits that can be stored, processed, and prepared for food much like grains. They belong to several plant families. Many grow under conditions not suitable for the major cereal crops. Buckwheat (*Fagopyrum esculentum*), of the *Polygonaceae* family, probably originated in China. It tolerates cool conditions and is adapted to short growing seasons, thus permitting it to be grown in the temperate regions of North America and Europe. In the United States, it is often associated with pancakes but is used in larger quantities for livestock feed. In Eastern Europe, the milled grain is used for soups.

Quinoa (*Chenopodium quinoa*) of the goosefoot family, *Chenopodiaceae*, has been cultivated by Indians of the Andes Mountains for centuries. The leafy annual produces grainlike fruits (actually achenes) with a high protein content and exceptional quality, high in lysine and other essential amino acids. After its bitter saponins have been removed, it can be cooked and eaten like rice or made into a flour. Quinoa has been cultivated in the Rocky Mountains since the 1980's and has become a gourmet food in the United States.

Most amaranths (*Amaranthus*) plants are New World weeds. They belong to the amaranth family, *Amaranthaceae*. A few species were used by Aztecs and other North American peoples, but amaranth use was banned by the Spanish. Since the late 1970's, plant breeders have targeted several species for improvement. The results are highly nutritious grains, rich in lysine, that are suitable for making flour. Research in Pennsylvania and California has resulted in improved varieties.

Thomas E. Hemmerly

See also: African agriculture; North American agriculture.

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ANAEROBES AND HETEROTROPHS

Categories: Cellular biology; evolution; microorganisms

The first organisms to evolve on the earth are thought to have been heterotrophs and anerobes. Heterotrophs are organisms that cannot produce their own food but must fill their energy requirements by consuming organic molecules produced by other processes or organisms. Anaerobes are organisms that do not require free oxygen gas in order to survive; for some anaerobes, free oxygen may be poisonous.

Heterotrophs include many familiar organisms (such as animals) whose existence is tied to *primary producers*, those organisms that create energy-storing molecules, such as photosynthesizing plants. Anaerobes also are common, though less apparent. Typically, they are microscopic organisms restricted to living in a few surface environments where oxygen is absent. It may seem strange, then, that these organisms were perhaps the first organisms to have evolved on the earth. Yet the combination of the heterotrophic lifestyle and the anaerobic life requirement is consistent with what is known about the conditions of the early earth's surface environment.

The earliest anaerobic heterotrophs laid the biochemical foundations for the evolution of photosynthesis, free oxygen in the atmosphere, and the rise of complex organisms. All those events had the adverse impact of limiting the range of environments available to the anaerobes.

The world's first organism evolved in what has been called a "prebiotic soup" of energy-rich organic molecules. Heterotrophic organisms would exploit this environment by absorbing the molecules. A continuing supply of energy-rich molecules depended on the absence of free oxygen in the early atmosphere and the functioning of the *abiotic synthesis*.

Fermentation

The energy-rich molecules of the soup were converted to energy by a series of biochemical reactions. One of the simplest, and therefore perhaps one of the oldest, types of energy conversion reactions is *anaerobic fermentation*. During anaerobic fermentation, an energy-rich molecule, such as the simple sugar glucose, is dismantled to release energy and waste by-products. Several lines of evidence suggest that this form of energy conversion was utilized by the early heterotrophs.

One indicator that fermentation is a very ancient biochemical process is that the reaction used to release energy from the glucose molecule is very common among modern organisms. The ability to utilize the *fermentation* reaction is evident in the anaerobic reaction of yeast using sugar and releasing ethyl alcohol. Although it is not the primary energy-releasing reaction for most organisms, fermentation's widespread availability suggests that it is very old and perhaps inherited from an early, simpler ancestor.

The fermentation reaction is not very efficient. For example, it releases two units of energy for every glucose molecule, whereas oxidation of the same glucose molecule releases more than thirty energy units. Such an inefficient reaction for energy release could not be tolerated by an advanced organism with many energy demands. Alternatively, single-celled heterotrophs surrounded by, and absorbing, energy-rich molecules such as glucose (which is unlikely to decompose in an anoxic environment) do not expend much energy in gathering their food.

The Earliest Organisms

Thus, two very different types of evidence—that which points to an anoxic early atmosphere and evidence for the ancient ancestry of the glucose fermentation reaction—suggest that the earliest organism was a single-celled heterotroph that absorbed energy-rich molecules from the surrounding anaerobic environment. Modern analogues for such an organism exist. Single-celled bacteria, called *obligate anaerobes*, exist in a few anoxic environments today. It is likely that the modern obligate anaerobes have not changed significantly (especially in their morphology, or shape and size) from their Precambrian ancestors. Given this much information, paleontologists know that their search for early Precambrian fossils, the petrified remains of organisms, is not easy.

The process of fossilization—that is, the preservation of the shape of an organism in rock—is best at preserving the details of hard body parts. Hard skeletons and shells or their impressions are easier to preserve than are soft body parts. In the case of early Precambrian fossils, the most likely organisms (bacteria) not only are small but also contain no hard body parts.

Despite these barriers to preservation and despite the very poorly preserved Precambrian rock record, some early Precambrian fossil remains have been found and described. The fossils are usually found preserved in rock called chert, which probably began as a gelatinous material. Microscopic remains of organisms embedded in this gelatin were delicately preserved when the chert lost some of its water and solidified.

The oldest fossil remains identified have been found in cherts from southern Africa. These cherts, part of what is called the Fig Tree Formation, are more than three billion years old. The fossils consist of the wispy, spherical remains of what may have been a type of alga and the rod-shaped remains of a possible heterotrophic bacterium.

Richard W. Arnseth

See also: Anaerobic photosynthesis; *Archaea*; Bacteria; Cell theory; *Eukarya*; Glycolysis and fermentation; Molecular systematics; Photosynthesis; Phytoplankton; Prokaryotes; *Protista*.

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ANAEROBIC PHOTOSYNTHESIS

Categories: Photosynthesis and respiration; physiology

Anaerobic photosynthesis, also known as anoxygenic photosynthesis, is the process by which certain bacteria use light energy to create organic compounds but do not produce oxygen. Anaerobes are those bacteria that cannot use oxygen to generate energy.

The photosynthetic process in all plants and algae, as well as in specific types of bacteria, involves the reduction of carbon dioxide to carbohydrate and the removal of electrons from water, resulting in the release of oxygen. This process is known as oxygenic or *aerobic photosynthesis*. Water is oxidized by a multi-subunit protein located in the photosynthetic membrane. This is a molecular protein feature shared among more than 500,000 species of plants on earth.

While this is a common feature among nearly every form of plant life on earth, some photosynthetic bacteria can use light energy to extract electrons from molecules other than water. These bacteria are of ancient origin and are believed to have evolved before aerobic photosynthetic organisms. These anaerobic photosynthetic organisms occur in the domain *Bacteria*. Anaerobic photosynthetic bacteria, also known as anoxygenic photosynthetic bacteria, differ from aerobic organisms in that each species of these bacteria has only one type of reaction center. In some photosynthetic bacteria the reaction center involves the oxidation of water and the reduction of the aromatic molecule plastoquinone. In

Heliobacteria, *shown in this scanning electron micrograph, one of five groups of photosynthetic bacteria, are anaerobic photosynthetic bacteria.*

other species it involves the oxidation of plastocyanin and the reduction of ferredoxin protein.

Photosynthetic bacteria are typically aquatic microorganisms inhabiting marine and freshwater environments, including wet and muddy soils, stagnant ponds, sulfur springs, and still lakes. They are classified into five groups based on pigment composition, metabolic requirements, and membrane structure: green bacteria, purple sulfur bacteria, purple nonsulfur bacteria, heliobacteria, and halophilic archaebacteria. Some of these organisms are *strict anaerobes*; that is, they can grow only in the complete absence of oxygen. They cannot use water as a substrate, and they do not produce oxygen during photosynthesis. *Facultative anaerobes*, on the other hand, can grow either in the presence or in the absence of oxygen.

Green bacteria include two families, the *Chloroflexaceae* and the *Chlorobiaceae*. The *Chlorobiaceae* are strict anaerobes that grow by utilizing sulfide, thiosulfate, or organic hydrogen as an electron source. *Chloroflexaceae* are facultative aerobes which use reduced carbon compounds as electron donors. Purple sulfur bacteria uses an inorganic sulfur compound, such as hydrogen sulfide, as a photosynthetic electron donor. Purple nonsulfur bacteria depend on the availability of simple organic compounds such as alcohols and acids as electron donors, but they can also use hydrogen gas. Purple sulfur bacteria must fix carbon dioxide to live, whereas nonsulfur bacteria can grow aerobically in the dark by respiration on an organic carbon source.

Heliobacteria are anaerobic photosynthetic bacteria that contain a special type of bacteriochlorophyll, BChl *g*, that works as both antenna and reaction center pigment. *Halobacteria* are very unusual. They cannot grow in low salt concentrations (or their cell walls collapse). Typically, they are heterotrophs with an aerobic electron-transport chain, but they can also respire anaerobically, with nitrate or sulfur. In the absence of suitable electron acceptors they can ferment carbohydrates. Halobacteria, when exposed to light in the absence of oxygen, can synthesize a purple membrane containing a single photosensitive protein called bacteriorhodopsin which, when illuminated, begins cyclic bleaching and regeneration, extruding protons from the cell. This light-stimulated proton pump operates without electron transport. The mechanism by which halobacteria convert light is fundamentally different from that of higher organisms because there is no oxidation/reduction chemistry, and halobacteria cannot use carbon dioxide as their carbon source. As a result, some scientists do not consider halobacteria as being photosynthetic.

Process

The common features to both aerobic and anaerobic photosynthesis have been known since the mid-twentieth century:

Green plants:

$$CO_2 + 2H_2O + \text{light} \rightarrow (CH_2O) + O_2 + H_2O$$

Green sulfur bacteria:

$$CO_2 + 2S + H_2O + \text{light} \rightarrow (CH_2O) + 2S + H_2O$$

In each case, inorganic carbon (CO_2) is fixed into organic carbon (CH_2O), the source of reductant is hydrogen in either water or hydrogen sulfide, and the chemical energy required for this activity is derived from light energy. The sulfur produced anaerobically is analogous to the oxygen produced by the oxygenic photosynthesis of green plants. Photochemical processes in photosynthetic bacteria require three major components: an antenna of light-harvesting pigments, a reaction center within an intra-cytoplasmic membrane containing at least one bacteriochlorophyll, and an electron transport chain.

All photosynthetic bacteria can transform light energy into a transmembrane proton gradient used for the generation of adenosine triphosphate (ATP) and production of oxidase, but none of the anaerobic photosynthetic bacteria are capable of extracting electrons from water, so they do not evolve oxygen. Many species can only survive in low-oxygen environments. To provide the necessary electrons for carbon dioxide reduction, anoxygenic photosynthetic bacteria must oxidize inorganic or organic molecules from their immediate environment.

Despite basic differences, the principles of energy transductions are the same in anaerobic and aerobic photsynthesis. Anaerobic photosynthetic bacteria depend on bacteriochlorophyll, a group of molecules similar to chlorophyll, that absorbs in the infrared spectrum between 700 and 1,000 nanometers. The antenna systems in these bacteria consist of bacteriochlorophyll and carotenoids, serving a reaction center where primary charge separation occurs. Electron carriers include quinone and cytochrome *bc* complex. Electron transfer is coupled to the generation of electrochemical potential that drives phosphorylation by ATP synthase, and the energy required for the reduction of carbon dioxide is provided by ATP and dehydrogenase.

Randall L. Milstein

See also: *Archaea*; Bacteria; Bacterial genetics; Eutrophication; Molecular systematics; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Plasma membranes; Proteins and amino acids; Respiration.

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ANGIOSPERM CELLS AND TISSUES

Categories: Anatomy; angiosperms; cellular biology; physiology

Some cell types and tissues which are not found in any other groups of plants occur in angiosperms (flowering plants).

Angiosperms are a group of plants with seeds that develop within an ovary and reproductive organs in flowers. They are commonly referred to as flowering plants and represent the most successful group of plants on earth, with approximately 235,000 species. Various cell types and tissues, many of which are not found in any other groups of plants, occur in angiosperms. These cells and tissues perform varied functions, which are very efficient compared to their counterparts in other plants. These include *dermal*, *vascular* (xylem and phloem), and *ground tissues* (such as parenchyma, collenchyma, and sclerenchyma).

The growth of plants is carried on by a group of cells at their tips. These groups of cells are referred to as *apical meristems*, which are composed of *initials* and their most recent *derivatives*. The initials are the main source of body cells in plants, while the derivatives become any of the cells and tissues in the plant body. The apical meristems of both the shoot and the root show continued cell division, with cells enlarging, elongating, and differentiating in regular, distinctly organized patterns. Apical meristems bring about the increase in the length of the stems and roots and are responsible in the formation of the primary plant body. The shoot apical meristem may continually initiate the aerial components of the plant or may enter a state of periodic quiescence. In some plants, the shoot apical meristem transforms into a floral or inflorescence meristem that eventually terminates in a single flower or clusters of flowers, respectively. The *root apical meristem* is enclosed by a thimble-shaped *root cap* that hastens the penetration of roots between soil particles. Unlike the shoot apical meristem, the root apical meristem forms no appendages. In fact, the site of lateral root initiation is far removed from it.

Shoot Apex

The shoot apical meristem is typically dome-shaped but flattened, and concave outlines also exist. The outline is not constant but changes in response to *plastochron* (the time interval between the initiation of one leaf primordium and the next). At least three models describe the shoot apical meristems. Although each of these is based on one or two unique criteria, they also have a few overlapping features.

Cell Lineage Analysis

This model holds that three clonally related layers of cells characterize the shoot apical meristem. These layers can be more than one cell layer thick. L1 is the outermost layer and gives rise to the *epidermis*, L2 is the middle layer and gives rise to the *vascular tissues* and *cortex*, and L3 is the innermost layer and gives rise to the *pith*. This model was based on studies using periclinal chimeras (organs or parts of tissues of diverse genetic constitution), where one of the cell layers was genetically altered using drugs that inhibit separation of chromosomes.

Tunica-Corpus Concept

This model is based on microscopic analysis of constituent cells. It says that the shoot apical meristem is made up of two groups of cells. The *tunica*, a group of cells that form one or two stratified layers, undergoes anticlinal divisions only and gives rise to the epidermis. Partly enclosed by the tunica is the *corpus*, a group of loosely arranged cells that divide in various planes and give rise to the vascular and ground tissues. The tunica maintains its individuality by surface growth, whereas the corpus adds bulk by increase in volume.

Cytohistological Zonation

This model recognizes various definable zones in the shoot apical meristem. Three zone boundaries are distinguished by cell size: staining quality, degree of vacuolation, and frequency of cell division. The central (mother cell) zone represents a conspicuous group of enlarged and isodiametric cells that undergo infrequent cell division, possess prominent nuclei, and are often highly vacuolated. The flanking peripheral zone is derived from, and partly surrounds, the central zone. Cells of this zone are smaller, are mitotically active, and have dense cytoplasms. They give rise to the epidermis, vascular tissues, and cortex. The rib zone is located at the base of the central and peripheral zones. This zone is directly formed from the central zone, produces longitudinal files of cells by periclinal divisions, and gives rise to the pith.

Root Apex

The organization of the root apical meristem is different from that of the shoot apical meristem. Root apical meristems are commonly interpreted as having either a close or open type of organization. In a close type of organization, the dermal, vascular, and ground tissues each have their own set of initials. This organization shows a clear boundary between root cap and other tissues of the root apex. In an open type of organization, all of the root tissues share a group of initials, and therefore the boundary of the root cap is indistinguishable from the other tissues of the root apex.

Developmental Processes

The cells produced by apical meristems undergo several key developmental processes, which include growth, differentiation, and morphogenesis. Although each of these can be separated individually, they overlap in highly complex fashion. *Growth* refers to the quantitative increase in a cell's volume or mass due to enlargement and multiplication. *Differentiation* is the qualitative change in the form and function of organelles, cells, tissues, and organs, resulting in the establishment of new structures and functions. From an anatomical point of view, cell differentiation is related to changes in cell size and shape, modifications of the wall, and changes in staining characteristics of nucleus or cytoplasm, as well as the degree of vacuolation and the ultimate loss of the protoplast in some cases. *Morphogenesis* is the visible manifestation of all of the changes, brought about by growth and differentiation, as expressed in the overall morphology of the plant.

Dermal Tissues

The primary plant body is composed of three basic tissues: dermal, vascular, and ground tissues. The *dermal tissue* (or epidermis) is made up of several cell types and is involved in a variety of functions, including retention and absorption of water and minerals, protection against herbivores, and control of gas exchange. Each of these functions is attributable to one or more of the unique features of the epidermis. Most epidermal cells are flat and tightly packed, forming a single layer around stems, leaves, and other organs. The outer walls of epidermal cells are equipped with a waterproof layer made up of a fatty material called *cutin*. The tightly packed and cutinized epidermis protects the plants from desiccation by keeping moisture in.

Epidermal cells lack chloroplasts and are transparent. It is the underlying cells that give leaves and stems their green color. However, the vacuoles of some epidermal cells occasionally contain pigments and are responsible in the coloration of flowers and colored parts of variegated leaves.

Stomata are specialized structures that form part of the epidermis of leaves, stems, flowers, and fruits. They are involved in regulating the intake of carbon dioxide for photosynthesis as well as the release of oxygen. *Trichomes* are single-celled or multicellular outgrowths of epidermal cells that are involved in deterring herbivores and restricting transpiration. *Root hairs* are also outgrowths of epidermal cells that are specialized for absorbing water and minerals from soil. They occur near the tip of the root and function to increase its absorptive surface area several-thousandfold.

Vascular Tissues

Vascular tissues are of two types: xylem and phloem. *Xylem* occurs throughout the plant body, and the type that differentiates directly from the apical meristem is called primary xylem. (Secondary xylem is formed from the vascular cambium.) Primary xylem is formed as stems and roots elongate. The two kinds of conducting cells in xylem are tracheids and vessels, or vessel elements. Both are dead at maturity and have thick, lignified secondary cell walls. *Tracheids* are long, slender cells with tapered, overlapping ends. They are the only water-conducting cells in most gymnosperms (an evolutionary line of plants that includes conifers). Water moves upward in roots and stems from tracheid to tracheid through thin areas in their cell walls called pits. With only a few exceptions, all angiosperms contain vessel elements and tracheids. *Vessel elements* are short, wide in diameter, and connected end to end. Their end walls are partly or wholly dissolved, forming long hollow vessels through which water moves. All these features of vessels enable them to transport water more rapidly than tracheids.

Phloem transports dissolved organic materials throughout the plant. The conducting cells of the phloem are called *sieve elements*, which are devoid of nuclei but otherwise have intact cytoplasm. They also have thin areas along their cell walls called sieve areas that are perforated. Solutes move from sieve element to sieve element through these pores.

Ground Tissues

The three types of *ground tissue* are parenchyma, collenchyma, and sclerenchyma. *Parenchyma cells* are the most abundant and versatile cells in plants. These cells are isodiametric, are alive at maturity, are highly vacuolated, and have a primary cell wall. Parenchyma functions as food- and water-storage tissue as well as sites of metabolism in plants. Chlorenchyma cells are chloroplast-containing parenchyma specialized for photosynthesis.

Collenchyma cells are relatively long, with unevenly thickened primary walls. They support growing regions of shoots and are common in petioles, elongating stems and expanding leaves. Collenchyma cells are well adapted for support because their cell walls are able to stretch. They often form in strands or a cylinder just beneath the epidermis; such location maximizes support, as would a rod located in the center of a stem or petiole (leaf base).

Sclerenchyma cells are rigid; produce thick, nonstretchable secondary walls; and are usually dead at maturity. They occur in, support, and strengthen mature regions of plants, including stems, roots, and leaves. There are two types of sclerenchyma cells: sclereids and fibers. *Sclereids* are relatively short and variable in shape and usually occur in small groups. *Fibers* are long and slender and occur in strands or bundles. Sclereids are found in the roots, leaves, and stems. They produce the gritty texture of pears and mostly make up the tough core of apples as well as the seed coats of peanuts and walnuts. Fibers are often associated with vascular tissues and, compared to sclereids, are typically elongated cells that vary in length from a few millimeters to more than half a meter long.

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See also: Angiosperm plant formation; Angiosperms; Cell wall; Flower structure; Leaf anatomy; Plant fibers; Plant tissues; Root uptake systems; Roots; Shoots; Stems; Water and solute movement in plants; Wood.

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ANGIOSPERM EVOLUTION

Categories: Angiosperms; evolution

Angiosperms (flowering plants) appeared about 130 million years ago and today dominate the plant world, with approximately 235,000 species.

In early Devonian-age rocks, approximately 363-409 million years old, fossils of simple vascular and nonvascular plants can be seen. Ferns, lycopods, horsetails, and early *gymnosperms* became prominent during the Carboniferous period (approximately 290-363 million years ago). The gymnosperms were the dominant flora during the Age of Dinosaurs, the Mesozoic era (65-245 million years ago). More than 130 million years ago, from the Jurassic period to early in the Cretaceous period, the first flowering plants, or angiosperms (phylum *Anthophyta*), arose. Over the following 40 million years, angiosperms became the world's dominant plants.

The angiosperms show high species diversity, and they occupy almost every habitat on earth, from deserts to high mountain peaks and from freshwater ecosystems to marine estuaries. Angiosperms range in size from eucalyptus trees well over 100 meters (328 feet) tall with trunks nearly 20 meters (66 feet) in circumference to duckweed, simple floating plants barely 1 millimeter (0.003 inch) long.

Special Characteristics

Some of the defining characteristics of angiosperms involve their physical appearance or morphology and internal anatomy: the presence of flowers and fruits containing seeds, stamens with two pairs of pollen sacs, a microgametophyte (the male, haploid stage of the life cycle contained in the pollen) with three nuclei, a megagametophyte (the female, haploid stage of the life cycle enclosed in the ovary) with eight nuclei, companion cells, and sieve tubes in the phloem (vascular tissue important in the transport of organic molecules). Some of these characteristics involve life-cycle features, such as *double fertilization*, that are distinct from almost all other members of the plant kingdom. (Double fertilization is also known in the genera *Ephedra* and *Gnetum*, members of the gymnosperms.)

Because angiosperms possess so many unique features, plant taxonomists have long believed that angiosperms originated from a single common ancestor. Because the first flowers and pollen grains appear in fossils from the early Cretaceous period, up to about 130 million years ago, it is probable that angiosperms actually arose more than 130 million years ago. As the findings of *paleobotanists* (botanists who study plants in the fossil record) have been combined with more recent knowledge from evolutionary genetics and biochemistry, a clearer picture of angiosperm evolution has emerged.

Proposed Ancestors

Because gymnosperms (the other large group of seed plants) have long been considered ancestral to the angiosperms, researchers have attempted to develop models for the evolution of the ovule-bearing structures of flowering plants from the similar, naked ovule-bearing structures of gymnosperms. Some lines of evidence indicate that groups of extinct cycad-like gymnosperms known as the *Bennettitales* and the *gnetophytes*, a modern division of the gymnosperms which show up in the fossil record about 225 million years ago, are the seed plants most closely related to angiosperms. All three groups, the *Bennettitales*, the gnetophytes, and the angiosperms, share, or shared, superficially similar flowerlike reproductive structures. The strobili, or cones, of some gnetophytes closely resemble flowers, and the xylem (vascular tissue specialized for transporting water) of some gnetophytes is similar to the xylem found in angiosperms.

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Seed Ferns

Other lines of evidence suggest that a group of plants called the seed ferns, or *pteridosperms*, might represent the ancestors of the angiosperms. The seed ferns, which predate the angiosperms by many millions of years, had seed-bearing cupules and specialized organs that produced pollen. Many plant taxonomists believe that the seed-bearing cupules in some groups of seed ferns could have evolved into the carpels of flowers.

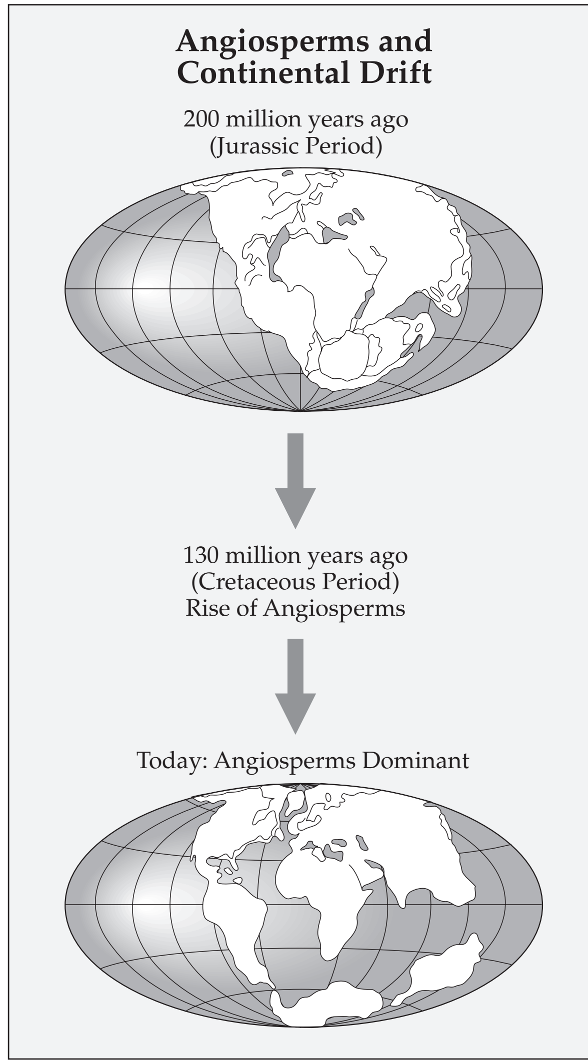
Earliest Flowers

Most paleobotanists assume that the first flowers were small, simple, and green in color and by modern standards were rather unattractive. Their petals and sepals were probably not clearly differentiated. In November of

1998, Ge Sun and David Dilcher and their colleagues published their discovery of the oldest angiosperm fossil to date, estimated to be at least 122 million years old and possibly as old as 145 million years. Either age qualifies it as the oldest. The fossils were discovered in China, and the fruits show the characteristic enclosed ovule (a *carpel*) that is distinctive to angiosperms. It was given the scientific name *Archaefructus liaoningensis*. Given its great age, this find implies that angiosperms may have arisen as early as the Jurassic period, more than 145 million years ago.

Other early flowers produced pollen with a single *aperture*, or opening, a trait that the monocot branch of the angiosperms shares with cycads and ginkgos. Plant taxonomists believe that pollen with a single opening is an ancestral feature that some plants have kept as they evolved. The pollen of eudicots, with its three apertures, is thought to be a derived feature (that is, a later evolutionary development).

Recent studies of angiosperm evolution, using data from deoxyribonucleic acid (DNA) sequences, have led to the proposal that an obscure shrub from the South Pacific island of New Caledonia, called *Amborella trichopoda*, represents what is left of the ancestral *sister group* (a related organism that branched off before the evolution of another group of organisms) to all the angiosperms. As a sister group to all the angiosperms, it is considered to be the most primitive (in an evolutionary sense) of the angiosperms and therefore should resemble what the ancestor to the angiosperms was like. It does possess some of the expected primitive traits for a primitive angiosperm, such as small, greenish-yellow flowers and a lack of vessels for conducting water from the ground to the leaves.



Angiosperms are proposed to have evolved approximately 130 million years ago, sometime between the Late Jurassic period (208-144 million years ago) and the Early Cretaceous period (144-65 million years ago), when South America, Africa, and India were much closer together.

Angiosperm Classification

Approximately 97 percent of angiosperm species are classified as either *Monocotyledones* (monocots), with approximately 65,000 species, or *Eudicotyledones* (eudicots), with about 165,000 species. The monocots include such familiar plants as the grasses, lilies, irises, orchids, cattails, and palms. The more diverse eudicots include most of the familiar trees and shrubs (other than the conifers) and many of the herbaceous plants. The remaining 3 percent of angiosperms are called the *magnoliids*, a group of plants considered to have primitive features, among them pollen with a single aperture. Many magnoliids also feature oil cells with ether-containing oils providing the characteristic scents of laurel and pepper, for example. The magnoliids are typically divided into the woody magnoliids and paleoherbs.

Woody magnoliids have large, often showy, bisexual flowers with multiple free parts. Magnolia trees and tulip trees (both in *Magnoliaceae*, or the magnolia family) are examples of this group. The *paleoherbs* have small, often unisexual flowers and usually just a few flower parts. Modern paleoherbs include the pepper family (*Piperaceae*), the birthwort family (*Aristolochiaceae*), and the water lily family (*Nymphaeaceae*).

Recent studies of angiosperm evolution, using data from DNA sequences, have also sharpened the understanding of some of the relationships among monocots, eudicots, and magnoliids. If these groups are displayed as an evolutionary tree (or *phylogenetic* tree), the magnoliids are *polyphyletic* (that is, they do not share a single common ancestor). The magnoliids branch off near the base of the tree on several different branches. The monocots are monophyletic (that is, they share a single common ancestor) and form a separate branch from among the magnoliid branches. The eudicots branch off last and represent the most diverse and evolutionarily complex group.

Geographic Origins

As hotly debated, perhaps, as exactly which group of plants were ancestral to the angiosperms is the question of where the angiosperms first evolved. Some botanists believe that angiosperms first developed in the Northern Hemisphere; others look at the Southern Hemisphere. At the time angiosperms are proposed to have evolved, the continents were not arranged the way they are now. At that time, all of the world's major landmasses were grouped into a supercontinent called Pangaea. The southern part of this continent is referred to as Gondwanaland, and the northern part is called Laurasia. Based on what is known about late Cretaceous angiosperms and their habitats, some scientists suggest that the westernmost, semiarid regions of Gondwanaland may be the place where angiosperms first evolved.

As Pangaea broke up, the separate continents moved in different positions, resulting in new configurations. India collided with Asia, raising the Himalaya Mountains and the Tibetan Plateau. Antarctica slipped over the South Pole, and Australia became isolated. These plate movements created new climatic regimes, opening up new niches that were rapidly exploited by the angiosperms.

Diversification and Spread

Regardless of their geographic origins, by about ninety million years ago the flowering plants were well on their way to dominating the world's flora. The early angiosperms were well adapted to drought and cold. Adaptations that conferred resistance to these conditions included strong leaves, efficient water-conducting cells, and tough, resistant seed coats. Some woody flowering plants evolved the ability to lose their leaves, called the *deciduous habit*. This characteristic allows the shutdown of metabolism during adverse environmental conditions, such as during seasonal droughts or winter weather. Because of greater climate instability during the past fifty million years or so compared to earlier times, the above-mentioned traits were important in allowing the flowering plants to adapt to different and often harsher climatic conditions.

Pollination

A major innovation that likely led to some of the great diversity seen in angiosperms was pollination by insects or other animals. As plants adapted to the various available pollinators, the pollinators also adapted to the plants, sometimes in very specific ways. Many pollination systems include specialized colors or markings, flower shapes, and flower scents. This process of evolving "together" is called *coevolution*. Coevolution has also occurred between plants and their predators. Evolution of chemical compounds to deter herbivory have, in turn, led to adaptations in many animal groups to circumvent the toxicity of the chemical compounds.

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See also: Algae; Angiosperm life cycle; Bacteria; Biochemical coevolution in angiosperms; Cell wall; Coevolution; Eukaryotic cells; Flower structure; Green algae; Photosynthesis; Plant tissues.

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ANGIOSPERM LIFE CYCLE

Categories: Anatomy; angiosperms; physiology; reproduction and life cycles

The word "angiosperm" comes from the Greek words for "vessel" and "seed" and translates roughly as "enclosed seed." In part, angiosperms (the flowering plants, phylum Anthophyta*) are defined by the fact that their seeds are enclosed by an ovule. The life cycle of an angiosperm is defined by the formation of the seed and its development to a full-grown plant which, in turn, produces seeds.*

Angiosperms are vascular plants with flowers that produce seeds enclosed in an *ovule*—a fact that is recognized as the *angiospermy condition*.

Reproductive Flower Parts

In general, angiosperms have a floral axis with four floral parts, two of which are fertile. At the receptacle, or tip, of the axis there is an ovule-bearing leaf structure known as the carpel. The ovule or ovules can be found inside the *pistil*. Three portions compose the pistil: the ovary, the style, and the stigma, where the pollen usually germinates. The mature ovule consists of the placenta, the integuments that are modified leaves that cover the entrance to the embryo sac, the micropyle, and the chalaza. These latter two parts of the ovule complement each other in their positions and functions. While the micropyle receives and guides the pollen tube, the chalaza relates to the vascular supply of the ovule, nutrition, and support. The *stamens*, which are often composed of the filament and sporangia sacs that make up the anther, surround the pistil. Stamens carry the male gametes, and the pistil carries the female gamete needed for sexual reproduction.

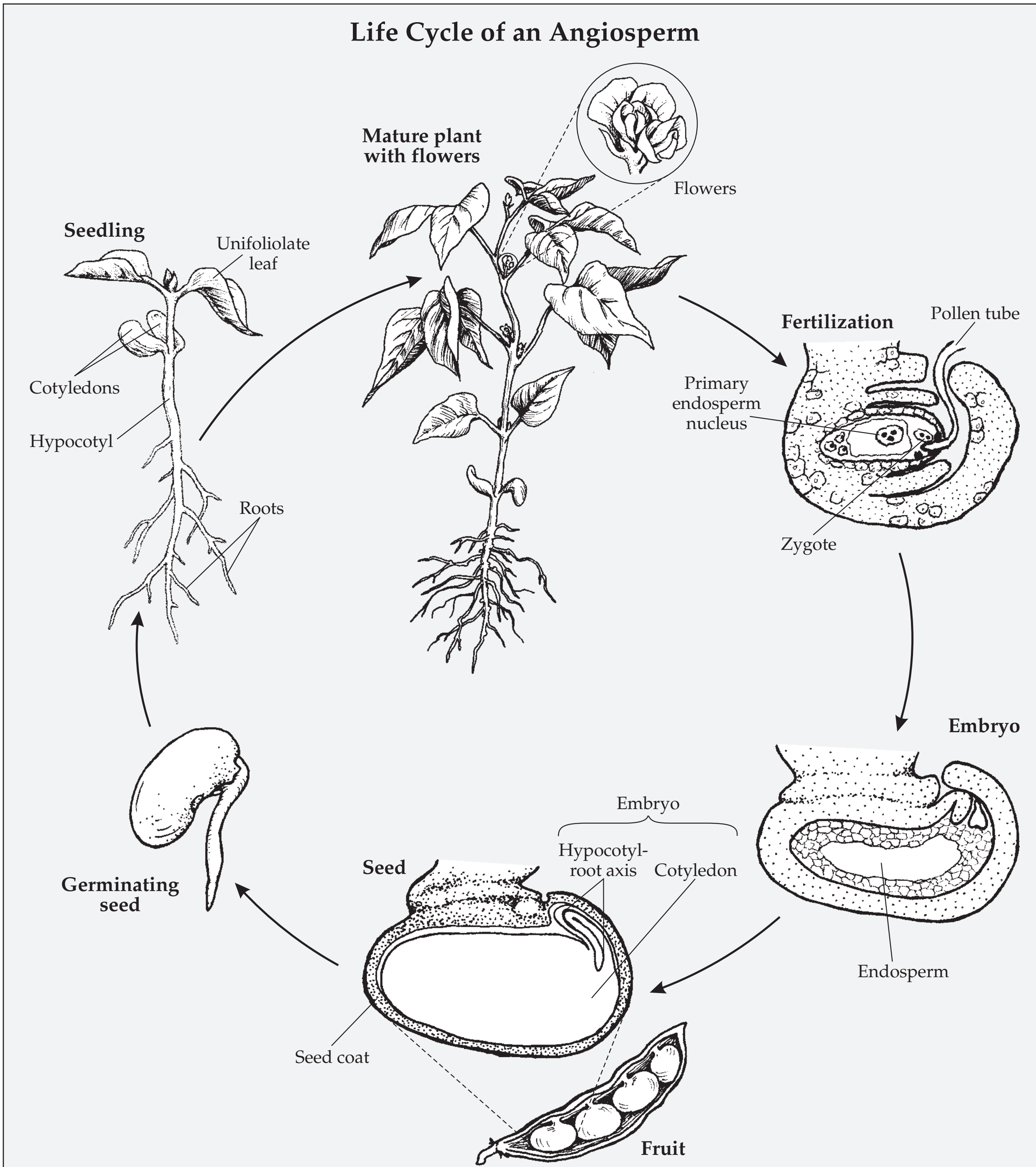
It is believed that the great diversity and adaptability of the angiosperms is related to the presence of a unique reproductive cycle. This cycle consists of an *alternation of generations* and the production of a pair of spores on two types of sporophylls: microspores (which become male gametophytes) and megaspores (which become female gametophytes).

Male Gamete Development

The angiosperm reproductive cycle begins with the process of *microsporogenesis*, or microspore formation. The stamen consists of a filament and the anther, also known as the *microsporangium*. In most of the cases, the anther consists of four pollen sacs, or locules. Within each locule, the archesporial cell develops through mitosis and extends as a row of cells throughout the entire length of the young anther. These mitotic cell divisions generate the anther wall, which is made up of several cell layers, the outermost of which transforms itself into the epidermis. The layer of cells below the epidermis is known as the endothecium. During anther development, the endothecial cells acquire thickenings whose function is related to anther opening and pollen release. The innermost layer of the anther wall is the tapetum, whose primary function correlates with the nourishment of the young pollen and the deposition of the exine, a coating of the pollen grain.

As development proceeds, the sporogenous cells located below the tapetum transform into microsporocytes. These microsporocytes will undergo meiosis, and tetrads (units of four) of microspores will form. Shortly after their formation, the tetrads separate into individual microspores. Each microspore is haploid, and often it will enlarge and separate from the tetrad, becoming sculptured by the deposition of sporopollenin and other substances that will turn into the ornamented surface of the pollen grain.

The second phase of pollen development is known as *microgametogenesis*. The microspore is the first cell of the gametophytic generation, the cell that generates the mature pollen. The single-nucleus microspore develops into the male gametophyte before the pollen is released. This developmental process occurs through two or three unequal mitotic divisions of the nucleus and subsequent cytokinesis (cell separation). The two daughter nuclei and cells differ in size and in form. The larger cell represents



Kimberly L. Dawson Kurnizki

the tube cell and nucleus, while the smaller cell represents the generative cell and nucleus. At maturity, the grain can be shred in two or three nucleate conditions. When the anther opens, the mature male gametophytes or pollen grains will be disseminated and ready for germination.

Female Gamete Development

The ovule (female sex organ) consists of two opposite ends: the micropyle, where the integuments come together, and a more distant end, where the ovular tissue is more massive. This part is also known as the chalaza, and it lies directly opposed to the micropyle. The mature ovule is composed of three layers: the outer integument; the inner integument; and, underneath the integuments, the nucellus. During ovular development, one cell lying below the nucellar epidermis changes into a primary archesporial; this will divide to form the primary parietal cell and primary sporogenous cell. The primary sporogenous cell functions as the megaspore mother cell, which divides meiotically, originating four haploid megaspores. In the majority of angiosperms, three of the megaspores will degenerate, and only the chalazal one will develop into the megagametophyte (embryo sac).

After the completion of the embryo sac stage, a series of cellular events occurs, ending with the formation of the mature embryo sac, ready for fertilization by the male gametes. The chalazal megaspore enlarges and undergoes three mitoses, giving rise to eight haploid cells. The mature megagametophyte consists of two groups of four cells located at both ends of the embryo sac. The result is three antipodals at the chalazal end: the egg apparatus (consisting of the egg and two synergids at the micropylar end) and the polar nuclei. These two cells, present at both ends, usually fuse before pollination, and during fertilization they form the primary endosperm nucleus.

Pollination

The plant reproductive structures are now ready for the union of male and female gametes or fertilization, which eventually will produce a seed with a viable embryo and cotyledons. Before that step takes place, however, the pollen must be transferred from the anther to the stigma. Biotic agents (such as birds, insects, or mammals) or abiotic agents (such as wind or water) can accomplish this transfer process, known as *pollination*.

After landing on the stigma, pollen tubes will emerge through the grain apertures if the environment is high in humidity. Successful germination of the pollen in the stigma requires nutrients. In most plants, growth of the pollen tube lasts between twelve and forty-eight hours, from pollen germination to fertilization. Pollen germination starts with pollen-tube initiation, elongation, and penetration of the stigmatic tissue. During this period intense metabolic activity takes place, for the tube must synthesize membrane material and cell wall for growth and expansion. Simultaneously, at its tip the tube carries the vegetative cell nucleus, followed by the germinative cell.

Angiosperms have evolved complex breeding systems that ensure they will be pollinated by their own species. Today it is recognized that two pollination syndromes exist: *self-pollination* and *cross-pollination*. In self-breeding species, the pollen comes from the anther of the same flower. In cross-pollination (or outcrossing) species, the pollen comes from the anthers of a different flower or even a different plant of the same species. In these plants, incompatibility in the stigma guarantees that only pollen from other flowers will germinate.

Fertilization

The union of one sperm with the egg is known as *fertilization*. However, several developmental processes in the vegetative and germinative cells prepare the two sperms for a process known as *double fertilization*. A mitotic division of the germinative cell generates the sperm cells. This process that can take place on the growing pollen tube or inside the pollen grain. In a growing pollen tube, the vegetative nucleus disintegrates and the sperm cells will take the lead and enter the embryo sac for successful fertilization. Usually, the interactions between the pollen grain and the pistil ensure that the sperm cells will often reach the micropyle of the ovule.

Once the sperm reach the micropyle, the growth of other tubes stops. In the embryo sac (female gametophyte), four cells are located at the micropylar side. Of those four, the first pair that the sperm cells will encounter are the synergids. One of these is always bigger than the other and carries the filiform apparatus, a structure resembling hairs that degenerates after pollination and before fertilization. The synergids act as chemical attractants to the pollen tube, which penetrates the synergids via the filiform apparatus and then releases the two sperm cells. One of the sperm cells will fuse with the egg, producing the zygote; the other sperm cell will fuse with the primary endosperm nucleus, generating the endosperm. The remaining cells of the female gametophyte are the antipodals; they usually degenerate after fertilization has taken place.

Seed and Fruit Formation

Once fertilization has occurred, the ovule will go through a series of metabolic steps ending with the formation of the *seed* and the *fruit*. The recently created zygote transforms into a multicellular and complex *embryo* that has two well-defined polar ends: the radicle, or primary root, and the embryonic apical meristem with the first leaves. After successive mitosis, the mature endosperm usually grows close to the embryo and may provide nutrients needed for germination. The integuments will undergo further transformation, replication, and elongation and will become the seed coat—of variable texture, consistency, and colors, depending on the type of plant.

In general, after pollination or during fertilization, the ovary undergoes a series of physiological changes regulated by synchronized hormonal and genetic alterations that will modify the size of the parenchyma cells and its sugar and organic acids contents. This process turns the ovary into fruit—in many cases familiar as the edible fruits familiar in human diets. The fruit provides nourishment for the seed until it ripens and drops to the ground, where the next stage in the life cycle begins.

Germination, Seedling Development, and Maturation

Seeds are released from the fruit in a large variety of ways that have evolved to ensure the survival of species. Whether ingested by mammals and passed through their feces to the ground, borne by wind on feathery "wings," or simply falling from rotting fruit that has abscissed and dropped from the plant, the seed must next undergo a process called *germination*, in which the embryo enclosed in the seed begins its growth. The embryo develops a *hypocotyl* (root axis) and a fleshy part known as the *cotyledon*; in monocots there is one cotyledon, in dicots, two.

Germination requires certain conditions, such as the softening of the seed coat, moisture, and adequate warmth, to occur. During germination, the hypocotyl begins growing downward to become the root; the cotyledon(s) will develop into the shoot, stems, and leaves. The process of germination results in the sprouting through the ground's surface of the *seedling*, which will develop into the mature plant with flowers. The cycle then begins again.

Miriam Colella

See also: Angiosperm cells and tissues; Angiosperm evolution; Angiosperm plant formation; Angiosperms; Dormancy; Flower structure; Flower types; Flowering regulation; Fruit: structure and types; Germination and seedling development; Plant life spans; Reproduction in plants; Seeds.

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ANGIOSPERM PLANT FORMATION

Categories: Anatomy; angiosperms; physiology; reproduction and life cycles

Angiosperms are flowering plants. Their formation entails development from embryo to seed, through germination to seedling, and finally to mature plant.

The life cycle of angiosperms (flowering plants) involves an alternation of generations between a dominant sporophytic (spore-producing) phase and a reduced gametophytic (gamete-producing) phase. The first cell of the sporophyte is the fertilized egg, or *zygote*, which undergoes repeated divisions, growth, and differentiation to form an embryo enclosed in the ovule. After fertilization, the ovule is transformed into the seed, which germinates into a seedling. The seedling becomes the adult plant; the plant produces flowers in which the sperm and egg—representing, respectively, the male and female gametophytic generations—are formed. Fertilization occurs, and seeds are produced to continue the life cycle.

Dicot Embryo Formation

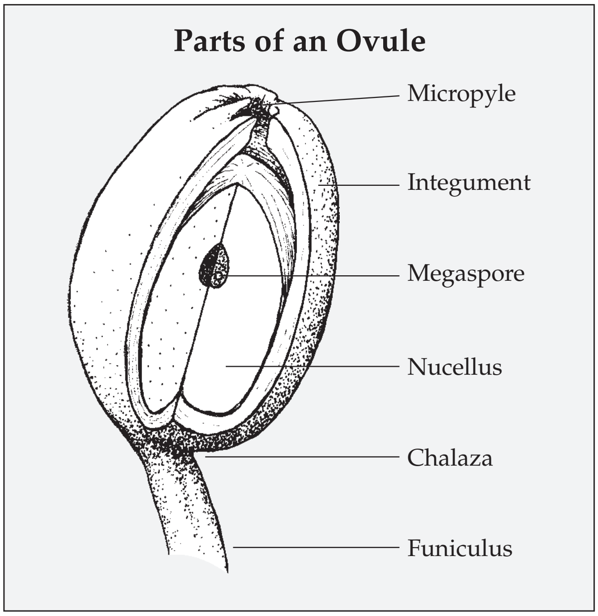
In most angiosperms, embryo development, or *embryogenesis*, is initiated with a division of the fertilized egg into a small apical cell and a large basal cell, forming a two-celled proembryo. The apical cell generates the embryo proper, and the basal cell forms a filamentous *suspensor* that anchors the embryo. Two weeds, *Capsella bursa-pastoris* (shepherd's purse) and *Arabidopsis thaliana* (mouse ear cress or wall cress), both belonging to the *Brassicaceae* family, have attained prominence as textbook examples of embryogenesis in typical *dicots* (plants with two *cotyledons*, or seed leaves; a *monocot* has one seed leaf).

In these plants, the apical cell of the proembryo divides by two successive longitudinal walls to form a quadrant that is immediately partitioned by transverse walls into an octant, composed of an upper and lower tier of four cells each. The fates of the two tiers are already fixed in the octant embryo, as the upper tier forms the *shoot apex* and much of the cotyledons. The lower tier, in addition to providing derivatives to the remaining part of cotyledons, generates the *hypocotyl*, the *radicle*, and the *root apex*. However, the central region of the root cap, known as the columella, and the quiescent center of the root apical meristem are derived from the terminal cell of the *suspensor* closest to the embryo, known as the *hypophysis*. The apicobasal pattern of the future seedling plant is established in the octant embryo.

A series of divisions separating eight peripheral cells from a core of eight inner cells heralds histogenesis in the embryo. The result is the formation of a sixteen-celled, globular embryo, in which the peripheral cells form the protoderm (precursor cells of the embryonic epidermis), and the inner cells differentiate into the procambium and ground meristem (precursors of the vascular tissues and ground tissues, respectively) of the mature embryo. This initiates the formation of radial-pattern elements made up of concentric tissue layers in the basal part of the embryo.

The globular stage of the embryo is completed by approximately three additional rounds of divisions, mostly in the inner core of cells. The suspensor attains its genetically permissible number of six to nine cells by this stage. Gradually the cells begin to lose connection from one another and from the embryo and disintegrate.

Emerging from the globular stage, the embryo expands laterally by cell divisions to form the cotyledons and becomes heart-shaped. The heart-shaped stage is followed by the torpedo-shaped



Angiosperms are vascular plants with flowers that produce seeds enclosed in an ovule (female sex organ), a fact that is recognized as the "angiospermy condition." The ovule consists of two opposite ends: the micropyle, where the integuments come together, and the chalaza, where the ovular tissue is more massive. The mature ovule is composed of three layers: the outer integument; the inner integument; and, underneath the integuments, the nucellus (megasporangium), in which the megaspore, which will become the female gametophyte, is embedded. The stalk to which the ovule is attached is the funiculus.

stage, in which elongation of the cotyledons and hypocotyl, as well as extension of the vascular tissues, occurs. The basic body plan of a shoot-root axis becomes unmistakably clear at this stage, with the establishment of the shoot apical meristem in the depression between the cotyledons and the organization of a root apex by incorporation of derivatives of the hypophysis at the opposite end of the embryo.

During further growth, the cotyledons bend toward the hypocotyl (bent cotyledon or walking-stick shaped stage), and the embryo is phased into the mature stage. A mature embryo of *Arabidopsis* has fifteen thousand to twenty thousand cells and, under favorable conditions of growth, develops in about nine days from the time of fertilization to the mature embryo stage. Sensitive genetic screens have led to the isolation of *Arabidopsis* mutants defective in apicobasal and radial patterning of embryos. Characterization of the mutant genes and their protein products has unraveled to some extent the molecular components of the embryonic pattern-forming system in this plant.

Monocot Embryo Formation

The early divisions of the zygote in monocots follow the same pattern as in dicots. However, in the *Poaceae* (grasses) family, which includes wheat and the other cereals, the sequence and orientation of later divisions in the proembryo are irregular, resulting in highly complex mature embryos. The main feature of the cereal embryo is the development of an absorptive organ known as the *scutellum* (considered equivalent to the single cotyledon). Other organs of the embryo for which there are no counterparts in the dicot embryo are a sheathlike tissue covering the root (*coleorhiza*), a tissue that covers the shoot (*coleoptile*), and an internode known as the *mesocotyl*. On one side of the coleorhiza there is also a small, flaplike outgrowth called the *epiblast*.

Embryo Maturation to Seed

As the embryo matures, the ovule progressively desiccates to become the seed enclosed within the ovary. Concomitantly, the integuments of the ovule harden to form the protective seed coat. Within the ovule itself, the primary endosperm nucleus formed after double fertilization begins to divide, ahead of the zygote, to produce the endosperm charged with nutrient substances. In seeds of many plants, including *Arabidopsis*, *Capsella*, bean, and pea, the endosperm is utilized by the developing embryo.

In other plants, especially the cereals, the bulk of the seed (grain) is made up of the endosperm surrounding the small embryo. The mature embryo enclosed in the seed consists of an axis bearing the *radicle* (embryonic root) at one end and the *plumule* (the embryonic shoot consisting of the shoot apex and one or two leaves) at the other end, and one (in monocots) or two (in dicots) cotyledons. The part of the embryo axis above the point of attachment of the cotyledon(s) is known as the *epicotyl*, whereas the part below the attachment point connecting to the radicle is called the *hypocotyl*.

Seed Germination

The dry seed enclosing the mature embryo may not germinate immediately; if it does not, it enters a period of *quiescence* or dormancy. Quiescent seeds germinate when provided with the appropriate conditions for growth, such as water, a favorable temperature, and the normal composition of the atmosphere. Dormant seeds germinate only when some additional hormonal, environmental, metabolic, or physical conditions are met. In almost all seeds, the first part of the embryo to emerge during germination is the radicle. It forces it way through the soil and forms the primary root of the seedling. However, the manner in which the shoot emerges and develops varies considerably in different seeds.

In the *epigeous* type of germination (for example, in beans), emergence of the radicle is followed by the elongation of the hypocotyl, which arches above the soil surface as a hook. As the hook straightens, it pulls out the cotyledons and plumule above the soil surface. In the *hypogeous* type of germination (in peas, for example) the cotyledons enclosed within the seed coat remain in the soil during germination. It is the epicotyl that arches above the soil surface, and as the hook straightens out, it carries the plumule along with it to the surface of the soil. In the monocot, such as the onion, after emergence of the radicle the single cotyledon arches aboveground and subsequently straightens.

Members of the *Poaceae* display a type of germination in which, following the outgrowth of the radicle, the coleoptile enclosing the plumule grows out of the grain and appears above the soil. The seedling leaves force their way, breaking the coleoptile, and appear outside as the first photosynthetic organs. The growth of the coleoptile during germination of grains is facilitated by the elongation of the mesocotyl. These various types of germination ensure an efficient use of food materials stored in the embryo or in the endosperm for the growth of the seedling until it becomes autotrophic.

Embryo to Adult Plant

Although the question as to whether the seedling will become a gigantic tree or a small, herbaceous plant is determined by its genetic blueprint, certain common postgermination growth and developmental episodes mark the development of the seedling into an adult plant. In dicots, continued growth of the primary root produces an extensively branched root system consisting of secondary roots or lateral roots. In monocots, the primary root disintegrates shortly after it is formed, and so the root system is constituted of numerous adventitious roots which arise from the base of the stem.

Although the cotyledons retain their photosynthetic capacity for some time after germination of the seed, the seedling becomes completely autotrophic as the shoot apex produces new leaves and branches arise in the axils of leaves. These activities are coordinated by the division of cells in the root and shoot apical meristems and the differentiation of cells into specialized tissues and organs. The shoot and root apical meristems, considered analogous to the stem cells of animals, remain active throughout the life of the plant and, hence, are known as indeterminate meristems.

V. Raghavan

See also: Angiosperm cells and tissues; Angiosperm evolution; Angiosperm life cycle; Angiosperms;

Digital Stock

As the angiosperm embryo matures, the ovule progressively desiccates to become the seed enclosed within the ovary. These milkweed seeds will germinate when particular hormonal, environmental, metabolic, or physical conditions are met.

Dormancy; Flower structure; Flower types; Flowering regulation; Germination and seedling development; Plant life spans; Pollination; Reproduction in plants; Seeds.

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ANGIOSPERMS

Categories: Angiosperms; economic botany and plant uses; food; medicine and health; *Plantae*; taxonomic groups

The name "angiosperms" has long been used by botanists to refer to the flowering plants, a group of approximately 235,000 species. All angiosperms are members of the phylum Anthophyta.

The name "angiosperm" is actually derived from two Greek words, *angeion*, meaning "vessel" or "container," and *sperma*, meaning "seed." The name was given in reference to the fact that the seeds of all flowering plants develop from *ovules* that are enclosed in a structure called a *carpel*. This characteristic sets the angiosperms apart from all other plants, which either do not have seeds or have seeds that are not developed in structures resembling a carpel. Although the name angiosperm is used widely, plant taxonomists and many botanists typically refer to them by the more formal name *Anthophyta*, the phylum that contains the flowering plants.

Unique Features of Angiosperms

In addition to possessing enclosed seeds, *Anthophyta* differs from other plant phyla in a number of ways. The most obvious distinguishing feature is the *flower*, a complex structure containing the reproductive parts of the plant. The reproductive structures in other plants are much less complex and showy. The angiosperm life cycle differs from that of almost all other plants. The *sporophyte* is the dominant, *diploid* stage and is the more visible form of the plant, with the leaves, stems, roots, and flowers. The *haploid gametophyte* is confined to life inside the *ovary* or *anther* of the flower, unlike the typically free-living gametophytes of most other plants.

Fertilization is also unique in angiosperms. Many angiosperms rely on insects or other animals to transfer pollen from one flower to another. *Pollen grains* produce two haploid *sperm* that travel through a *pollen tube* from the *stigma* into the ovary of the flower and into one of the *embryo sacs*. Within the embryo sac one of the sperm fertilizes the egg, which will lead to formation of the diploid embryo, and the other sperm fuses with two or more polar nuclei to form the *endosperm*, which will nourish the embryo and young seedling. This process is often referred to as *double fertilization*. Other, less obvious features set *Anthophyta* apart as well, including a unique *vascular anatomy*, pollen structure, and various biochemical characteristics.

Size and Geographic Diversity

There are approximately 235,000 species of flowering plants, and they are found in almost all terrestrial habitats, with the exception of extremely high elevations and some polar regions. A small proportion of flowering plants are aquatic (that is, found in

Common Monocot Families

There are at least four major taxonomic systems for classifying flowering plants, as well as less formal systems. While names of phyla (divisions), subdivisions, classes, subclasses, and orders vary, along with the placement of families within those larger groups, the names of families, genera, and species remain fairly constant, with fewer alterations and controversies (although subject to changes as well). Families found in the United States are followed by their common names in parentheses.

Acoraceae (calamus)
Agavaceae (century plant)
Alismataceae (water plantain)
Aloeaceae (aloe)
Aponogetonaceae (cape pondweed)
Araceae (arum)
Arecaceae (palm)
Bromeliaceae (bromeliad)
Burmanniaceae (burmannia)
Butomaceae (flowering rush)
Cannaceae (canna)
Centrolepidaceae
Commelinaceae (spiderwort)
Corsiaceae
Costaceae (costus)
Cyanastraceae
Cyclanthaceae (Panama hat)
Cymodoceaceae (manatee grass)
Cyperaceae (sedge)
Dioscoreaceae (yam)
Eriocaulaceae (pipewort)
Flagellariaceae
Geosiridaceae
Haemodoraceae (bloodwort)
Hanguanaceae (hanguana)
Heliconiaceae (heliconia)
Hydatellaceae
Hydrocharitaceae (tape grass)
Iridaceae (iris)
Joinvilleaceae (joinvillea)
Juncaceae (rush)
Juncaginaceae (arrow grass)
Lemnaceae (duckweed)
Liliaceae (lily)
Limnocharitaceae (water poppy)
Lowiaceae
Marantaceae (prayer plant)
Mayacaceae (mayaca)
Musaceae (banana)
Najadaceae (water nymph)
Orchidaceae (orchid)
Pandanaceae (screw pine)
Petrosaviaceae
Philydraceae (philydraceae)
Poaceae (grass)
Pontederiaceae (water hyacinth)
Posidoniaceae (posidonia)
Potamogetonaceae (pondweed)
Rapateaceae
Restionaceae
Ruppiaceae (ditch grass)
Scheuchzeriaceae (scheuchzeria)
Smilacaceae (catbrier)
Sparganiaceae (bur reed)
Stemonaceae (stemona)
Strelitziaceae
Taccaceae (tacca)
Thurniaceae
Triuridaceae
Typhaceae (cattail)
Velloziaceae
Xanthorrhoeaceae
Xyridaceae (yellow-eyed grass)
Zannichelliaceae (horned pondweed)
Zingiberaceae (ginger)
Zosteraceae (eelgrass)

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA, and the Texas A&M Bioinformatics Working Group, Texas A&M University, http://www.csdl.tamu.edu/FLORA/newgate.

freshwater habitats), and an even smaller number are marine (found in saltwater habitats). The greatest species richness is in tropical regions, especially tropical rain forests, and species richness steadily decreases at increasing latitudes north and south of the equator.

Angiosperms have been so successful in terrestrial ecosystems that they represent the majority of the herbs and shrubs and many of the trees as well. The diversity of growth forms is tremendous, represented by such diverse families as *Poaceae* (grasses and bamboos), which have greatly reduced and modified flowers; *Cactaceae* (cactuses), which have spines instead of leaves and very showy flowers; and *Lemnaceae* (duckweed), which has a highly reduced plant body sometimes comprising a single leaf with no true roots or stem and the smallest flowers of any angiosperm. Other families include *Asteraceae* (sunflower or aster family), with reduced disc and ray flowers crowded together into *inflorescences* called heads; *Salicaceae* (willow family), a widespread, water-loving family of trees and shrubs with reduced flowers arranged in catkins; and *Orchidaceae* (orchid family), with some of the showiest and most intricate flowers of all, which have extremely numerous and minute seeds.

Economic Importance

Economically, angiosperms have made a profound impact. Essentially all of the world's food crops, from rice, wheat, and corn to other fruits and vegetables, are derived from flowering plants. In fact, it is almost impossible to think of more than a handful of foods or food ingredients from plants that are not flowering plants. The same is true of ornamental plants. Although a few gymnosperms (such as conifers) and ferns are common as ornamentals, most of the remaining plants, even many valued for their foliage rather than their blooms, are flowering plants. The only area where angiosperms do not dominate economically is in forest products, where conifers account for a significantly larger proportion of the harvest, but even there, hardwoods predominate for certain applications.

Medicine has also reaped many benefits from angiosperms. In fact, it was primarily the herbalists, from the Middle Ages to the Scientific Revolution, who expanded humankind's understanding of flowering plants. Knowledge of flowering plants for food and medicine among many indigenous peoples has always been widespread. Modern medicine has capitalized on much of this knowledge and has

Common Dicot (Eudicot) Families

There are at least four major taxonomic systems for classifying flowering plants, as well as less formal systems. While names of phyla (divisions), subdivisions, classes, subclasses, and orders vary, along with the placement of families within those larger groups, the names of families, genera, and species remain fairly constant, with fewer alterations and controversies (although subject to changes as well). Families found in the United States are followed by their common names in parentheses.

Acanthaceae (acanthus)
Aceraceae (maple)
Achariaceae
Achatocarpaceae (achatocarpus)
Actinidiaceae (Chinese gooseberry)
Adoxaceae (moschatel)
Aextoxicaceae
Aizoaceae (fig marigold)
Akaniaceae
Alangiaceae
Alseuosmiaceae
Alzateaceae
Amaranthaceae (amaranth)
Amborellaceae
Anacardiaceae (sumac)
Ancistrocladaceae
Anisophylleaceae
Annonaceae (custard apple)
Apiaceae (carrot)
Apocynaceae (dogbane)
Aquifoliaceae (holly)
Araliaceae (ginseng)
Aristolochiaceae (birthwort)
Asclepiadaceae (milkweed)
Asteraceae (aster, also *Compositae*)
Austrobaileyaceae
Balanopaceae
Balanophoraceae (balanophora)
Balsaminaceae (touch-me-not)
Barbeyaceae
Barclayaceae
Basellaceae (basella)
Bataceae (saltwort)
Begoniaceae (begonia)
Berberidaceae (barberry)
Betulaceae (birch)
Bignoniaceae (trumpet creeper)
Bixaceae (lipstick tree)
Bombacaceae (kapok tree)
Boraginaceae (borage)
Brassicaceae (mustard, also *Cruciferae*)
Bretschneideraceae
Brunelliaceae (brunellia)
Bruniaceae
Brunoniaceae
Buddlejaceae (butterfly bush)
Burseraceae (frankincense)
Buxaceae (boxwood)
Byblidaceae
Cabombaceae (water shield)
Cactaceae (cactus)
Caesalpiniaceae
Callitrichaceae (water starwort)
Calycanthaceae (strawberry shrub)*
Calyceraceae (calycera)
Campanulaceae (bellflower)
Canellaceae (canella)
Cannabaceae (hemp)
Capparaceae (caper)
Caprifoliaceae (honeysuckle)
Cardiopteridaceae
Caricaceae (papaya)
Caryocaraceae (souari)
Caryophyllaceae (pink)
Casuarinaceae (she-oak)
Cecropiaceae (cecropia)
Celastraceae (bittersweet)
Cephalotaceae
Ceratophyllaceae (hornwort)
Cercidiphyllaceae (katsura tree)
Chenopodiaceae (goosefoot)
Chloranthaceae (chloranthus)
Chrysobalanaceae (cocoa plum)
Circaeasteraceae
Cistaceae (rockrose)
Clethraceae (clethra)
Clusiaceae (mangosteen, also *Guttiferae*)
Cneoraceae
Columelliaceae
Combretaceae (Indian almond)
Compositae (aster, also *Asteraceae*)
Connaraceae (cannarus)
Convolvulaceae (morning glory)
Coriariaceae
Cornaceae (dogwood)
Corynocarpaceae (karaka)
Crassulaceae (stonecrop)
Crossosomataceae (crossosoma)
Crypteroniaceae
Cucurbitaceae (cucumber)
Cunoniaceae (cunonia)
Cuscutaceae (dodder)
Cyrillaceae (cyrilla)
Daphniphyllaceae

(continued)

*Some systems classify magnoliids (about 3 percent of flowering plants) separately from monocots and dicots, including these families.

even expanded the search for new medicines. Flowering plants have been the original source of many precursors to modern medicines, including aspirin (willows, *Salix*), quinine (*Cinchona* species), and digitalin and digoxin (*Digitalis* species).

Lifestyle Diversity

Along with the diversity in structure comes a diversity in lifestyles. Most angiosperms are free-living, that is, receiving their primary energy and carbon from photosynthesis and their nutrients from the soil. A few groups of plants receive their energy or nutrients in other ways. Some are *saprophytes*, which receive their energy and carbon from decaying organic material in the soil and their nutrients from other soil components, much like other plants. Some of the best-known saprophytes are in *Ericaceae* (heath family). Their most distinc-

Datiscaceae (datisca)
Davidsoniaceae
Degeneriaceae
Dialypetalanthaceae
Diapensiaceae (diapensia)
Dichapetalaceae
Didiereaceae
Didymelaceae
Dilleniaceae (dillenia)
Dioncophyllaceae
Dipentodontaceae
Dipsacaceae (teasel)
Dipterocarpaceae (meranti)
Donatiaceae
Droseraceae (sundew)
Duckeodendraceae
Ebenaceae (ebony)
Elaeagnaceae (oleaster)
Elaeocarpaceae (elaeocarpus)
Elatinaceae (waterwort)
Empetraceae (crowberry)
Epacridaceae (epacris)
Eremolepidaceae (catkin-mistletoe)
Ericaceae (heath)
Erythroxylaceae (coca)
Eucommiaceae
Eucryphiaceae
Euphorbiaceae (spurge)
Eupomatiaceae
Eupteleaceae
Fabaceae (pea or legume, also *Papilionaceae*)
Fagaceae (beech)
Flacourtiaceae (flacourtia)
Fouquieriaceae (ocotillo)
Frankeniaceae (frankenia)
Fumariaceae (fumitory)
Garryaceae (silk tassel)
Geissolomataceae
Gentianaceae (gentian)
Geraniaceae (geranium)
Gesneriaceae (gesneriad)
Globulariaceae
Gomortegaceae
Goodeniaceae (goodenia)
Greyiaceae
Grossulariaceae (currant)
Grubbiaceae
Gunneraceae (gunnera)
Gyrostemonaceae
Haloragaceae (water milfoil)
Hamamelidaceae (witch hazel)
Hernandiaceae (hernandia)
Himantandraceae
Hippocastanaceae (horse chestnut)
Hippocrateaceae (hippocratea)
Hippuridaceae (mare's tail)
Hoplestigmataceae
Huaceae
Hugoniaceae
Humiriaceae
Hydnoraceae
Hydrangeaceae (hydrangea)
Hydrophyllaceae (waterleaf)
Hydrostachyaceae
Icacinaceae (icacina)
Idiospermaceae
Illiciaceae (star anise)
Ixonanthaceae
Juglandaceae (walnut)
Julianiaceae
Krameriaceae (krameria)
Lacistemataceae
Lamiaceae (mint, also *Labiatae*)
Lardizabalaceae (lardizabala)
Lauraceae (laurel)*
Lecythidaceae (brazil nut)
Leeaceae
Leitneriaceae (corkwood)
Lennoaceae (lennoa)
Lentibulariaceae (bladderwort)
Limnanthaceae (meadow foam)
Linaceae (flax)
Lissocarpaceae
Loasaceae (loasa)
Loganiaceae (logania)
Loranthaceae (showy mistletoe)
Lythraceae (loosestrife)
Magnoliaceae (magnolia)*
Malesherbiaceae
Malpighiaceae (barbados cherry)
Malvaceae (mallow)
Marcgraviaceae (shingle plant)
Medusagynaceae
Medusandraceae
Melastomataceae (melastome)
Meliaceae (mahogany)
Melianthaceae
Mendonciaceae
Menispermaceae (moonseed)
Menyanthaceae (buckbean)
Mimosaceae
Misodendraceae
Mitrastemonaceae
Molluginaceae (carpetweed)
Monimiaceae (monimia)
Monotropaceae (Indian pipe)
Moraceae (mulberry)
Moringaceae (horseradish tree)
Myoporaceae (myoporum)
Myricaceae (bayberry)
Myristicaceae (nutmeg)
Myrothamnaceae
Myrsinaceae (myrsine)
Myrtaceae (myrtle)
Nelumbonaceae (lotus lily)
Nepenthaceae (East Indian pitcher plant)
Neuradaceae
Nolanaceae

(continued)

*Some systems classify magnoliids (about 3 percent of flowering plants) separately from monocots and dicots, including these families.

tive feature is that they are either white or some shade of pink or red and are never green. *Monotropa uniflora* (Indian pipes), for example, is a ghostly white and has no chlorophyll.

Parasitism is an alternative for some angiosperms. One well-known parasite is the mistletoe (*Loranthaceae*), popular as a Christmas decoration, which is a branch parasite on trees. Many types of mistletoe have green foliage and therefore receive some of their energy from photosynthesis, but their primary nourishment comes from the host tree. Some species have foliage that is brown or yellow and do not photosynthesize much at all. The seeds of mistletoe are spread from tree to tree when birds eat their berries and defecate the seeds on the branch of another tree. Probably the most unusual

Common Dicot (Eudicot) Families *(continued)*

Nothofagaceae
Nyctaginaceae (four-o'clock)
Nymphaeaceae (water lily)
Nyssaceae (sour gum)
Ochnaceae (ochna)
Olacaceae (olax)
Oleaceae (olive)
Oliniaceae
Onagraceae (evening primrose)
Oncothecaceae
Opiliaceae
Orobanchaceae (broom rape)
Oxalidaceae (wood sorrel)
Paeoniaceae (peony)
Pandaceae
Papaveraceae (poppy)
Paracryphiaceae
Passifloraceae (passionflower)
Pedaliaceae (sesame)
Pellicieraceae
Penaeaceae
Pentaphragmataceae
Pentaphylacaceae
Peridiscaceae
Physenaceae
Phytolaccaceae (pokeweed)
Piperaceae (pepper)
Pittosporaceae (pittosporum)
Plantaginaceae (plantain)
Platanaceae (plane tree)
Plumbaginaceae (leadwort)
Podostemaceae (river weed)
Polemoniaceae (phlox)
Polygalaceae (milkwort)
Polygonaceae (buckwheat)
Portulacaceae (purslane)
Primulaceae (primrose)
Proteaceae (protea)
Punicaceae (pomegranate)
Pyrolaceae (shinleaf)
Quiinaceae
Rafflesiaceae (rafflesia)
Ranunculaceae (buttercup or ranunculus)
Resedaceae (mignonette)
Retziaceae
Rhabdodendraceae
Rhamnaceae (buckthorn)
Rhizophoraceae (red mangrove)
Rhoipteleaceae
Rhynchocalycaceae
Rosaceae (rose)
Rubiaceae (madder)
Rutaceae (rue)
Sabiaceae (sabia)
Saccifoliaceae
Salicaceae (willow)
Salvadoraceae
Santalaceae (sandalwood)
Sapindaceae (soapberry)
Sapotaceae (sapodilla)
Sarcolaenaceae
Sargentodoxaceae
Sarraceniaceae (pitcher plant)
Saururaceae (lizard's tail)
Saxifragaceae (saxifrage)
Schisandraceae (schisandra)
Scrophulariaceae (figwort)
Scyphostegiaceae
Scytopetalaceae
Simaroubaceae (quassia)
Simmondsiaceae (jojoba)
Solanaceae (potato)
Sonneratiaceae (sonneratia)
Sphaerosepalaceae
Sphenocleaceae (spenoclea)
Stachyuraceae
Stackhousiaceae (stackhousia)
Staphyleaceae (bladdernut)
Sterculiaceae (cacao)
Stylidiaceae
Styracaceae (storax)
Surianaceae (suriana)
Symplocaceae (sweetleaf)
Tamaricaceae (tamarix)
Tepuianthaceae
Tetracentraceae
Tetrameristaceae
Theaceae (tea)
Theligonaceae
Theophrastaceae (theophrasta)
Thymelaeaceae (mezereum)
Ticodendraceae
Tiliaceae (linden)
Tovariaceae
Trapaceae (water chestnut)
Tremandraceae
Trigoniaceae
Trimeniaceae
Trochodendraceae
Tropaeolaceae (nasturtium)
Turneraceae (turnera)
Ulmaceae (elm)
Urticaceae (nettle)
Valerianaceae (valerian)
Verbenaceae (verbena)
Violaceae (violet)
Viscaceae (Christmas mistletoe)
Vitaceae (grape)
Vochysiaceae
Winteraceae (wintera)
Xanthophyllaceae
Zygophyllaceae (creosote bush)

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA, and the Texas A&M Bioinformatics Working Group, Texas A&M University, http://www.csdl.tamu.edu/FLORA/newgate.

parasite is *Rafflesia*, from Malaysia and Sumatra. It parasitizes species of *Tetrastigma*, a vine that grows on the forest floor and has no stems or leaves of its own. When it blooms it has the largest flowers in the world, and it is often called the corpse flower because it has a very strong odor, like that of rotting flesh.

Other parasites receive varying proportions of their energy and nutrients from their host and conventional means, and when the contributions are nearly equal they are referred to as *hemiparasites*. Hemiparasites are common in *Castilleja* (paintbrushes), and many species invade the roots of other plants to obtain part of their nutritional needs.

A unique approach to obtaining nutrients is represented by *insectivorous plants*, commonly known as *carnivorous plants* These plants use a variety of adaptations for trapping and absorbing nutrients from insects. Sundews (*Droseraceae*) have special glands on their leaves that excrete a sticky fluid that traps insects like flypaper. Pitcher plants (*Nepenthaceae* and *Sarraceniaceae*) have special tubular leaves that resemble cups or pitchers. The inside of the leaves fill with water near the base, and the lip and inside surface of the pitcher are slippery. Once an insect gets inside, it slips into the water at the bottom. Venus's flytrap (*Dionaea*, also in *Droseraceae*) is even more intricate, with leaves specially modified with traps that spring shut when an insect lands or walks on them. There is even an aquatic carnivore, the bladderwort (*Utricularia*), which has saclike leaves with small openings that can close after a small aquatic insect or crustacean is sucked in. Although insectivorous plants do obtain some of their nutrients from insects, they also obtain nutrients from the soil or, in the case of bladderworts, surrounding water.

Angiosperm Classification

Traditionally *Anthophyta* has either been considered as a single class *Angiospermae* or *Magnoliopsida*, with two subclasses, or has been divided into two classes, *Eudicotyledones,* or *Magnoliopsida*, and *Monocotyledones*, or *Liliopsida*. The second of these two options is more commonly accepted by contemporary plant taxonomists, and the two classes are often referred to by the common names dicotyledons or dicots and monocotyledons or monocots, respectively.

The monocot/dicot dichotomy has long been considered a major evolutionary split in the angiosperms. The two classes a differ from each other in a number of ways. Monocots generally have bladelike leaves with parallel venation, whereas dicots more typically have pinnate or palmate venation. Monocots have fibrous root systems without taproots; dicots typically have taproots. The flower parts in monocots occur typically in threes, whereas they occur most often in fours and fives in dicots. Monocots lack cambial secondary growth, which is common in dicots. Monocots have scattered vascular bundles in their stems, as opposed to the more orderly arrangement seen in dicot stems.

It has long been proposed that the monocots branched off from the dicots very early in the evolution of the angiosperms, but until recently it was difficult to sort out the probable events and the resulting classification system that would be needed to reflect them. With the advent of molecular tools, such as deoxyribonucleic acid (DNA) sequencing, the study of early angiosperm evolution is getting much more attention. It has now become clear that, if the classification system is to reflect evolutionary history, *Anthophyta* must be divided into more than just two classes. Currently there is no agreement on how many other classes there should be, but *Monocotyledones* and *Eudicotyledones* will retain most of the taxa. This new approach to the classification of *Anthophyta* has also resulted in changing the common name of the "dicots" to "eudicots," meaning "true dicots."

Many of the remaining taxa not included in the monocots or eudicots are now often referred to as *magnoliids* and are considered to represent taxonomic groups that have branched off from the early angiosperms before the monocot/eudicot split. Some of these groups include the orders *Magnoliales* (which includes *Magnoliaceae*, long considered as having many primitive characteristics), *Winterales*, and *Laurales*. The placement of a few taxa, such as *Ceratophyllaceae* and *Chloranthaceae*, is particularly controversial. With continued analyses of DNA sequences it is hoped that a clearer picture of the relationships among the magnoliids and related taxa will be obtained and a more phylogenetically based classification system can be devised.

Bryan Ness

See also: Angiosperm evolution; Angiosperm life cycle; Angiosperm plant formation; Biochemical coevolution in angiosperms; Cacti and succulents; Carnivorous plants; Eudicots; Flower structure;

Flower types; Fruit: structure and types; Garden plants: flowering; Germination and seedling development; Grasses and bamboos; Growth habits; Inflorescences; Legumes; Medicinal plants; Monocots vs. dicots; *Monocotyledones*; Orchids; Parasitic plants; Pollination; Reproduction in plants.

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ANIMAL-PLANT INTERACTIONS

Categories: Animal-plant interactions; ecology; ecosystems; evolution

The ways in which certain animals and plants interact have evolved in some cases to make them interdependent for nutrition, respiration, reproduction, or other aspects of survival.

Ecology represents the organized body of knowledge that deals with the relationships between living organisms and their nonliving environments. Increasingly, the realm of ecology involves a systematic analysis of plant-animal interactions through the considerations of nutrient flow in *food chains* and *food webs*, exchange of such important gases as oxygen and carbon dioxide between plants and animals, and strategies of mutual survival between plant and animal species through the processes of *pollination* and *seed dispersal*.

A major example of animal-plant interactions involve the continual processes of photosynthesis and cellular respiration. Green plants are classified as ecological *producers*, having the unique ability, by photosynthesis, to take carbon dioxide and incorporate it into organic molecules. Animals are classified as *consumers*, taking the products of photosynthesis and chemically breaking them down at the cellular level to produce energy for life activities. Carbon dioxide is a waste product of this process.

Mutualism

Mutualism is an ecological interaction in which two different species of organisms beneficially reside together in close association, usually revolving around nutritional needs. One such example is a small aquatic flatworm that absorbs microscopic green algae into its tissues. The benefit to the animal is one of added food supply. The mutual adaptation is so complete that the flatworm does not actively feed as an adult. The algae, in turn, receive adequate supplies of nitrogen and carbon dioxide and are literally transported throughout tidal flats in marine habitats as the flatworm migrates, thus exposing the algae to increased sunlight. This type of mutualism, which verges on parasitism, is called *symbiosis*.

Coevolution

Coevolution is an evolutionary process wherein two organisms interact so closely that they evolve together in response to shared or antagonistic selection pressure. A classic example of coevolution involves the yucca plant and a species of small, white moth (*Tegitecula*). The female moth collects pollen grains from the stamen of one flower on the plant and transports these pollen loads to the pistil of another flower, thereby ensuring cross-pollination and fertilization. During this process, the moth will lay her own fertilized eggs in the flowers' undeveloped seed pods. The developing moth larvae have a secure residence for growth and a steady food supply. These larvae will rarely consume all the developing seeds; thus, both species (plant and animal) benefit.

Corbis

Nonsymbiotic mutualism, one kind of animal-plant interaction, can be demonstrated in the often unusual shapes and colorations that flowering plants have developed to attract birds, such as this hummingbird, as well as insects and mammals, for pollination and seed dispersal purposes.

Although this example represents a mutually positive relationship between plants and animals, other interactions are more antagonistic. *Predator-prey relationships* between plants and animals are common. Insects and larger herbivores consume large amounts of plant material. In response to this selection pressure, many plants have evolved *secondary metabolites* that make their tissues unpalatable, distasteful, or even poisonous. In response, herbivores have evolved ways to neutralize these plant defenses.

Mimicry and Nonsymbiotic Mutualism

In *mimicry*, an animal or plant has evolved structures or behavior patterns that allow it to mimic either its surroundings or another organism as a defensive or offensive strategy. Certain types of insects, such as the leafhopper, walking stick, praying mantis, and katydid (a type of grasshopper), often duplicate plant structures in environments ranging from tropical rain forests to northern coniferous forests. Mimicry of their plant hosts affords these insects protection from their own predators as well as camouflage that enables them to capture their own prey readily. Certain species of ambush bugs and crab spiders have evolved coloration patterns that allow them to hide within flower heads of such common plants as goldenrod, enabling them to ambush the insects that visit these flowers.

In *nonsymbiotic mutualism*, plants and animals coevolve morphological structures and behavior patterns by which they benefit each other but without living physically together. This type of mutualism can be demonstrated in the often unusual shapes, patterns, and colorations that more advanced flowering plants have developed to attract various insects, birds, and mammals for pollination and seed dispersal purposes. Accessory structures, called fruits, form around seeds and are usually tasty and brightly marked to attract animals for seed dispersal. Although the fruits themselves become biological bribes for animals to consume, often the seeds within these fruits are not easily digested and thus pass through the animals' digestive tracts unharmed, sometimes great distances from the parent plant. Some seeds must pass through the digestive plant of an animal to stimulate germination. Other types of seed dispersal mechanisms involve the evolution of hooks, barbs, and sticky substances on seeds that enable them to be easily transported by animal fur, feet, feathers, or beaks. Such strategies of dispersal reduce competition between the parent plant and its offspring.

Pollinators

Because structural specialization increases the possibility that a flower's pollen will be transferred to a plant of the same species, many plants have evolved a vast array of scents, colors, and nutritional products to attract *pollinators*. Not only does pollen include the plant's sperm cells; it also represents a food reward. Another source of animal nutrition is a substance called nectar, a sugar-rich fluid produced in specialized structures called nectaries within the flower or on adjacent stems and leaves. Assorted waxes and oils are also produced by plants to ensure plant-animal interactions. As species of bees, flies, wasps, butterflies, and hawkmoths are attracted to flower heads for these nutritional rewards, they unwittingly become agents of pollination by transferring pollen from stamens to pistils.

Some flowers have evolved distinctive, unpleasant odors reminiscent of rotting flesh or feces, thereby attracting carrion beetles and flesh flies in search of places to reproduce and deposit their own fertilized eggs. As these animals copulate, they often become agents of pollination for the plant itself. Some tropical plants, such as orchids, even mimic a female bee, wasp, or beetle, so that the insect's male counterpart will attempt to mate with them, thereby encouraging precise pollination.

Among birds, hummingbirds are the best examples of plant pollinators. Various types of flowers with bright, red colors, tubular shapes, and strong, sweet odors have evolved in tropical and temperate regions to take advantage of hummingbirds' long beaks and tongues as an aid to pollination. Because most mammals, such as small rodents and bats, do not detect colors as well as bees and butterflies do, some flowers instead focus upon the production of strong, fermenting, or fruitlike odors and abundant pollen rich in protein. In certain environments, bats and mice that are primarily nocturnal have replaced day-flying insects and birds as pollinators.

Thomas C. Moon, updated by Bryan Ness

See also: Parasitic plants; Trophic levels and ecological niches.

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ANTARCTIC FLORA

Categories: Ecosystems; world regions

The harsh climate of Antarctica makes it one of the most inhospitable places on the earth, allowing only a relatively small number of organisms to live there. Permanent terrestrial (land) animals and plants are few and small. There are no trees, shrubs, or vertebrate land animals. Native organisms are hardy, yet the ecosystem is fragile and easily disturbed by human activity, pollution, global warming, and ozone layer depletion.

The Antarctic continent has never had a native or permanent population of humans. In 1998 the United States, Russia, Belgium, Australia, and several other countries signed one of an ongoing series of treaties to preserve Antarctica. The continent is used for peaceful international endeavors such as scientific research and ecotourism.

Terrestrial Flora

There are only two types of flowering plants in Antarctica, a grass and a small pearlwort (*Deschampsia antarctica*). These are restricted to the more temperate Antarctic Peninsula. Antarctic hairgrass (*Colobanthus quitensis*) forms dense mats and grows fairly rapidly in the austral summer (December, January, and February). At the end of summer, the hairgrass's nutrients move underground, and the leaves die. Pearlwort forms cushion-shaped clusters and grows only 0.08 to 0.25 inch (2 to 6 millimeters) per year.

Numerous species of primitive plants, such as lichens, mosses, fungi, algae, and diatoms, live in Antarctica. *Lichens* are made up of an alga and a fungus in a symbiotic (interdependent) relationship. They can use water in the form of vapor, liquid, snow, or ice. Lichens grow as little as 0.04 inch (1 millimeter) every one hundred years, and some patches may be more than five thousand years old. Mosses are not as hardy as lichens and also grow slowly; a boot print in a moss carpet may be visible for years. Fungi are found in the more temperate peninsula, and most are microscopic.

Algae grow in Antarctic lakes, runoff near bird colonies, moist soil, and snow fields. During the summer, algae form spectacular red, yellow, or green patches on the snow. Bacteria are found in lakes, meltwater, and soils. As elsewhere on the earth, bacteria play a role in decomposition. Because of the extreme conditions, they are not always as efficient in Antarctica as they are in warmer climates, and carcasses may lie preserved for hundreds of years.

Kelly Howard

See also: Arctic tundra.

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AQUATIC PLANTS

Categories: Economic botany and plant uses; *Plantae*; water-related life

Aquatic plants are any "true" plants, members of the kingdom Plantae*, that are able to thrive and complete their life cycle while in water, on the surface of water, or on hydric soils.*

Hydric soils develop when the ground is flooded or ponded long enough during the growing season to become anaerobic (depleted of oxygen) in the rooting zone. These soils include organic (peats and mucks) and inorganic (mineral) sediments. Aquatic plants grow in fresh, brackish, and salt water but are most common in fresh water. Their habitats include flowing waters (rivers, streams, brooks), standing waters (lakes, ponds), and *wetlands* (bogs, fens, marshes, swamps), which are categorized as *riverine*, *lacustrine*, and *palustrine* communities, respectively. Wetland plants are sometimes referred to as *helophytes*. Marshes are dominated (that is, more than half covered) by herbaceous species and swamps by woody species. Bog plants are aquatics that grow in acidic organic soils. Fen plants occur in alkaline organic soils.

Aquatic plants (also known as *hydrophytes*, *macrophytes*, and *water plants*) occur throughout the plant kingdom. The term "macrophyte" distinguishes them from microscopic aquatic algae, which are not true plants. Aquatic plants have evolved repeatedly, having more than 250 independent origins by some estimates. They occur occasionally in spore-producing plants such as ferns, liverworts, lycopods, and mosses but are relatively rare among nonflowering seed plants (gymnosperms), with bald cypress (*Taxodium*) a notable exception. Flowering plants (angiosperms) contain the greatest hydrophyte diversity, with more species proportionally in monocotyledons than in dicotyledons. Nevertheless, fewer than 2 percent of flowering plant species are aquatic.

Life-Forms

Regardless of their taxonomic affinities, aquatic plants are often classified ecologically by their life-forms. Categories include the following:

- Floating (*acropleustophytes*), with stems and leaves floating completely on the water surface and stems not rooted in the bottom, such as duckweed (*Lemna*) and water hyacinths (*Eichhornia*).
- Emergent (*hyperhydrates*), with stems and leaves extending mainly above the water surface and stems rooted in the bottom, such as cattails (*Typha*) and reeds.
- Phragmites (*planmergents* or *ephydrates*), floating-leaved, with some or all leaves floating on the water surface and stems rooted in the bottom, such as floating-leaved pondweed (*Potamogeton natans*), water chestnut (*Trapa natans*), and water lily (*Nymphaea*).
- Submersed (*hyphydrates*), with stems and leaves completely under water and stems rooted in the bottom, such as Eurasian water milfoil (*Myriophyllum spicatum*) and wild celery (*Vallisneria*).
- Suspended (*mesopleustophytes*), with stems and leaves completely under water and stems not rooted in the bottom, such as the bladderwort (*Utricularia vulgaris*) and the coontail (*Ceratophyllum*).

Benthophyte and *pleustophyte* are used respectively to differentiate between forms that are either rooted in the substrate or unrooted. Species with elongate, leafy stems are termed *vittate* or *caulescent* (such as coontail). Those with leaves clustered in a basal rosette are *rosulate* (such as wild celery), and those not clearly differentiated into stems and leaves are *thalloid* (such as duckweed). Species whose floating or emergent leaves differ morphologically from their submersed leaves are *heterophyllous* (such as floating-leaved pondweed).

Adaptations

Water plants are anatomically and structurally reduced. Watermeal (*Wolffia*), the world's smallest angiosperm, contains plants only 0.4 millimeter long. Submersed species often lack water-conducting tissue (xylem), mechanical tissue (sclerenchyma), and cuticle. Some lack roots entirely. Support and floatation of underwater stems are accommodated by buoyant tissue (aerenchyma) and extensive air spaces (lacunae) which also transport oxygen throughout the plant. Submersed plants usually possess either highly dissected (compound) or thin, ribbonlike leaves. Some leaves become fenestrate, that is, lacking tissue between the veins. Such leaf shapes increase surface area-to-volume ratios for more efficient nutrient uptake and to reduce damage from water currents.

Floating leaves are normally flat and circular, with stomata on their upper surfaces. They may reach 2.5 meters in diameter (such as *Victoria*). For stability, the stalks (petioles) of most floating leaves are positioned centrally by emargination of the base, as in the water lily, or are peltate by complete fusion of leaf lobes, as in the water shield (*Brasenia*) and *Victoria*. Physiological adaptations enable aquatic plants to tolerate deleterious effects of anaerobic hydric soils.

Reproduction

Most aquatic plants are perennials that reproduce vegetatively (asexually). Species survive winters or other unfavorable periods as intact plants, by dying back to dormant stem apices, by means of modified stems (rhizomes, stolons, tubers), or by use of specialized dormant structures (*hibernacula*) in the sediment. "Winter buds" are a kind of hibernaculum; buds are insulated by normal foliage leaves on shortened internodes. They usually remain attached to the plant. *Turions* are specialized hibernacula that produce modified, morphologically distinct leaves to protect the enclosed buds. Turions always detach from the plant and function as propagules for dispersal. Water plants also disperse vegetatively by fragmentation of stems, which are characteristically brittle, due to the lack of mechanical tissue. Detached stems can establish themselves by production of adventitious roots.

The few aquatic plants that are annuals produce seeds as their dormant stage. Some aquatic annuals also multiply vegetatively by fragmentation during the growing season. Generally, sexual reproduction is rare in submersed species, more common in floating-leaved species, and quite common in emergent species (and annuals).

Pollination in water plants is facilitated by insects (entomophily), wind (anemophily), and water (hydrophily). Most aquatics are insect-pollinated; about one-third of them are wind-pollinated. Less than 5 percent of aquatic species are hydrophilous, with pollen transported on the water surface (ephydrophily) or under the water surface (hyphydrophily). Most marine angiosperms (seagrasses) are hydrophilous.

Seeds, fruits, and vegetative propagules are dispersed locally by water currents and more widely by waterfowl. Waterfowl transport propagules in plumage, in mud adhering to their feet, and by excretion of seeds consumed as food. Many water plants are distributed broadly, with some species achieving worldwide distributions.

NOAA/National Estuarine Research Reserve Archive

A freshwater pond with large water lilies near Charleston, South Carolina.

Uses

Aquatic plants are important economically. Foods include rice (*Oryza sativa*), which sustains more human life than any other plant on earth. Aquatic plants are important horticulturally as aquarium and water-garden ornamentals. Some aquatic plants, such as the water hyacinth, are invasive weeds that interfere with shipping, irrigation, or recreation and cost millions of dollars to eradicate. The beauty of many water plants, especially water lilies, has inspired art and religion since ancient times.

Donald H. Les

See also: Adaptations; Angiosperm evolution; Angiosperms; Eutrophication; Invasive plants; Marine plants; Peat; Pollination; Rice; Wetlands.

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ARCHAEA

Categories: Bacteria; evolution; paleobotany; taxonomic groups

The domain Archaea *represents a diverse group of prokaryotes originally found in environments once considered to be hostile to life, now known to be widely distributed in nature.*

The cycling of plant nutrients, such as carbon, nitrogen, and sulfur, requires the activity of microorganisms that convert these elements to forms readily available to plants. These microorganisms, which are generally found in both soil and water, include both prokaryotic organisms of the domain *Bacteria* and the domain of prokaryotes called *Archaea*, which play significant roles in nutrient cycling. Along with *Eukarya*, to which protists, fungi, plants, and animals belong, the *Archaea* form one of the three domains of life. The *Archaea* are related to both *Bacteria* and *Eukarya* and, in some respects, appear to be more closely related to *Eukarya*. Biochemical and genetic studies, including information obtained from whole genome sequencing, suggest that *Archaea* may be closely related to an ancestor that gave rise to both *Bacteria* and *Eukarya*. Thus, *Archaea* may provide some insight into the processes that resulted in the evolution of higher lifeforms, including plants and animals.

A Third Domain

For more than fifty years, biologists categorized living organisms into two groups based on their cellular organization and complexity: prokaryotes (originally all classified in kingdom *Monera*), the single-celled organisms whose chromosomes are not compartmentalized inside a nucleus (which include the domain *Bacteria*), and eukaryotes, consisting of all other organisms, whose cells contain a nucleus. In the late 1970's studies on a unique group of microorganisms led investigators to question the accepted classification of prokaryotes. Originally called *Archaebacteria* by molecular biologist Carl Woese and his colleagues in 1977, these microorganisms were isolated from environments characterized by extremes in heat, acidity, pressure, or salinity, and many were found to be able to utilize sulfur and molecular hydrogen as part of their growth process.

Like all prokaryotes, *Archaea* do not have a nucleus. However, in their biochemistry and the structure and composition of their molecular machinery, they are as different from bacteria as they are from eukaryotes. Woese and his colleagues analyzed and compared specific molecules of ribonucleic acid (RNA) present within the ribosome in all organisms, called *ribosomal RNA* (rRNA). Their findings suggested that all extant life is composed of three distinct groups of organisms: the eukaryotes, or domain *Eukarya*, which includes plants and animals, and two different prokaryotes, domains *Bacteria* and *Archaea*. In 1990 Woese and others recommended the replacement of the simple prokaryote/eukaryote view of life with a new tripartite scheme based on three domains: the *Bacteria*, *Archaea*, and *Eukarya*. Since 1990 the three-domain classification has been the subject of considerable debate, and as a consequence, both old and new terminology are used in scientific and popular literature.

Characteristics

Generally, the size and shape of *Archaea* are similar to those of *Bacteria*. They are single-celled microscopic organisms that, in some cases, are motile (capable of self-movement) and may be found in chains or clusters. *Archaea* multiply in the same manner as bacteria: via *binary fission*, budding, or fragmentation. Like *Bacteria*, archaeal chromosomes are circular, indicating the absence of breaks or discontinuities, and many genes are organized in the same fashion as those found in *Bacteria*. On the other hand, the specific chemical composition of *Archaea* plasma membranes and cell walls is unique to the *Archaea* and is quite different from the composition of these structures typically found in either *Bacteria* or *Eukarya*. In fact, the distinctive ether-linked isoprenoid lipids that compose the external membranes of *Archaea* are a hallmark of these microorganisms.

Another unique characteristic of *Archaea* is the composition of the molecular genetic machinery, which is a mosaic of the components found in *Bacteria* and *Eukarya*. For example, the ribosomes (which are responsible for protein synthesis) of *Archaea* resemble the ribosomes of *Bacteria* in shape and composition and are distinct from the ribosomes of *Eukarya*. On the other hand, the enzyme utilized by *Archaea* in the production of RNA, namely RNA polymerase, is quite different from the enzyme found in *Bacteria*. In *Bacteria*, RNA polymerase molecules are composed of four major proteins, while in the *Archaea*, RNA polymerase molecules consist of more than ten proteins and are surprisingly similar to the enzyme found in *Eukarya*. In fact, archaeal RNA polymerase is so similar to the eukaryotic enzyme that combining certain proteins from both archaeal and eukaryotic sources results in a functional enzyme, a manipulation that is not possible with any bacterial RNA polymerases.

Among species of the *Archaea*, there is a variety of metabolic processes that differ greatly from the better-known metabolic routes of *Bacteria* and *Eukarya*. Many of the archaeal pathways used to convert food sources to energy and building blocks for growth involve enzymes having biological activities not found in any other biological systems. In some cases, the enzymes require the involvement of rare metals, such as tungsten. While a requirement for metals in the activity of many bacterial and eukaryotic enzymes is ubiquitous, the use of tungsten appears to be unique to *Archaea*.

Diversity

A fascinating feature of *Archaea* is that they are found in niches that support the growth of few other organisms. These include highly reduced (oxygen-free) environments or very high-temperature environments found near hot springs or undersea hydrothermal vents as well as sites that are sulfur-rich and highly acidic. *Archaea* are also found in highly saline marine environments and hypersaline lakes where the salinity is as much as ten times that in seawater.

Based on the comparison of ribosomal RNA sequences as well as physiological and metabolic characteristics, the *Archaea* have been divided into three subdomains: *Euryarchaeota*, *Crenarchaeota*, and *Korarchaeota*. The *Euryarchaeota* includes members of the *methanogenic* (methane-producing) and halophilic (salt-requiring) *Archaea* as well as many that grow at very high temperature, the thermophilic and extremely thermophilic, or hyperthermophilic, *Archaea*. Representatives of hyperthermophilic *Archaea* are found in the *Crenarchaeota*, which also includes cold-dwelling *Archaea* that have been isolated in association with certain marine sponges. The *Korarchaeota* also includes hyperthermophilic

Archaea, although these were not isolated or characterized as of 2001, but whose presence in hot spring and deep-sea samples has been identified by molecular biological techniques.

Methanogenic *Archaea*

Methane-producing *Archaea* are found in strictly anaerobic environments. They have no tolerance for oxygen: Trace amounts are inhibitory for growth, and too much is lethal. These *Archaea* obtain energy for growth by a process called *methanogenesis*, which results in the conversion of carbon dioxide to methane gas.

Methane production requires several enzymes that use coenzymes unique to methanogenic *Archaea*. The production of methane is of great importance to carbon cycling in many anaerobic environments, and microorganisms that produce this gas have been known for centuries. In 1776 the scientist Alessandro Volta demonstrated that air generated from sediments rich in decaying vegetation, such as those present in bogs, streams, and lakes, could be ignited. It is now known that methanogenic *Archaea* are responsible for generating this "marsh gas."

Because methanogens require an oxygen-free environment for growth, they are found only where carbon dioxide and hydrogen are available and oxygen has been excluded. Thus, methanogens thrive in stagnant water, natural wetlands, paddy fields, and in the rumen of cattle and other ruminants as well as in the intestinal tracts of animals and the hindguts of cellulose-digesting insects, such as termites. Methanogens are also found in hot springs and the deep ocean and are major components of the anaerobic process in waste treatment facilities. It has been estimated that production of methane by the methanogenic *Archaea* may account for almost 90 percent of the total methane released into the atmosphere each year. In addition to playing a role in carbon cycling, several methanogenic *Archaea* are also involved in nitrogen cycling, as they are able to convert molecular nitrogen into organic nitrogen via nitrogen fixation, a process that is shared by only a few prokaryotes.

Thermophilic *Archaea*

Thermophilic *Archaea* live in environments ranging in temperature from 55 degrees Celsius (131 degrees Fahrenheit) to 80 degrees Celsius (176 degrees Fahrenheit). Hyperthermophilic *Archaea* grow at temperatures near or greater than the boiling point of water and as high as 113 degrees Celsius (235 degrees Fahrenheit). These *Archaea* have been isolated from hot sulfur springs, sulfur-laden mud at the base of volcanoes, and near very hot deep-sea hydrothermal vents where superheated water is emitted at very high temperatures under pressure. Species that can use oxygen, as well as those that have no tolerance for oxygen, are known. Many of the anaerobic representatives obtain energy for growth by the metabolism of elemental sulfur.

In addition, many are found in environments that are extremely acidic, including those that are members of *Thermoplasmatales*. This group is noted for its ability to grow at a pH of 2.0 and below (on a scale where pH 7.0 is neutral), which is equivalent to the acid in car batteries. A representative is *Thermoplasma*, which does not possess a cell wall but has


PhotoDisc

Hyperthermophilic Archaea *grow at temperatures as high as 113 degrees Celsius.* Archaea *have been isolated from hot sulfur springs, such as those at Yellowstone National Park.*

a chemically unique structure composed of a lipid-polysaccharide (tetraether lipid with mannose and glucose units) that is distinctly different from the unusual ether-linked lipids found in the membrane components of typical *Archaea*.

Halophilic *Archaea*

The salt-dependent halophilic *Archaea* require extremely high concentrations of salt for survival, and some grow readily in saturated brine, where the salt concentration reaches 32 percent (in seawater it is approximately 3.5 percent) and where very alkaline conditions are not uncommon. Halophilic *Archaea* are found in salty habitats along ocean borders and inland waters such as the Dead Sea and the Great Salt Lake.

The reddish-purple color observed in salt evaporation ponds is due to production of red- and orange-colored carotenoids and other pigments associated with the massive growth of halophilic *Archaea*.

Some halophilic *Archaea* are capable of harvesting light to provide energy for growth by a mechanism that does not involve chlorophyll pigments. Light harvesting by these halophilic *Archaea* is done by a membrane-bound protein called *bacteriorhodopsin* that is equivalent to the mammalian eye pigment *rhodopsin* in both function and structure. Bacteriorhodopsin contains retinal, a purple carotenoidlike molecule used for light trapping. Interestingly, retinal is produced via a pathway that contains many of the same enzymes used for the production of lycopene by tomatoes during ripening.

Window to the Past

The extreme conditions in which *Archaea* are found suggests that these organisms have adapted to environments thought to exist during early life on earth, three billion to four billion years ago. Thus, the *Archaea* might be considered as a window into the past, and they may shed light on the processes involved in evolution as well as their relationships with *Bacteria* and *Eukarya*. In order to survive in their unique environments, *Archaea* possess molecules that withstand heat or cold, acids, salt, and in some cases, pressure—characteristics that are tailor-made for specific applications in molecular biology and biotechnology.

Uses

A number of important applications have been developed as a consequence of studying the *Archaea*. These include the identification of heat-stable enzymes for analyses used in genetic fingerprinting and cancer detection (certain polymerase chain reaction enzymes), the use of halophilic pigments for holographic applications, optical signal processing and photoelectric devices, and methanogenesis as an alternative fuel source.

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See also: Bacteria; Biotechnology; Carbon cycle; DNA in plants; Environmental biotechnology; *Eukarya*; Eukaryotic cells; Molecular systematics; Nitrogen cycle; Nitrogen fixation; Nucleus; Photorespiration; Prokaryotes; Ribosomes; RNA.

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ARCTIC TUNDRA

Category: Biomes

The Arctic tundra is a biome representing the northernmost limit of plant growth on earth. Arctic tundra has a circumpolar distribution in the Northern Hemisphere, extending from the ice cap southward to the forested taiga of North America, Europe, and Asia. Tundra is also found on islands within the Arctic Ocean and along coastal Greenland.

The term "tundra" was derived from the Finnish word for a treeless or barren landscape. The Arctic tundra biome is located within one of the harshest climates on earth for plant growth, with winter temperatures averaging –34 degrees Celsius (–30 degrees Fahrenheit). The climate is comparatively dry, with annual precipitation of 150 to 250 millimeters (6 to 10 inches). Locked in snow or frozen within soil, the majority of moisture is not available for plant use.

In addition to surviving extreme temperatures and dry conditions, plants must adapt to seasonal variation in available sunlight; winter nights, for example, last twenty-four hours. The tundra's growing season is very short, extending over only about sixty days. Continuous sunlight during warmer months, July and August, contributes to the productivity of tundra plant communities that can yield 227-454 kilograms (500-1,000 pounds) of vegetation per acre. This *biomass* serves as an important food source for caribou, musk ox, and migratory waterfowl. Tundra vegetation is made up of *herbaceous* plants (grasses, forbs, and sedges), mosses, lichens, and shrubs that grow close to the ground, where temperatures are highest. By providing an insulating layer, snowfall is advantageous for tundra plants during cold winter months.

Herbaceous Plants

Rushlike tundra sedges belong to the flowering plant family *Cyperacaeae*. Common to the tundra, cottongrass is really a sedge within the genus *Eriophorum*. Perennial forbs are broadleaf plants that survive winter months as bulbs that are protected below the ground level. During warm months the plants begin to grow rapidly and will develop flowers and seeds when temperatures climb above 10 degrees Celsius (50 degrees Fahrenheit).

Lichens and Low-Growing Shrubs

Acting as a single organism, pioneering lichens growing on rock surfaces represent a symbiotic relationship between fungi and algae. The fungi anchor to the rock, absorbing water directly into their cells, while the algae occupy this moist area, creating food through photosynthesis that is shared with the fungi. Tundra lichens are found in fruiticose (stalklike), crustose (crustlike), or foliose (leaflike) forms.

The heath (*Ericaceae*) family includes several species of shrub, many of which have tough, evergreen leaves. Examples include rhododendron, cranberry, blueberry, and Labrador tea. Another heath, the alpine azalea (*Loiseleuria procumbens*), forms a mat or cushion where several plants clump tightly together.

Adaptations

In many ways tundra vegetation must adapt to many of the same environmental conditions as *grasslands* or *deserts*, such as little precipitation, strong winds, and extreme temperature variations. As a result of the brief growing season, plant reproduction in the tundra must take place rapidly. Other adaptations include compact plant size that protects from cold temperatures, hairy stems that help retain heat, and dark-colored leaves that absorb sunlight. Some plants have hollow stems that require fewer nutrients to grow. A unique adaptation made by the Arctic poppy (*Papaver radicatum*) and mountain aven (*Dryas integrifolia*) allows them to orient their flowers to track the sun's movement across the sky, maximizing solar radiation received.

Although sunlight is usually beneficial to plant growth, some plants such as Arctic algae must implement protective measures to avoid damage from ultraviolet radiation. The green alga *Ulva rigida*, also called sea lettuce, produces amino acids and carotenoid pigments that absorb harmful radiation. Cushion plants grow in tight but low-profile clumps, forming windbreaks that protect them from the cold, and may trap airborne dust and soil used as a source of nutrients. Many tundra plants are capable of carrying out photosynthesis under relatively low light intensities. With short growing seasons, some plants reproduce by budding and division instead of by the creation of seeds. Plants may also store nutrients in *rhizomes*, underground stems that survive after root systems die.

Edaphic Influences

Soils of the tundra are principally thin soils (inceptisols). Contributing to the lack of soil development are cold temperatures that inhibit the growth of soil-producing organisms such as bacteria. The tundra's treeless plain may be interrupted by patterned ground made up of stone polygons, soil circles, or soil stripes. These unusual features are formed by the thrusting action of repeated freezing and thawing in soil that overlies rock or permanently frozen ground called *permafrost*. Impenetrable permafrost that inhibits root system development, rather than cold temperatures, is thought to be responsible for the lack of tree growth in the tundra. Warmer summer temperatures lead to a thaw in permafrost that extends only about a meter below the surface. Ponds and boggy areas form in places where soil above the permafrost melts and cannot move downward, creating a source of moisture for plants.

Environmental Concerns

As a result of growing under harsh conditions, tundra plants are slow to recover from disturbances. Vehicles can destroy tundra plants. Other concerns include oil spillage, damage caused by pipeline construction, and other impacts tied to petroleum production.

Thomas A. Wikle

See also: Adaptations; Antarctic flora; Asian flora; Biomes: definitions and determinants; Biomes: types; European flora; North American flora; Tundra and high-altitude biomes.

Image Not Available

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ASCOMYCETES

Categories: Economic botany and plant uses; fungi; microorganisms; taxonomic groups

The ascomycetes are fungi (phylum Ascomycota *or* Ascomycotina*) that produce sexual spores in a specialized cell called an ascus. These diverse fungi, with more than thirty thousand species, can be found in almost every ecosystem worldwide. One of the most famous members of the ascomycetes is the truffle.*

Ascomycetes, one of the four phyla of the fungus kingdom, by definition possess an *ascus*, a single cell inside of which sexual spores are produced. The reproductive process has been well documented and occurs when the *dikaryotic mycelium* (the mass of hyphae forming the body) undergoes changes that precede the formation of the ascus. Dikaryotic is the genetic state in which two haploid nuclei are present in the cell. One nucleus is donated by each parent.

The first change occurs when the end cell of a hyphal strand begins to form a small bend. The cell divides into three cells; the outer two cells are haploid, and the middle cell is dikaryotic. The middle cell then elongates, and the nuclei migrate into its center. The two haploid nuclei then fuse to form a single diploid nucleus, which undergoes mitosis and meiosis to form eight haploid nuclei. Cell walls form around the nuclei producing eight haploid *ascospores*. The ascospores are then liberated from the ascus.

The ascus wall determines the kind of dispersal of the spores. Some asci have a thin, single-layer wall, which breaks down to liberate spores. *Unitunicate* asci have a multilayer cell wall with a pore at the end of the ascus. Spore release is active through the pore. *Bitunicate* asci have multilayer cell walls, and release of spores is by the separation of the layers of the cell wall, with the inner layer inflating to several times its normal size and then lifting off of the ascus, allowing the spores to be released. The spores are released into the environment, where they germinate and produce haploid hyphae. The haploid hyphae fuse with compatible haploid hyphae, forming dikaryotic hyphae, and the process begins to repeat itself.

There are five different ways in which asci are formed in nature. First, asci can be produced by exposure to the environment, as are the asci of yeasts or the ascus of the peach leaf-curl pathogen *Taphrina deformans*. With these fungi, the ascospores are released by the breakdown of the ascus wall.

The other four ways of production of asci all take place inside structures made from mycelium, called *ascocarps*. These structures range from totally closed to open, like a cup. The totally closed ascocarps are called *cleistothecia*. Within these, the asci are scattered, and the spores are released by breakdown and decomposition of the fungal tissue.

Ascomycetes as Pathogens

Some members of the ascomycetes are very important plant and animal pathogens, causing serious diseases. One of the more impressive plant pathogens is the ergot fungus (*Claviceps purpurea*). This fungus colonizes the ovaries of grains, such as rye (*Secale cereale*). It produces a mass of mycelium, called a *sclerotium*, which is hard and has a density similar to that of a seed. Because of this, the sclerotia are often found in the threshed grain. Sclerotia contain an accumulation of alkaloids and other secondary metabolites. When the sclerotia are ground into flower and baked into bread, many of these secondary metabolites are passed into the bread. During the Middle Ages this fungus was responsible for a human disease called St. Anthony's Fire. Today, this fungus is used for the natural production of a coagulant which is used in medicine.

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Another group of plant pathogens are the powdery mildews. There are several hundred species of these fungi, which produce a powdery spore mass on the outer surfaces of plant leaves. If a leaf is infected before it has expanded, it will remain small and puckered and may drop from the plant. The powdery mildews are superficial and send hyphae through the leaf cuticle into the epidermis. The fungus then grows over the surface of leaf, giving it a powdery appearance. During the winter, the fungus produces cleistothecia on the surface of the leaf. Powdery mildew can occur on most plant species and can be very damaging to crop and ornamental plants.

Economic Uses

Truffle is a generic term for fungi that form mycorrhizae (a symbiotic association) with the roots of various trees. The fungus grows into the roots and helps the plant tolerate stress, providing the plant with increased absorption of phosphorus from the soil. In return, the plant gives the fungus metabolites that it needs for growth. These fungi then produce fruiting bodies, either in the soil or upon the surface of the soil. The truffles are produced in the soil up to a depth of 1 foot.

Truffles can be located in the soil using a trained sow or dog that is able to sniff out the volatile chemicals that are produced. However, it is important to note that edible fungi such as truffles can often be mistaken for highly toxic fungi and should never be gathered or eaten without expert identification. Truffles are used as condiments and are able to impart unique aromas and sensations to food. They are shaped like small balls, varying in size from that of a pea to that of a golf ball. Truffles are only produced in nature and therefore fetch high prices. The price of truffles depends on the species, size, and freshness. Prices of the famous French Black Périgord truffle (*Tuber melanosporum*) can reach into thousands of dollars per kilogram (2.2 pounds). In the United States, the Oregon white truffle is quite appealing and can be found in the Pacific Northwest.

Morels (*Morchella*) are another choice edible ascomycete. Shaped like a little hat sitting upon a stalk, they are brown in color and have an appealing aroma. They add flavor to any food and are a favorite of many wild animals.

Scientific Uses

Some members of the ascomycetes are used for genetic studies. Such is the case for *Neurospora*, a common fungus found growing on soil and organic matter and one of the first organisms to be found in an area after a fire. As with all ascomycetes, there are two compatible mating types, which makes for easy genetic study. Using spore characteristics of shape, color, and texture, it is possible to see how mitosis and meiosis occur in the ascus by determining the placement of the spores. The fungus is readily mutated, which further enhances genetic study.

J. J. Muchovej

See also: *Basidiomycetes*; Basidiosporic fungi; Chytrids; Deuteromycetes; Fungi; Lichens; Mitosporic fungi; Mushrooms; Mycorrhizae; Yeasts; Zygomycetes.

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ASIAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

Land constraints and growing population and urbanization throughout Asia underscore the need for environmentally sound technologies to sustain agricultural growth.

The first agricultural revolution occurred in Asia and involved the domestication of plants and animals. It is believed that *vegeculture* first developed in Southeast Asia more than eleven thousand years ago. In vegeculture, a part of a plant—other than the seed—is planted for reproduction. The first plants domesticated in Southeast Asia were taro, yam, banana, and palm. *Seed agriculture*, now the most common type of agriculture, uses seeds for plant reproduction. It originated in the Middle East about nine thousand years ago, in the basins of the two major rivers of present-day Iraq, the Tigris and the Euphrates. Wheat and barley were probably the first crops cultivated there. Although many plants were domesticated simultaneously in different parts of the world, rice, oats, millet, sugarcane, cabbage, beans, eggplant, and onions were domesticated originally in Asia.

Asia supports about 60 percent of the global population on only about 23 percent of the world's agricultural land. As a result, Asian agriculture is far more intensive than on any other continent. Despite the population pressure on arable land, Asia has made remarkable progress in agricultural productivity. Between 1966 and 1995, wheat production grew 5.5 percent annually, and rice production 2.2 percent. In Asia as a whole, food production has outpaced the growth of population. In most Asian countries, particularly in the low-income countries of South Asia, per-capita food availability has risen.

Agrarian Structure

Most people in Asia are farmers, owning an average of about 2.5 acres (1 hectare) of land per family. Topographic and climatic conditions, to a large extent, determine farm size. Agricultural potential is limited in Nepal, for example, because of the Himalaya Mountains, and in Saudi Arabia because of the Arabian Desert. In these countries, average farm size is larger relative to countries like Bangla-

Leading Agricultural Crops of Asian Countries with More than 15 Percent Arable Land

Country	*Products*	*Percent Arable Land*
Armenia	Fruit, vegetables	17
Azerbaijan	Cotton, grain, rice, grapes, fruit, vegetables, tea, tobacco	18
Bangladesh	Rice, jute, tea, wheat, sugarcane, potatoes	73
Burma (Myanmar)	Paddy rice, corn, oilseed, sugarcane, pulses, hardwood	15
India	Rice, wheat, oilseed, cotton, jute, tea, sugarcane, potatoes	56
Israel	Citrus and other fruits, vegetables, cotton	17
Korea, South	Rice, root crops, barley, vegetables, fruit	19
Lebanon	Citrus, vegetables, potatoes, olives, tobacco, hemp (hashish)	21
Nepal	Rice, corn, wheat, sugarcane, root crops	17
Pakistan	Cotton, wheat, rice, sugarcane, fruits, vegetables	27
Syria	Cotton, wheat, barley, lentils, chickpeas	28
Thailand	Rice, rubber, corn, tapioca, sugarcane, soybeans, coconuts	34
Turkey	Cotton, tobacco, cereals, sugar beets, fruits, olives, pulses, citrus	32
Vietnam	Rice, corn, potatoes, rubber, soybeans, coffee, tea, bananas	17

Source: Data are from *The Time Almanac 2000*. Boston: Infoplease, 1999.

desh, which contains a vast, fertile floodplain and receives abundant rainfall.

Another feature of Asian agrarian structure is the inequitable distribution of farmland. For example, in India more than 25 percent of cultivated land is owned by less than 5 percent of farming families. Farm holdings in most Asian countries are highly fragmented, and tenancy is widespread. Fragmentation of farms inhibits agricultural mechanization, and land consolidation efforts have had limited success in most Asian countries.

Most Asian farmers are subsistence farmers, cultivating crops for family consumption. Almost all farm operations are done manually or with the help of draft animals. Exceptions are found in Japan, South Korea, and Taiwan, where small-scale equipment similar to garden tractors is widely used. Only recently have Asian farmers started to use chemical fertilizer; for water, they largely depend on rain. As a result, yields are low, which compels farmers to cultivate the land intensively. Double-cropping is the norm; some farmers grow three crops a year. Therefore, only a small fraction of the arable land in humid regions of Asia remains fallow. Farming is labor-intensive, and the extended family is the main source of labor. This helps to explain why family size is generally large in agrarian countries of Asia.

Rice and Wheat

The coastal areas and inland river valleys of East, Southeast, and South Asia are the agricultural cores of the continent. More than half of the crop area of these regions is used to cultivate food crops such as rice and wheat. Rice is the principal food crop of all Asian countries located east and north of India and for the people of southern and eastern India.

Rice is the staple food of more than half of the world's population, and 90 percent of it is grown in coastal and deltaic plains and in the river valleys of Monsoon Asia. This region encompasses a broad geographic area characterized by a distinctive climate, stretching from Japan in the east, through Indonesia in the south, and west to Pakistan. Rice farming there is practiced mostly at the subsistence level, using traditional methods.

Wheat is the primary food crop of northern and western India and all Asian countries located west of India. People of the wheat-producing region consume rice as a secondary staple. Eighteen of the twenty-five top rice-producing countries of the world are in Asia. India has the largest area devoted to rice cultivation of the world's countries, but China is first in total production. Indonesia and Bangladesh rank third and fourth in world rice production.

With the exceptions of Japan, South Korea, China, and Taiwan, yields of all crops—particularly rice and wheat—are low in Asia compared to world standards. Although crop yields increased significantly after 1970, typical yields in Asia remained low for several reasons: Fertilizer use and the area under irrigation are among the lowest in the world. Also, most Asian farmers practice traditional farming methods, where high yields are atypical. Another major obstacle to increasing crop yields is the preponderance of small farms. Because small farms do not have access to assured irrigation and cannot afford modern agricultural inputs, their average yield is generally much lower than that of medium and large farms.

Slash-and-Burn Agriculture

In the tropical rain forests of Southeast Asia, the mountainous and hilly parts of South Asia, and in southern China, a type of primitive agriculture known as *shifting cultivation* or *slash-and-burn agriculture* is practiced. Shifting cultivators plant different crops, such as rice, corn, millet, yams, sugarcane, oilseeds, potatoes, taro, vegetables, and cotton, on one site. These farmers must abandon their fields and establish new ones every few years. As a result, a large area of land is required to support a small population. The land devoted to shifting cultivation is declining at a rapid rate worldwide because of the demand for forest resources for other uses.

Dry Agriculture

Farmers in the colder, drier parts of Asia (northeastern China, northern Japan, southeastern East Asia, northeastern Southeast Asia, and the western half of South Asia) and the river valleys of the Middle East practice a system of intensive subsistence agriculture called peasant grain-and-livestock farming, or *dry agriculture*. The dominant grain crops are wheat, barley, sorghum, millet, oats, and corn, while cotton, tobacco, and sugarcane are grown as cash crops. In arid areas, such as the Middle Eastern river valleys, irrigation helps support dry farming. Traditional water-lifting devices, such as the shaduf (a counterweighted, lever-mounted bucket), and the naria (waterwheel), permit limited double-cropping in the dry season near the rivers of the Middle East.

In the arid and semiarid parts of South Asia and the Middle East, and in the dry and cold western two-thirds of East Asia, nomadic herders graze cattle, sheep, goats, and camels. Nomadic herders move from place to place with their livestock in search of forage. As in other places, nomadic herding is declining in Asia.

Mediterranean Agriculture

A distinctive type of subsistence agriculture, called *Mediterranean agriculture*, is practiced along the Mediterranean coast of the Middle East and in the northern part of Turkey that borders the Black Sea. Traditional Mediterranean agriculture is based on wheat and barley cultivation in the rainy winter season. Farmers of this region also cultivate vine and tree crops, such as grapes, olives, and figs, and raise small livestock.

Export Crops

Plantation crops such as tea, rubber, coconuts, and coffee are grown in Asia. Tea is indigenous to China, which is the world's largest producer, fol-

PhotoDisc

An elephant works a rice field in Thailand.

lowed by India, Sri Lanka, and Bangladesh. Tea is Sri Lanka's largest export crop, accounting for about one-third of annual exports by value. Tea is grown in the central highlands of Sri Lanka and in the hilly regions of northeastern India and Bangladesh. Rubber is grown in Malaysia and Indonesia—which account for about 75 percent of total world production—and Cambodia, India, and Sri Lanka. Malaysia, Indonesia, and Sri Lanka are world-leading exporters of coconuts and coconut products.

Green Revolution

A dramatic growth in food production in Asia began with the *Green Revolution* in the late 1960's, particularly for wheat and rice. Cultivation of the new varieties of rice and wheat caused an impressive increase in the use of fertilizer and the expansion of irrigation, particularly the exploitation of groundwater through tube wells. With proper and timely application of fertilizers and water, yields of wheat can be tripled, and yields of rice can be doubled.

Critics of the Green Revolution have concentrated on the negative impacts of increased use of fertilizer and pesticides, which causes surface water pollution. With high-yield seeds, three crops a year can be cultivated. Adopting this practice has two consequences: It causes overuse of land, a major source of land degradation, and it leads to increasing monocultures of rice and wheat, reducing the genetic diversity of food crops.

Without the Green Revolution, feeding current Asian populations at prevailing nutritional standards would have been impossible. New agricultural practices enabled Asia to avoid the famine that was widely predicted in the 1970's. The new rice and wheat varieties also have stimulated agricultural employment, because more people are needed to cultivate, harvest, and handle the increased production.

Throughout Asia, agricultural growth and the increase in food production were somewhat slower in the 1990's than in the 1980's. The opportunity for bringing more land under cultivation has largely been exhausted. Therefore, any increase in crop output will have to come largely from an increase in yields. Rice and wheat yields are still relatively low in many Asian countries, primarily because of low use of modern agricultural inputs. For example, the use of chemical fertilizer in South Asian countries has not reached the levels of neighboring regions.

Demand for fruits, vegetables, meat, fish, milk, and eggs is likely to grow with the increased urbanization and industrialization of Asia. This will reduce the demand for cereal crops. In Japan, South Korea, and Taiwan, consumption of rice has already begun to decline. Increased crop production is required to feed the growing populations of most Asian countries. While increasing agricultural production, Asian policymakers must also promote environmentally sound technologies and implement effective land reforms to address the problems of inequality and poverty caused by landlessness. Better crop management and better management of irrigation water are also needed to sustain agricultural growth in Asian countries.

Forestry

Forests of significant economic importance are found primarily in northeastern East Asia and Southeast Asia. The softwood forests of northeastern East Asia cover most of Japan and parts of North Korea. Trees grown there are used for construction lumber and to produce pulp for paper. Tropical hardwood forests cover all Southeast Asian countries and the south central part of China, several places in India, and the northern part of Iran.

Trees grown in those forests are used primarily for fuel wood and charcoal, although an increasing quantity of special-quality woods are cut for export as lumber. Nearly 80 percent of the world's hardwood log exports in the early 1990's came from Malaysia. Cambodia, Malaysia, Indonesia, the Philippines, Thailand, and Myanmar export large quantities of forestry products.

Overexploitation of hardwoods and conversion of forest lands for other uses have become serious concerns. Rates of forest conversion are most rapid in continental Southeast Asia, averaging about 1.5 percent a year. *Deforestation* has important local, regional, and global consequences, ranging from increased soil and land degradation to greater food insecurity, escalating carbon emissions, and loss of biodiversity. Small-scale, poor farmers clearing land for agriculture to meet food needs and the gathering of wood to be used for cooking account for roughly two-thirds of the deforestation in Southeast Asia. Commercial logging and urban expansion account for most of the remaining deforestation.

Bimal K. Paul

See also: Asian flora; Deforestation; Green Revolution.

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ASIAN FLORA

Category: World regions

Asia has the richest flora of the earth's seven continents. Because Asia is the largest continent, it is not surprising that 100,000 different kinds of plants grow within its various climate zones, which range from tropical to Arctic.

Asian plants, which include ferns, gymnosperms, and flowering vascular plants, make up 40 percent of the earth's plant species. The endemic plant species come from more than forty plant families and fifteen hundred genera. Asia is divided into five major vegetation regions based on the richness and types of each region's flora: tropical *rain forests* in Southeast Asia, temperate *mixed forests* in East Asia, tropical rain/dry forests in South Asia, *desert* and *steppe* in Central and West Asia, and *taiga* and *tundra* in North Asia.

Tropical Rain Forests

The Asian regions richest in flora, tropical rain forests, are found in the island nations of Southeast Asia, which extend from Kinabalu in the north to Java in the south, and from New Guinea in the east to Sumatra in the west. In this vast archipelago, the longest island chain between Asia and Australia, are thirty-five thousand to forty thousand vascular plant species. Tropical rain forests grow there year-round because of the region's warm temperatures and plentiful rainfall. The forests contain great varieties of tall trees, some towering 148 feet (45 meters) high. Within any 1-square-mile area, one can see as many as one hundred tree species with no single species dominant.

The rain forests have mostly broad-leafed *evergreens*, with some palm trees and tree ferns. The uppermost branches of the trees form *canopies* that cover and protect the earth below. Because little sunlight penetrates the dense canopies, few shrubs or herbs grow in the rain forests. Instead, many vines, *lianas*, *epiphytes*, and *parasites* are twined on tree branches and trunks. Mangroves fringe the tropical rain forests along the coasts.

Temperate Mixed Forests

Second in floral richness, East Asia's temperate mixed forests contain thirty thousand to thirty-five thousand plant species. This region ranges from Japan in the east to the Himalayan nations (Bhutan, Sikkim, and Nepal) in the west, and from Russia's Amur River Valley in the north to China's Hainan Island in the south. East Asia's temperate weather is similar to the climate of eastern North America, with hot summers and cool winters. From south to north and from the east coasts to lower elevations in mountainous areas in the west, the vegetation changes from evergreen to *deciduous* broad-leafed forests, with dense shrubs, bamboo, and herbs in different layers beneath the forest canopy. The major tree species are of the magnolia, oak, tea, laurel, spurge, azalea, and maple families. Herbs include members of the primrose, gentian, pea, carrot, foxglove, composite, buttercup, and rose families.

The Himalayan range is the point where the regions of South Asia, East Asia, and Central and West Asia join. From the Qinghai-Tibet Plateau in southwest China to the lower areas of the Himalayas, elevation usually is between about 5,000 and 13,000 feet (1,500 and 4,000 meters). Mountains with deep valleys showcase complex, multiple vegetation types—from mixed forests and dense shrubs to alpine meadows in mountain plains. Many *primary seed plants* (gymnosperms and flowering plants), grow there.

Untouched native vegetation in East Asia is usually found only in mountainous or remote areas. On mountains at high elevations, the points where the temperatures are so cold that trees cannot grow form what is called the *tree line*. Near the tree line, only plants related to *coniferous* and *alpine* species grow. Above about 13,000 feet (4,000 meters) in high mountain areas, no vegetation grows. Instead, snowcaps or icebergs exist year-round.

Tropical Rain/Dry Mixed Forests

The third-richest region, tropical rain/dry forests, is found in South Asia, which reaches from the Philippines in the east to Pakistan in the west, and from the Himalayas in the north to Thailand in the south. Twenty-five thousand to thirty thousand species of plants grow there. This region has both tropical rain forests and tropical seasonal dry forests. The tropical rain forest is mainly found in the region's lowlands and the seasonal dry forests in the highlands or mountainous areas. More often, these two types of forests are combined.

The tropical seasonal dry forests usually grow in a climate with wet and dry seasons or under a somewhat cooler climate than the tropical rain forests. The canopy, formed from primarily deciduous broad-leafed species, is much thinner than the canopy in the tropical rain forest, so more sunlight reaches plants below. Many different plant species live together, forming tropical jungles. Tall, thick-trunked trees, colorful orchids, ferns, dense mosses, and twined vines and lianas dominate this vast region. The major components of these kinds of forests are members of the dipterocarpas, sweetsop, laurel, piper, fig, dissotis, akee, gardenia, periwinkle, milkweed, African violet, palm, and aroid families. In central and southern India and in some areas of Pakistan there are tropical *grasslands*, called the *savanna*. Because of the savanna's hot, dry weather, mainly coarse grasses grow there.

Desert and Steppe

The desert and steppe region in Central and West Asia has twenty to twenty-five thousand species of plants. This region stretches from north and northwest China and Mongolia in the east to Turkey in the west, and from Kazakhstan in the north to the Arabian Peninsula in the south. This region's vegetation changes from semidesert or desert to the temperate grassland called the steppe.

Central and West Asia contains the largest desert-steppe landscape in the Northern Hemisphere. Few plant species grow in the steppe and nearly none in the desert. The herbs and few woody plants that grow in these dry areas are members of the grass, pink, mustard, pea, saxifrage, stonecrops, lignum vitae, forget-me-not, and lily families. Because the desert environment is so dry, plant species must be able to survive in the arid weather for long periods of time. Central and West Asia—with its steppe between the desert in the south and coniferous forests in the north—forms one of the world's largest foraging areas, providing food resources for both wild and domestic animals, such as camels, sheep, goats, cows, and horses.

Taiga and Tundra

The poorest region in floral richness, with only about five thousand vascular plant species, is North Asia. This region is primarily Siberia, the eastern part of Russia, reaching from the Ural Mountains in the west to the Bering Strait in the east and from the Arctic Circle in the north to Mongolia and Kazakhstan in the south. The region's weather is temperate, with short, mild summers and long, cold winters. The predominant vegetation in North Asia is *coniferous* (boreal) forest. This region, called the taiga, contains mainly pine, spruce, fir, larch, and some species in the birch, aspen, and willow families. Because the trees there are straight and tall, the taiga provides timber for Russia's forestry industry. Small, perennial herbs and a few types of shrubs grow in the taiga's swamps or marshes.

Farther north is the cooler Arctic area called the tundra. Plants that grow in tundra are resistant to the cold climate. During the summer they complete their life cycle quickly, before winter comes. Tundra plant species are members of such common families as composites, peas, grasses, and reeds. Far beyond the tundra is Arctic ice.

Asia's native plant species provide shelter and food for animals. For example, arrow bamboo and umbrella bamboo, found in the forests of central to southwest China, are the main food of the giant panda. Many plants in Asia also provide food, ornaments, or medicine for humans.

Food Crops

Rice is the main food for humans in Asia, especially in the tropics. In temperate Asia, wheat—one of the world's main food sources—joins rice as a primary food source. Various beans and peas provide plant protein in the human diet and are eaten with vegetables and grains. Asia has many tropical fruit plants, such as the mango, banana, litchi, citrus fruits, and breadfruit. Pears, apples, grapes, peaches, and strawberries are temperate fruits. The kiwi, one of the most nutrient-rich fruits, is cultivated in New Zealand but originally came from central China. The Chinese not only eat kiwi but also make kiwi wine. Palm dates are another important fruit in West and Southwest Asia (the Arabian Peninsula). Vegetables grown in Asia include various cabbages, lettuce, onions, garlic, celery, carrots, soybeans, cucumbers, and squash. Ginger originally came from Asia.

Soybean oil is the major cooking oil in Asia. Although soybeans are native to Asia, they have become the biggest crop grown in the United States. According to the U.S. Department of Agriculture, in 1999 U.S. farmers harvested 73.3 million acres of soybeans, 2.3 million acres more than corn and 18.6 million acres more than wheat. Another oil plant, the sunflower, is grown in temperate Asia. In tropical Asia, people use mustard oil, palm oil, cotton oil, and peanut oil. In Central and West Asia, the most popular oil is olive oil. Many other foods people enjoy throughout the world are native Asian plants, for example, tea and coconuts. Black pepper and sugarcane also are grown in tropical Asia.

Ornamental and Medicinal Plants

Many of Asia's plant species have great ornamental value. Azaleas, dogwood, primroses, camellias, peonies, roses, lotus, daisies, cherries, and begonias are frequently planted in gardens. Ornamental conifers from Asia include pines, spruces, cedars, junipers, umbrella pines, and yews. Thousands of wildflowers originating in Asia include poppies, snapdragons, slippers, columbine, trillium, marigolds, buttercups, gentian, lilies, bluebells, and violets. Europeans who explored Asia centuries ago brought ornamental plants back to their home countries. As a result, many of these plants are now grown throughout the world. The world's largest flower, *rafflesia*, grows in the tropical rain forests of Sumatra. In full bloom, the flower's diameter is about 3 feet (1 meter).

Plants make up a large part of traditional Chinese medicine, which has been practiced for thousands of years. Today, some of these plants are used in alternative medicine in the West. They include ephedra, eucommia, cinnamon, ginseng, sanqi, and ginkgo.

Scientific Value

Botanists view the region ranging from central China to the Himalayas to the northern part of South Asia as a key area for research into the origin of flowering plants. Native plant species in Asia are numerous; botanists also study Asian plants that are relics of ancient times, from millions of years ago, as well as fossils.

Ancient species include such gymnosperms as the dawn redwood of central China. Dawn redwood is similar to California's redwood and giant sequoia. Another fossil-like tree is East Asia's ginkgo. This species not only has great ornamental value but also has great commercial value as an alternative medicine. Ginkgo trees are also dust-resistant, which makes them a favorite in urban landscaping and the ornamental industry. Other Asian plants such as the magnolia and its allied families may represent the most primitive flowering plants.

Introduced Plants

Asian flora today also includes introduced plant species from other parts of the world that play important roles in people's lives. For example, the rubber tree of South America is cultivated in tropical Asia. This tree produces raw material for the natural rubber industry, in which Asia is the largest producer in the world. Cacao, a tree species that provides the basis of chocolate, was introduced from tropical America. Corn, one of the most common crops in Asia, was introduced from America several thousand years ago. Several vegetables, including the tomato, potato, eggplant, green pepper, hot pepper, and chili (all from the nightshade family), were introduced to Asia long ago. Peanuts, originally from Brazil, are also cultivated in Asia.

Coffee, an increasingly popular beverage in Asia, came originally from Africa. An introduced fruit is the pineapple, which came from tropical America but now is popular in tropical Asia. The sweet potato, from Central America, is also cultivated in Asia. Tobacco is another crop introduced to and cultivated in Asia. It originally came from tropical America, but its yield in China has made that nation a leading producer.

Impact of Human Activity

Asia's highly diversified flora have contributed positively to the daily lives of people around the world, but the demands of a rapidly growing population are a constant threat. *Deforestation*, *overgrazing*, and *urbanization* have become major reasons for heavy losses of Asian flora, especially in South and East Asia. In China alone, eight key plant species were added to the first-class protection list in the Red Book of 1992 (equivalent to the U.S. endangered species list). Among them are the Chinese silver fir, dawn redwood, and ginseng. These plants only grow in several isolated locations and are rare in their original range. As natural vegetation is cut for farming, grazing, or simply for cooking and heating fuel, fewer plants remain. Although scientists from around the world have worked on this problem for decades, the situation has not improved.

Guofan Shao and Jinshuang Ma

See also: Asian agriculture.

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ATP AND OTHER ENERGETIC MOLECULES

Categories: Cellular biology; physiology

All cells contain a small collection of compounds called common intermediates. These compounds transfer energy between processes that produce energy and those that require it. The best-known example is adenosine triphosphate (ATP), but several other esters play a similar role. Because of their function in energy transfer, cells are absolutely dependent on such compounds, and a cell deprived of ATP will quickly die.

ATP (adenosine triphosphate) is the principal energy carrier for most life processes, including those carried out within plant cells, including the chemical reactions of photosynthesis. The central importance of *common intermediates* (energy-transferring compounds) is evident in the effects of various chemicals that prevent ATP synthesis. For example, in cells that require oxygen, ATP synthesis is coupled to the oxidation of food-related molecules. Cyanide and carbon monoxide interfere with such cellular oxidations and, therefore, completely prevent the ATP synthesis that is coupled to them. Thus, these compounds are extremely toxic, and cells are often killed by them in a matter of seconds.

Free Energy

Many biological processes require energy in order to occur; that is, they are not by themselves spontaneous. Examples of energy-requiring processes include contraction of muscle, beating of cilia, emission of light by fireflies, heat production by birds and mammals, and establishment of a voltage difference across a cellular membrane. The synthesis of proteins from their constituent amino acids, the formation of complex membrane fats, and, indeed, the synthesis of many other chemical compounds are not themselves spontaneous and, hence, require energy. Energy-dependent processes and reactions are referred to as *endergonic*.

On the other hand, many processes in organisms are spontaneous and do occur without any other energy source. Most of these are chemical reactions, and all such reactions, being spontaneous, can serve as energy producers. For this reason, they are often called *exergonic*. They can, in principle, provide energy for events, such as the secretion of nectar or aromatic oils by flower cells, that require it. The form of that energy is *free energy*.

There is a change in free energy, measured in units of calories or joules, associated with any chemical reaction or physical event. If the change in free energy is more than zero, the process requires energy to proceed; if less than zero, it yields energy and is spontaneous. Thus, the numerical value for the change in free energy of a reaction is very useful for predicting whether it can occur.

The other important aspect of free energy is that its numerical value can be altered by changing the concentrations of the chemicals reacting or the product formed when the chemicals react. For example, consider a hypothetical biochemical reaction in which A is the reactant and B is the product. Imagine that this reaction is not spontaneous; therefore, its free energy change is greater than zero, and it does not "go." Yet, though A becoming B is not spontaneous, its reverse, B becoming A, is. In other words, if a reaction in one direction has a change in free energy greater than zero, the reverse reaction will have one less than zero. Most important, if a reaction in a particular direction is not spontaneous, it can be made to "go" anyway, simply by increasing the concentration of the reactant until the change in free energy falls below zero. This is called the *law of mass action*: Adding more reactant (or subtracting some of the product) will often force a reaction. Stubborn reactions can be pushed or pulled.

Spontaneous Reactions

A second law explains completely how spontaneous reactions can provide energy for those that are not spontaneous. It is called the *law of the common intermediate* and states that reactions can be linked, as far as energy is concerned, by the products of one reaction serving as the reactants of another. Here are two biochemical reactions:

$$A + B \leftrightarrow C + D$$

$$X + D \leftrightarrow Y + Z$$

If the first reaction is spontaneous, with a change in free energy less than zero, it produces a substantial amount of C and D. The second reaction would not normally be spontaneous (with its positive change in free energy), but notice that D, the product of the first reaction, is a reactant in the second. When the two reactions are together in the same cell, the buildup of D tends to push the second reaction, reducing the difference in free energy between reactants and products. In other words, the energy produced by the first reaction is being transferred to the second reaction, allowing it to occur. In this case, D is the common intermediate that connects the two.

ATP

In organisms, the sum of all chemical reactions is called *metabolism*. All the systems of reactions that require energy are called *anabolism* and those producing it, *catabolism*. Anabolism and catabolism are tightly linked by common intermediates. A good example of a common intermediate is ATP. Using ATP as an example, it can be seen that the linkage between anabolism and catabolism is a two-way street. ATP is synthesized from adenosine diphosphate (ADP) and phosphate, with the required energy often coming from light (photosynthesis) or from the oxidation of foods (respiration). When ATP is used to provide energy for muscle, for example, it is broken down by hydrolysis to ADP plus phosphate. Thus, the product of catabolism (ATP) is utilized in anabolism, and the products of anabolism (ADP plus phosphate) are utilized in catabolism to regenerate ATP. Thus, the role of ATP is cyclic.

Most common intermediates are *phosphate esters* such as ATP, although a few are *thioesters*. It was once thought that such ester bonds were somehow unusual, perhaps containing an abnormally large amount of available free energy. They were often called high-energy bonds. In fact, these ester bonds are not particularly abnormal in their energy; there are many esters with much more energy—compounds that are not important common intermediates. Apparently, the reason that so few compounds have evolved as links between catabolism and anabolism is that their chemical structures are unique in enabling them to participate readily in both.

It appears likely that a very early common intermediate in ancient cells was not ATP but pyrophosphate, which is simply two phosphates hooked together by an ester bond. Apparently, cells evolved the central role for ATP at a later stage. In all these cases, when the energy of a common intermediate is utilized in an anabolic reaction, it is by means of a *hydrolysis reaction*, the breaking of an ester bond by the addition of water. In many instances, the hydrolysis occurs in more than one step, but it is a hydrolysis, nevertheless, and the free energy that matters in such cases is the free energy of the hydrolysis.

Other Intermediary Compounds

ATP usually gets the most attention, which is proper, because evolution, over the long run, appears to have exhibited the same preference. There are, however, a few other compounds that serve as common intermediates. Several are quite similar to ATP, with a ring-shaped organic part and three phosphates attached in series at one end. The organic parts are a little different, however, and the compounds have different names, with abbreviations such as GTP, UTP, and ITP. These compounds, which are, with ATP, termed *nucleoside triphosphates*, are readily interchangeable with ATP. For example, ATP can be manufactured from ADP by a phosphate transfer reaction:

$$ADP + GTP \leftrightarrow ATP + GDP$$

In addition, pyrophosphate, a common intermediate in early cells, transfers energy today in a variety of plant, animal, and bacterial species. In some organisms, pyrophosphate is made (and used) under conditions in which it is, for whatever reason, difficult to make ATP. A few reactions use energy from the hydrolysis of acetyl phosphate, which can be chemically described as a derivative of acetic acid (the active ingredient of vinegar) with a phosphate attached. Also, a number of thioesters, esters with sulfur in place of oxygen, are important common intermediates; they are often large, complicated molecules.

Finally, one may wonder why ATP and similar compounds have as large negative free energies as they do. A complete answer would involve advanced chemistry, but one factor is both important and readily understood. When ATP is hydrolyzed,

$$\text{ATP} + \text{water} \leftrightarrow \text{ADP} + \text{phosphate}$$

both of the products happen to be negatively charged. It is well known that unlike charges attract each other and like charges repel. Therefore, the two products are driven apart from each other, and they are unlikely to react together to produce a back reaction. Thus, the reaction tends to go well in the direction of ADP and phosphate but not the reverse. Another way of saying it is that the reaction is highly spontaneous, or that the reaction exhibits a solidly negative change in free energy, making such compounds good candidates for energy transfer.

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See also: Active transport; Calvin cycle; Cell-to-cell communication; Cells and diffusion; Chloroplasts and other plastids; Energy flow in plant cells; Exergonic and endergonic reactions; Glycolysis and fermentation; Krebs cycle; Lipids; Mitochondria; Nitrogen fixation; Oxidative phosphorylation.

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AUSTRALIAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

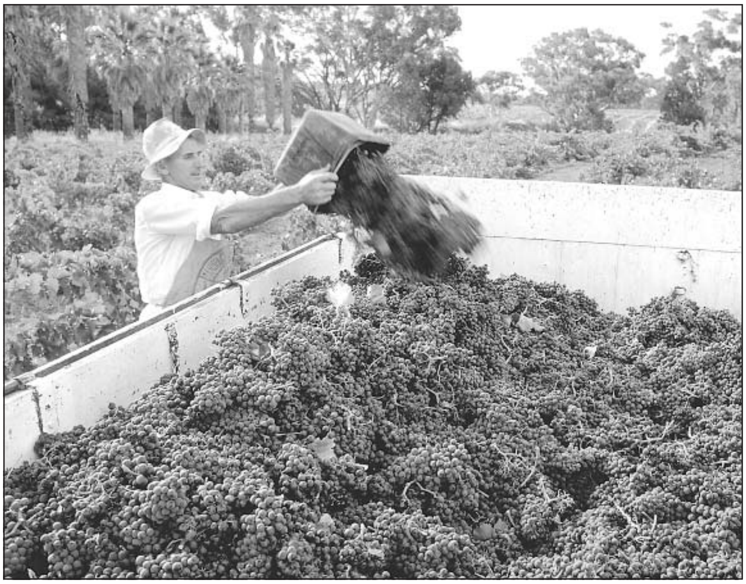
Agriculture is an important part of Australia's economy. Australia's exports were overwhelmingly agricultural products until the 1960's, when mining and manufacturing grew in importance.

Agriculture occupies 60 percent of the land area of Australia, but much of this is used for open-range cattle grazing, especially in huge areas of the states of Queensland and Western Australia. Only 5 percent of Australia's agricultural land is used for growing crops. Western Australia and New South Wales have the largest areas of cropland. The limited area suitable for growing commercial crops is limited mainly by climate, because Australia is the world's driest continent.

Annual rainfall of about 20 inches (500 millimeters) is necessary to grow crops successfully without irrigation; less than half of Australia receives this amount, and the rainfall is often variable or unreliable. Years of drought may be followed by severe flooding. High temperatures throughout most of Australia also mean high evaporation rates, so rainfall figures alone are not a good guide to the feasibility of agriculture.

Australian soils usually require the application of fertilizer to grow crops successfully. The east coast of Australia is suitable for growing sugarcane,

Selected Agricultural Products of Australia



Australia has 242,060 acres of vineyards and more than one thousand wineries.

while the cooler southern parts are suited to growing wheat. Irrigation has opened up large areas of drier land to agriculture, especially for growing fruit, but *salinization* (the buildup of salt in the soil) has become a major problem in some areas, especially near the mouth of the Murray River. Major agricultural plant exports from Australia are wheat and sugar. Other important agricultural exports are fruits, cotton, rice, and flowers.

Wheat

Long the most important crop of Australia, wheat is produced in the Wheat Belt, a crescent of land just west of the Eastern Highlands, or Great Dividing Range, which extends from central Queensland through New South Wales to Victoria, as well as in the south of South Australia and southwest Western Australia. More than 120,000 farms in Australia grow grains, and wheat is the principal crop on some 25,000 farms. The average Australian wheat farm is family-owned and has an area of 3,700 acres (1,500 hectares). Crops are rotated, usually because of low soil fertility.

Australian wheat is planted during the winter, which is much milder than winter on the prairies of North America. Harvesting begins in September in the warm state of Queensland and moves south to Victoria and Western Australia by January. Australian wheat is high in quality and low in moisture, so it is easy to mill. Wheat crops are frequently affected by drought; another problem is Australia's markets, because the nation competes with the United States in wheat export.

When the British first came to Australia, convicts planted wheat on a government farm in what is now inner Sydney. They had difficulty growing wheat because of poor soils, unfamiliar climate, and inexperience, causing fear of widespread hunger. As settlement spread beyond the coastal plain and into the interior, wheat production rose dramatically. The rapid increase in population after the gold discoveries of the 1850's also led to increased demand for wheat. Australia began exporting wheat in 1845 and is now the world's fourth-largest exporter of wheat.

Sugar

Sugarcane is grown in a series of small regions along the tropical coast of Queensland, extending slightly across the border into northern New South Wales. A warm, wet climate is required for successful cultivation of sugarcane, so it is confined to parts of the coastal plain with good, deep soils and reliable rainfall. Australia is the world's third-largest exporter of sugar. Sugar is grown on more than six thousand small, individually owned farms. Until the 1960's, cane was cut by hand. Now it is harvested mechanically and taken by light rail to a nearby mill. There are twenty-five mills in Queensland and three in New South Wales.

Fruit

Fruit growing has a long history in Australia and is strongly influenced by climatic considerations. In Queensland, tropical fruits such as bananas, pineapples, mangoes, and papaya (called pawpaw in Australia) are cultivated. In the cooler south, apples, peaches, apricots, cherries, and grapes are grown.

Grapes are grown for eating and are dried as raisins, but more important is wine production, especially in the Barossa Valley (South Australia), Hunter Valley (New South Wales), Margaret River area (Western Australia), and the Murrumbidgee Irrigation Area and Riverina. John Macarthur, the founder of the Australian wool industry, established the first commercial vineyard, in New South Wales. Later European settlers planted vineyards in Victoria and South Australia. In the 1960's modern plantings and production methods were introduced. Australia has 242,060 acres (98,000 hectares) of vineyards and more than one thousand wineries. Wine is an important export for Australia, with the European Union purchasing 60 percent of wine exported.

Other Agricultural Products

Cotton is grown in drier interior parts of northern New South Wales and in part of central Queensland. Cotton is usually grown in conjunction with sheep farming, on family farms. Indonesia is the major customer for Australian cotton. Rice has been grown commercially in Australia since 1924, using irrigation. New South Wales is the main producer, where the Murrumbidgee Irrigation Area dominates rice production. Australia exports most of its rice crop and in 1999 was the world's eighth-largest exporter of rice. Oats are grown where the climate is too cool and too moist for wheat. In Australia, this is in the interior southeast with a small area in Western Australia. This state and New South Wales are the biggest producers of oats, which is used mainly for livestock fodder.

Other agricultural products of Australia include barley; grain sorghum; corn, called maize in Australia; vegetables, including potatoes, peas, tomatoes, and beans; oil seeds such as sunflower; soybeans; and tea and coffee in northern Queensland. Australia is a major producer of honey, with more than eight hundred commercial apiarists. Blossoms of the eucalyptus tree produce distinctive-tasting honey, which is sold mainly to European Union countries.

Ray Sumner

See also: Australian flora.

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AUSTRALIAN FLORA

Category: World regions

Australia broke off from the supercontinent Pangaea more than fifty million years ago, and the species of plants living at that time continued to change and adapt to conditions on the isolated island. This led to distinctive plants, differing from those of the interconnected Eurasian-African-American landmass, where new immigrant species changed the ecology.

Many species of plants in Australia are found nowhere else on earth, except where they have been introduced by humans. Such species are known as endemic species. This distinctiveness is the result of the long isolation of the Australian continent from other landmasses. Australian vegetation is dominated by two types of plants—the eucalyptus and the acacia. There are 569 known species of eucalypts and 772 species of acacia. Nevertheless, a great deal of botanical diversity exists throughout this large continent.

Climate and Ecology

Climate is a major influence on Australian flora, and the most striking feature of the Australian environment as a whole is its aridity. Nutrient-poor soils affect the nature of Australia's vegetation, especially in arid areas. Half of the continent receives less than 11.8 inches (300 millimeters) of rainfall per year; small parts of Australia receive annual rainfall of 75 inches (800 millimeters). Therefore, forests cover only a small percentage of Australia. A close correlation exists between rainfall and vegetation type throughout Australia. Small regions of tropical *rain forest* grow in mountainous areas of the northeast, in Queensland. In the cooler mountains of New South Wales, Victoria, and Tasmania, extensive temperate rain forests thrive.

More extensive than rain forest, however, is a more open forest known as *sclerophyllous forest*, which grows in the southern part of the Eastern Highlands in New South Wales and Victoria, in most of Tasmania, and in southwest Western Australia. A huge crescent-shaped region of woodland vegetation, an open forest of trees of varying height, with an open canopy, extends throughout northern Australia, the eastern half of Queensland and the inland plains of New South Wales, and to the north of the Western Australian sclerophyllous forest.

Beyond this region, the climate is arid, and shrubs, forbs (smaller herbaceous plants), and grasses predominate. The tropical north of inland Queensland, Northern Territory, and a smaller part of Western Australia have extensive areas of *grassland*. Much of Western Australia and South Australia, as well as interior parts of New South Wales and Queensland, are *shrubland*, where grasses and small trees grow sparsely. In the center of the continent is the desert, which has little vegetation, except along watercourses.

Eucalypts

Many people familiar with the song "Kookaburra Sits in an Old Gum Tree," may not realize that *gum tree* is the common Australian term for a eucalyptus tree. When the bark of a eucalyptus tree is cut, sticky drops of a transparent, reddish substance called *kino* ooze out. In 1688 the explorer William Dampier noticed kino coming from trees in Western Australia and called it "gum dragon," as he thought it was the same as commercial resin. Kino is technically not gum, as it is not water-soluble.

The scientific name *Eucalyptus* was chosen by the first botanist to study the dried leaves and flowers of a tree collected in Tasmania during Captain James Cook's third voyage in 1777. The French botanist chose the Greek name because he thought that the bud with its cap (*operculum*) made the flower "well" (*eu*) "covered" (*kalyptos*). The hard cases are commonly called gum nuts.

The more than five hundred species of eucalypts in Australia range from tropical species in the north to alpine species in the southern mountains. Rainfall, temperature, and soil type determine which particular eucalypt will be found in any area. Eucalyptus trees dominate the Australian forests of the east and south, while smaller species of eucalyptus grow in the drier woodland or shrubland areas. It is easier to mention parts of Australia where eucalypts do not grow: the icy peaks of the Australian Alps, the interior deserts, the Nullarbor Plain, and the tropical and temperate rain forests of the Eastern Highlands.

The scientific classification of the eucalypts proved difficult to European botanists. Various experts used flowers, leaves, or other criteria in their attempts to arrange the different species into a meaningful and useful taxonomy, or classification scheme. George Bentham eventually chose the shape of the anthers—the part of the *stamen* that holds the pollen—together with fruit, flowers, and nuts.

A simpler classification of the eucalypts, commonly used by foresters, gardeners, and naturalists, arranges them into six groups based on their bark: gums have smooth bark, which is sometimes shed; bloodwoods have rough, flaky bark; ironbarks have very hard bark with deep furrows between large pieces; stringybarks have fibrous bark that can be peeled off in long strips; peppermints have mixed but loose bark; boxes have furrowed bark, firmly attached. This system was devised in 1859 by Ferdinand von Müller, the first government botanist of the Colony of Victoria and the father of Australian botany.

A eucalyptus forest in Victoria, Australia.

Many of the native plants of Australia, along with eucalypts, show typical adaptations to the arid climate, such as deep taproots that can reach down to the water table. Another common feature is small, shiny leaves, which reduce transpiration. Eucalyptus leaves are tough or leathery and are described as sclerophyllous. Sclerophyllous forests of eucalypts cover the wetter parts of Australia, the Eastern Highlands, or Great Dividing Range, and the southwest of Western Australia. The hardwood from these forests is generally not of a quality suitable for building, so areas are cleared and the trees made into wood chips that are exported for manufacture of newsprint paper. This has been a controversial use of Australian forests, especially where the native forest has been cleared and replaced with pine plantations.

The southwest corner of Western Australia has magnificent forests featuring two exceptional species with Aboriginal names, *karri* and *jarrah*. Karri is one of the world's tallest trees, growing to 295 feet (90 meters) tall. This excellent hardwood tree is widely used for construction. The long, straight trunks are covered in smooth bark that is shed each year, making a colorful display of pink and gray. These forests are now protected. Jarrah grows to 120 feet (40 meters) in height and is a heavy, durable timber. It was used for road construction in the nineteenth century, but now the deep red timber is prized for furniture, flooring, and paneling.

During the nineteenth century, Australia could also claim to be home to the world's tallest trees, the mountain ash. The tallest tree, which observers claimed was 433 feet (132 meters) high and with the top broken away, was felled in 1872. The tallest accurately measured tree was 374 feet (114 meters) high.

The most widely distributed of all Australian eucalypts is the beautiful river red gum. These trees grow along riverbanks and watercourses throughout Australia, especially in inland areas; their spreading branches provide wide shade and habitat for many animals. Koalas eat leaves from this tree. In the song "Waltzing Matilda," Australia's unofficial national anthem, a man camps "under the shade of a coolabah tree." This word might apply to any eucalypt, but it is most likely a river red gum.

In drier interior areas and in some mountain areas, there are more than one hundred smaller species of eucalypts that are known by the Aboriginal name *mallee*. These many-trunked shrubs have underground lignotubers, roots that store water. Much of this marginal country was cleared for farming, creating a situation similar to that of the 1930's Dust Bowl in the United States. In the dry Australian summers bushfires are a great danger in the mallee and in any eucalyptus forest. The volatile oils of the eucalyptus trees can lead to rapid spread in the tree crowns, jumping across human-made firebreaks. On the other hand, several Australian trees not only can survive fires but actually require fire for their seeds to germinate. Eucalypts have been introduced to many countries, including Italy, Egypt, Ethiopia, India, China, and Brazil, and they are common in California, where they have been growing as introduced trees for 150 years.

Acacias

These plants are usually called *wattles* in Australia, because the early European convicts and settlers used the flexible twigs of the plant for wattling, in which twigs are woven together, making a firm foundation for a thatched roof or for walls. The walls are then covered inside and out with mud. This style of building, known as wattle-and-daub, was common throughout Australia in pioneering days.

Wattles frequently have masses of colorful flowers, usually bright yellow. One species is the national flower of Australia. Other interesting acacias include the mulga, which has an attractive wood.

Rain Forests

Although rain-forest vegetation covers only a small area of Australia, it is exceptionally varied and of great scientific interest. Neither of the two general types of rain forest found in Australia has eucalypts. Rain forests are located along the Eastern Highlands, or Great Dividing Range, where rainfall is heavy. In small areas of tropical Queensland, where rainfall is also heavy, true tropical rain forest is found. The flora are similar to those in Indonesian and Malaysian rain forests. The tropical rain forest contains thousands of species of trees, as well as lianas, lawyer vine, and the fierce *stinging tree*, whose touch could kill an unwary explorer. Toward the north of New South Wales, a kind of subtropical to temperate rain forest grows. Cool, wet Victoria and Tasmania have extensive areas of temperate rain forest, where only a few species dominate the forests. Arctic beech trees are found, as well as sassafras and tall tree ferns.

Sclerophyllous Forest

This is the typical Australian *bush*, which grows close to the coast of New South Wales, Victoria, and Tasmania. The bright Australian sun streams down through the sparse crowns and narrow leaves of the eucalypts. As the climate becomes drier, farther inland from the coast, the open forest slowly changes to a shrubbier woodland vegetation.

Grasslands

Moving farther inland, to still drier regions, woodlands give way to grasslands, where cattle are raised for beef in the tropics, and sheep are raised for wool in the temperate areas. Before Europeans came to Australia, there were native grasslands in the interior—tropical grasslands in the monsoonal north, and temperate grasslands in the south and southwest. Kangaroo grass and wallaby grass once grew in the temperate interior of New South Wales, but much of this has been cleared for agriculture, especially for wheat farming. Mitchell grass is another *tussock grass*, which grows in western Queensland and into the Northern Territory. Cattle and sheep graze extensively on this excellent native pasture.

The most common grassland type in Australia is dominated by *spinifex*, a spiky grass that grows in clumps in the arid interior and west. Even cattle cannot feed on spinifex grass, so this ecosystem is less threatened than most other grasslands. The northern grasslands are dotted with tall red termite mounds; those that are aligned north-south for protection from the hot sun are built by so-called magnetic termites.

Other Trees and Plants

Many people think that *macadamia* nuts are native to Hawaii, which produces 90 percent of the world's crop, but in fact, the tree is native to Australia. It was discovered by Ferdinand von Müller in 1857 on an expedition in northern Australia. Müller named the tree after his Scottish friend, John Macadam. The trees were introduced to Hawaii in 1882.

Cycads are plants from an ancient species which still thrive in Australia. The *Macrozamia* of North Queensland is a giant fernlike plant. Similarly old are the *Xanthorrhea* grass-trees, which used to be called "blackboys." A single spearlike stem rises from a delicate green skirt on this fire-resistant species.

In northwest Australia, the *baobab*, or bottle tree, can be found. This fat-trunked tree collects water in its tissue. One is said to have served as a temporary prison. The only other baobabs are found in Africa, a reminder that these continents were once joined. *Bottlebrush* is an Australian shrub with colorful flowers that has become popular with gardeners in many parts of the world.

Extinct and Endangered Plants

Human activities in Australia have led to the extinction of more than eighty species of plants, and the list of endangered plants contains more than two hundred species. Many nonnative species have been introduced to Australia by Europeans. Some have become pests, such as the blackberry in Victoria, the lantana in north Queensland, and water hyacinth, found throughout the continent. There are 462 national parks in Australia, as well as other conservation areas, where native flora are protected.

Aboriginal Plant Use

The Australian Aborigines used plants as sources of food and for medicinal purposes. Food plants included nuts, seeds, berries, roots, and tubers. Nectar from flowering plants, the pithy center of tree ferns, and stems and roots of reeds were eaten. Fibrous plants were made into string for weaving nets or making baskets. Weapons such as spears, clubs, and shields, as well as boomerangs, were made from hardwoods such as eucalyptus. The bunya pine forests of southeast Queensland were a place of great feasting when the rich bunya nuts fell.

Ray Sumner

See also: Australian agriculture.

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AUTORADIOGRAPHY

Category: Methods and techniques

Autoradiography produces an image formed by a substance's own radioactivity when exposed to a photographic film. This technique is often used for investigation of biological processes.

In 1896 Antoine-Henri Becquerel was working with rocks containing uranium ore. By chance, he put one rock sample into a dark drawer on top of a box of unexposed photographic film. When the film later was developed, it showed a clear outline of the uranium rock. Evidently, some radiation had been emitted from the rock, penetrated through the wrapping paper, and exposed the film inside. An autoradiograph, that is, an image produced by radioactivity, was visible on the film. Autoradiography, much refined, is now a valuable technique for investigating biological processes.

Hungarian chemist Georg von Hevesy pioneered the use of radioactive tracers in biological research in the 1920's, and two developments in the 1930's greatly expanded their use. First was the discovery of *induced radiation* by Frédéric Joliot-Curie and Irène Joliot-Curie, which raised the exciting possibility that artificially created radioactivity could be induced in almost any element found in nature. The second development was the invention of the *cyclotron*. The cyclotron beam was used to bombard various elements to produce new *radioactive isotopes*, including radioactive sodium, potassium, sulfur, and iron. After 1950 radioactive hydrogen and carbon also became available as *tracers*, allowing organic molecules such as carbohydrates and proteins to be labeled.

Macroautoradiography

Whole-body autoradiography has been widely used to trace the routes of molecules in *metabolism*. First, a radioactive tracer is administered to an organism by ingestion or injection. After a period of time, individual samples of tissue are removed and pressed directly against X-ray film for several days, to expose the film wherever the radioactivity has become concentrated. The film is then developed and viewed, frequently with the aid of a microscope. This process has been used to trace the uptake of nutrients by plants from the soil into the leaves or buds. Experimentation with whole organisms is called *macroautoradiography*.

Microautoradiography

A refinement of this methodology, called *microautoradiography*, has been developed for studying subcellular structures, even those as small as individual strands of deoxyribonucleic acid (DNA). Much interesting information has been learned about the mechanisms of cell division and other processes in cell biology. The cells being studied are given a nutrient solution containing molecules that have been labeled, usually with radioactive tritium, carbon, or phosphorus.

After a period of incubation, some cells are transferred to a glass slide. The slide is dipped into a liquid photographic emulsion containing light-sensitive silver bromide, which clings to the slide in a thin layer. The slide with the cells covered by emulsion is then placed into a light-tight box for several days to allow time for radioactive decay. The beta particles from tritium cause the photographic emulsion to become exposed.

The emulsion is then developed and fixed as any photographic negative would be. The developer washes the soluble silver bromide away and leaves behind the insoluble grains of silver, which show up as small black dots. A stain may be applied to show the outlines and structures within. Finally, the cell is examined with a microscope. Autoradiographs typically show the black dots of exposed silver grains against a faint background of the surrounding cell structure. When higher magnification and resolution are desired, an electron microscope can be used.

In some studies, the radioactive nutrient is supplied to the cell for a short time interval, perhaps only a few minutes. This procedure is called *pulse-labeling*. Only those molecules that are being freshly synthesized in the cell during the "pulse" will incorporate radioactive atoms. Autoradiography will then show which cells were active.

When autoradiography is applied to chromosomes or other subcellular structures, the matter of resolution becomes very important. For high resolution to be obtained, the radioactive particles should have a short range within the photographic emulsion; the black dots of silver in the developed film should pinpoint the source of radioactive decay as precisely as possible. Tritium works very well because it emits low-energy beta particles, which travel only a few millimeters in the emulsion, producing a well-localized image on the film. Radioactive carbon 14 emits higher-energy beta particles, so the silver grains in the film are more diffuse and the resolution is not as high.

Autoradiography and Electrophoresis

Autoradiography also has been very useful in biochemistry research when combined with the methodology of *electrophoresis*. Living cells are exposed to radioactively labeled amino acids, which are gradually absorbed into the proteins. For electrophoresis, the cells are transferred to a gel to which a voltage has been applied. The protein molecules will diffuse along the gel and be sorted out by their relative molecular weights. A photographic emulsion then is placed over the gel. Radioactivity from the proteins exposes the film, producing an image with black spots that show the distances that the different molecules drifted in the gel. The relative molecular weight of complex molecules that contain many thousands of atoms can be determined in this way.

One commercial catalog of radioactive materials lists many hundreds of organic chemicals that have been labeled with radioactive tritium. The other most common radioactive isotopes used for autoradiography are carbon 14, phosphorus 32, and sulfur 35. A large inventory of labeled chemicals has become available for the continuing use of radioactive tracers in biological research.

Applications

Autoradiography has been used in biology on the macroscopic level to study the uptake of radioactive tracers by both plant leaves and animal organs. Since the 1960's the technique has been applied to successively smaller structures, such as individual cells, chromosomes and organelles within a cell, strands of DNA, and protein molecules. It is easier to understand the microscopic applications after first looking at a large-scale example.

In one experiment, bean plants were grown in a nutrient solution containing radioactive phosphorus. The phosphorus moved from the roots to the leaves as expected, shown by an autoradiograph of a leaf pressed against photographic film. When the bean plant is allowed to continue growing in a nonradioactive solution, autoradiography shows that radioactive phosphorus is withdrawn from older leaves and translocated to new leaves and buds. Evidently, nutrients not only travel up from the roots but also move around the plant. In another experiment, a solution containing phosphorus was sprayed directly onto the leaf surface and was shown to migrate away from it. Redistribution of nutrients on an even larger scale takes place in deciduous trees, where as much as 90 percent of some minerals are withdrawn from leaves before they fall.

Practical Applications

In agricultural research, the effectiveness of herbicides, insecticides, and fertilizers is studied to determine which ones can increase productivity without causing serious environmental problems. Radioactive phosphorus can be used in this regard to study plant metabolism. The uptake of iron or zinc from the soil and their circulation in a plant can be studied to ascertain the effect of soil acidity and chemical form. Sometimes the presence or absence of other elements can inhibit translocation of an essential nutrient. New plant growth regulators may move from one plant through the soil to a nearby untreated plant. Autoradiography is an important analytical technique for observing the route of micronutrients and discovering what factors can change their mobility in a plant.

The sequence of bases in DNA molecules can be decoded by using electrophoresis combined with autoradiography, and the study of DNA sequences is crucial to research in many diverse areas of biology. Although alternatives to using autoradiography in DNA sequencing are now common, autoradiography is still a standard technique used in many other aspects of molecular biology.

Hans G. Graetzer, updated by Bryan Ness

See also: Electrophoresis.

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BACTERIA

Categories: Bacteria; medicine and health; microorganisms; taxonomic groups

The earliest organisms to appear on earth, bacteria form one of the three domains of life in the three-domain system. They are structurally the smallest, physiologically the simplest, and ecologically the most widespread and abundant of all living organisms.

Although only a few thousand species are known, Bacteria are often extremely abundant; a handful of soil or a spoonful of the organic muck at the bottom of a pond may hold several million bacteria. So tiny are these smallest of living organisms that a quarter of a million of them can be squeezed into the period at the end of this sentence. Bacteria are undoubtedly the most widely distributed of all organisms in nature. They occur everywhere: in soil, water, and in the air, as well as within the bodies of virtually all plants and animals.

Bacteria represent the earth's earliest, and in many ways the earth's simplest, living organisms. Fossils of bacteria have been found in rocks estimated at 3.5 billion to 3.7 billion years old. Thus, bacteria predate eukaryotic cells by at least a billion years.

Although small and simple, bacteria are ecologically and economically among the most important of all living organisms. They are the major organisms of decay and decomposition, fermentation, and nitrogen fixation. Activities such as spoiling of food, rotting of flesh, decomposition of plants, and causing of disease are all evidence of bacterial activity; although the smallest, bacteria are hardly the safest of organisms. While the vast majority of bacteria are harmless or helpful, a small percentage causes serious and often fatal diseases in humans, other animals, and plants.

Algae and Bacteria

Bacteria are traditionally included in botany studies because they show a number of structural and physiological similarities to algae. One group, the blue-green bacteria (formerly called the blue-green algae), contain chlorophyll and manufacture food via photosynthesis. The bacterium *Prochloron* exemplifies the prochlorophytes, which are a group of photosynthetic bacteria that have chlorophylls *a* and *b* and carotenoids, which are precisely the same pigments that are found in green algae and plants. Other similarities to plants include flagella, found in some bacteria, that are similar to the paired flagella found in some algae but unlike the flagella characteristic of some of the simplest animals, the protozoa.

Characteristics and Classification

All bacteria are single-celled prokaryotic organisms (a prokaryote is a cell that lacks a nucleus). Traditionally, there are two groups of prokaryotic bacteria, the *Archaea* or *Archaebacteria* (ancient bacteria), and the true bacteria, which are classed as *Bacteria* or *Eubacteria*. Both groups comprise minute organisms that vary in size from about 0.2 to 10 micrometers in diameter. In comparison, eukaryotic cells range from about 10 to 100 micrometers in diameter.

Bacteria number some four thousand to five thousand species, but evidence based on recent deoxyribonucleic acid (DNA) studies indicates that many more species probably await identification. Part of the problem in discovering new species of bacteria is their lack of sexual reproduction, which is often an important criterion used in identifying species in other organism groups.

Known bacteria are classified on the basis of shape, DNA or ribonucleic acid (RNA) arrangements, locomotion, pigments, and staining properties. Taxonomists increasingly rely on DNA and RNA comparisons to identify new species and determine relationships among bacteria.

In the five-kingdom classification scheme, all bacteria are placed in the kingdom *Monera*, which consists of all of the prokaryotic animals. In the three-domain classification of life, the bacteria are placed in the domain *Bacteria*, while the other group of prokaryotes, the *Archaebacteria* (ancient, simple bacteria thought to represent earliest forms of life but now limited in distribution) are placed in the domain *Archaea*. All other living organisms, including the protistans, fungi, plants, and animals, are classed in the domain *Eukarya* (because they are formed by eukaryotic cells, that is, cells that have a nucleus).

Structure

Bacteria are single-celled organisms encased within a cell wall and lacking a central nucleus. They have a relatively homogenous cytoplasm devoid of membrane-bound organelles, such as Golgi bodies, endoplasmic reticulum, mitochondria, or plastids, but sites along the cell membrane perform some of these organelle functions. Bacteria do have ribosomes for protein synthesis, but these are about half the size of ribosomes that are found in the eukaryotic cells of higher plants and animals.

The nucleic acid of bacterial DNA occurs as a single naked, ringlike form called a nucleoid, which is attached to the cell wall. Bacteria also have small rings of DNA called plasmids, which are dispersed within the cytoplasm. The plasmids replicate separately from the nucleoid, suggesting that they were originally separate organisms that were somehow incorporated into the bacterial system.

The cell walls of bacteria help maintain shape and provide rigid protection. Unlike cell walls of plants, which are composed mostly of cellulose, bacterial cell walls contains *peptidoglycans*, which consist of large amino acid molecules cross-linked to molecules of polysaccharides. Antibiotics, such as penicillin, work by inhibiting cell wall formation and repair, thereby destroying the bacterial cell.

Reproduction

Most bacterial reproduction is asexual, with individual cells undergoing a form of mitosis called binary fission, during which the nucleoid and plasmids replicate themselves and then migrate to opposite ends of the dividing cell. The cell wall pinches inward to form an interior wall that separates the dividing cell into the two new daughter cells. Under ideal conditions, binary fission can take place every ten to twenty minutes.

Some species can also exchange genetic material by a process called *conjugation*. Conjugation occurs when two compatible bacteria come into close contact with each other. The cell wall of one of the two bacteria evaginates (grows outward) toward its partner and merges with it to form a hollow, connecting tube called a pilus. When the tube is complete, the DNA segment migrates through the tube to the recipient cell, where it merges with and becomes part of the recipient cell's nucleoid.

Another process of genetic transfer occurs when a bacterium picks up fragments of DNA released by fragmented dead bacterial cells and incorporates the fragments into its own nucleoid. The absorbed DNA increases the genetic variability of the bacterial cell, and new characteristics may result from the interactions of the original genetic material with the newly acquired genetic material.

Shapes

Bacteria occur in three basic body forms, which also serve as a simple method for recognizing and classifying them. *Cocci bacteria* are round, elliptical, or spheroid in shape. Rod-shaped bacteria are called *bacilli*. The third bacterial form, called *spirilla*, are greatly elongated coils and are often corkscrew-shaped. Spiral bacteria are often twisted in the form of a helix or spiral. Cocci bacterial cells may occur in several different forms; in irregular clusters they are called staphylococci, which cause the well-known staph infections. Those in filimentlike chains or beadlike chains are called streptococci, which cause strep throat, while cocci that occur in pairs are called diplococcus. In all of these forms, each cell is completely independent.

Sheaths and Surfaces

Bacteria can develop slimy or gummy capsule-like sheaths around their cells, which, in addition to body shapes and pigments, helps taxonomists to classify them. Outside the cell walls of some bacteria are sticky capsules, or slime layers, that are made up of polysaccharide or protein. These capsules help certain bacteria that cause disease avoid being detected by an animal's immune system.

Some bacteria have a mass of hairlike projections called *pili* covering their surface. They are made of protein, and they generally function to attach to the bacteria of other cells. The tubelike pili found in some bacteria serve as attachment structures that enable the bacteria to remain fastened in place to a suitable substrate. Infectious bacteria, such as the bacteria involved in the sexually transmitted disease gonorrhea, use the pili to attach to the cell membranes of the host, causing infection.

Motility

Although many bacteria are nonmotile, some filamentous bacteria have slender flagella that slowly rotate, propelling them through the medium in a spiraling glide. Flagella help bacteria to move into new habitats, to follow nutrients, and to leave environments that are nonbeneficial. Flagellated bacteria may move toward or away from stimuli, a behavior which is known as a *taxis*. Bacteria that move in response to chemicals in their environment are called chemotactic; those that move toward or away from light are *phototactic*, while *magnetotatic* bacteria respond to the earth's magnetic field. Occurring in aquatic habitats, the magnetotatic bacteria are able to detect the earth's magnetic field using iron crystals within their cytoplasm that act as tiny magnets.

If environmental conditions become unfavorable, some bacteria form structures called endospores, which consist of genetic material along with a few enzymes enclosed inside a thick protective layer. Endospores can survive for long periods of time in extremely unfavorable conditions and are also important dispersal mechanisms because they can travel for long distances in the air or water, then produce new bacteria quickly as soon as they find conditions that are favorable.

Nutrition

A major reason for the success of the bacteria is in their various forms of nutrition. All bacteria are either autotrophic (able to manufacture their own food) or heterotrophic (obtaining food by feeding on plants or animals or their remains). The majority of heterotrophic bacteria are saprobes that obtain food directly from the environment by absorbing it across the cell wall, but some are important parasites that cause disease. Other types of bacteria are *chemosynthetic*, gaining energy through reactions that combine oxygen with inorganic molecules, such as sulfur, ammonia, or nitrite. During the process, they release sulfates and nitrates, crucial plant nutrients, into the soil.

Certain types of bacteria have the ability to break down cellulose, the primary component of plant cell walls. Some of these types of bacteria have formed a symbiotic relationship with mammals called ruminants, which include deer, sheep, and cows. The cellulytic bacteria manufacture and release cellulose-digesting enzymes. They are considered symbiotic because they provide enzymes that enable the animal to digest food it would otherwise be unable to process. In turn, they inhabit an optimum environment deep within the animal's stomach and have nutrients supplied directly to them. Other symbiotic bacteria live in the intestines of humans and other animals. They feed on undigested food passing through the gut and synthesize vitamins K and B_{12}, which are absorbed into the human body.

Another extremely important group of symbiotic bacteria are the *nitrogen-fixing bacteria*, which are one of the very few groups of organisms able to extract molecular nitrogen from the atmosphere and incorporate it in organic compounds. This ecologically and economically important group grows within root nodules—small, rounded clumps that cluster along the roots of certain plants, such as alfalfa, soybeans, lupines, and clover.

Archaea

Classed as either the *Archaebacteria* or *Archaea* and considered to be the most primitive prokaryotes, the *Archaea* differ from true bacteria (in some classification schemes) in the unique structure of their RNA molecules, in lacking muramic acid in their cell walls, and in the production of distinctive lipids. The *Archaea* are usually divided today into three groups: methane bacteria, salt bacteria, and thermophilic bacteria.

Methane bacteria are the most diverse *Archaea*. They are anaerobic organisms that live in the mud of swamps and marshes, in the murky debris of ocean floors, hot springs, lake sediments, animal intestines, sewage treatment plants, and other areas in which free oxygen is not available. Methane bacteria are so-named because they metabolically generate methane gas from carbon dioxide and hydrogen during their energy-producing process.

The salt bacteria, or *halophiles*, are another ancient group that today are mostly confined to life in shallow, saltwater evaporation ponds common in parts of the western United States. When abundant, salt bacteria can give these ponds a distinctive red color. Their metabolism enables them to thrive under conditions of extreme salinity. Salt bacteria carry on simple photosynthesis using a red pigment called bacterial rhodopsin.

The *thermophiles*, or heat-loving bacteria, consist mostly of the sulfur-metabolizing bacteria that

Some Bacterial Diseases of Plants

Bacterium	*Diseases*
Argobacterium	Cane gall, crown gall, hairy root, twig gall
Clavibacter, Rhodococcus	Fasciation, spots, ring rots, tomato cankers, wilts
Erwinia	Blights, wilts, soft rots
Pseudomonas	Banana wilts, bud blasts, cankers, leaf spots, lilac blights, olive galls
Xanthomonas	Black venation, bulb rots, citrus cankers, cutting rots, walnut blights
Rhizobium	Root nodules (legumes)
Streptomyces	Potato scabs

Source: Data are from Peter H. Raven et al., *Biology of Plants*, 6th ed. (New York: W. H. Freeman/Worth, 1999).

thrive in sulfur hot springs, thriving at temperatures ranging from 80 degrees Celsius to 100 degrees Celsius. Some of the thermophilic bacteria are heterotrophic, but most are chemosynthetic and obtain their metabolic energy by forming hydrogen sulfide from elemental sulfur and water.

Cyanobacteria

The true bacteria have muramic acid in their cell walls. The majority are heterotrophic or parasitic, but some very important groups are autotrophic. Two groups of true bacteria are recognized, eubacteria and the cyanobacteria or blue-green bacteria.

The *cyanobacteria*, or blue-green bacteria, formally known as the blue-green algae, are different from true algae as they are prokaryotic, while all of the green algae are eukaryotes. Blue-green bacteria possess chlorophyll *a*, which is also found in green plants. Many blue-green bacteria also have a blue pigment called phycobilin, a red pigment called phycoerythrin, and carotenoids, which help gather light energy for photosynthesis. Their distinctive blue-green color is caused by the combination of chlorophyll and phycocyanin pigments. Blue-green bacteria are the only organisms that can fix nitrogen and produce oxygen at the same time, producing a nitrogenous food reserve called cyanophycin. They are also able to produce and store carbohydrates and lipids.

Blue-green bacteria occur in chains or hairlike filaments. Some form irregular, spherical, or plate-like colonies held together by gelatinous sheaths. These sheaths may be colorless or pigmented with shades of yellow, red, brown, green, blue, violet, or blue-black. Blue-green bacteria lack flagella but move by rotating on their longitudinal axis, which gives them a forward-gliding motion.

Blue-green bacteria occur in soil, in water, on moist surfaces, and in root nodules of plants. They are common in temporary pools and ditches and often very abundant in freshwater habitats. Blue-green bacteria are among the first invaders of newly formed habitats, such as the ash fields around volcanoes and newly opened fissures along deep-sea volcanic ridges and mounts. They are even found in tiny fissures in desert rocks. Some species occur in jungle soils and on the shells of turtles and snails. Others live as symbionts within amoebae, protozoans, diatoms, sea anemones, fungi, and the roots of tropical cycads.

Over billions of years, the photosynthetic activity of blue-green bacteria transformed the oxygen-free early atmosphere into the modern atmosphere, in which oxygen plays such an important role for all higher plants and animals. The accumulation of oxygen in the upper atmosphere produced the high-altitude ozone layer, which shields animals and terrestrial plants from the damaging effects of ultraviolet radiation.

Ecologically, blue-green bacteria form the base of many food chains, especially in freshwater and marine habitats. During the warm months of the year, blue-green bacteria can temporarily become abundant and form floating mats of pond scum that often cover quiet waters of ponds and wetlands in late summer. The sudden increase of populations produce algal blooms (eutrophication) that cause massive die-offs of plant and animal populations because the bacteria populations consume all of the available oxygen in the water, thereby asphyxiating other organisms. In reservoirs and other human water supplies, large populations of blue-green bacteria clog filters, corrode steel and concrete structures, and cause a natural softening of water.

They produce odors and discoloration which sometimes make water unpalatable.

Eubacteria

The *eubacteria* include the unpigmented bacteria, purple bacteria, green sulfur bacteria, and the prochlorophytes. The eubacteria also include two groups of uncertain relationships: the mycoplasmas and the prochlorophytes. Most eubacteria are heterotrophic saprobes that absorb food directly from their environment. Many of these bacteria are extremely important decomposing organisms which, along with soil fungi, are responsible for the decay of all types of organic matter and the release of minerals back into the soil.

A few eubacteria are autotrophic. The purple sulfur bacteria, the purple nonsulfur bacteria, and the green sulfur bacteria all are photosynthetic bacteria that use sunlight energy to fragment hydrogen sulfide into sugar, water, and sulfur. Chemoautotrophic bacteria obtain energy by oxidizing compounds of iron, hydrogen, and sulfur. Some of the true bacteria are parasitic, living in or on living organisms and depending on them for food. Many of these parasitic forms are responsible for serious diseases in humans and other animals.

Beneficial True Bacteria

The number of true bacteria that are beneficial organisms for humans is much greater than the number of disease-causing bacteria. The use of bacteria as biological control agents is typified by *Bacillus thuringiensis* (*B.t.*), bacteria available in garden shops as a spray or powder. Placed on plants, it kills caterpillars and worms. It is sold as a mass-produced, stable, moist dust containing millions of spores of the bacteria. It is harmless to humans, birds, earthworms, and other creatures, except moth or butterfly larvae. When the caterpillar ingests the bacterial spores, they develop into bacilli, which multiply in the digestive tract and paralyze the gut of the worm. The crop pest usually dies as a result of ingestion in two to four days. Other varieties, such as *Bacillus thuringiensis* (variety *israelensis*, or *B.t.i.*),is used to control mosquitoes, while Japanese beetles can be controlled by application of a bacterial power containing *Bacillus popilliae*, which is specific to this beetle.

Other bacteria have important uses in the service of humans. Some are used in bioremediation projects, such as the cleanup of oil spills, sewage treatment plants, and toxic waste dumps. *Pseudomonas capacia*, for example, is used to decompose oil spills. More benefits from bacteria are being developed using genetic engineering techniques.

Bacteria also play a major role in the dairy industry as cultures in the production of buttermilk, acidophilus milk, yogurt, sour cream, kefir, and cheese. Whey, the watery part of milk left in cheese production, is used in the manufacture of lactic acid. Lactic acid from lactate bacteria is also used in the textile industry, in the preparation of laundry products, in leather tanning, and in the treatment of calcium and iron deficiencies.

Bacteria are cultured in vats and used to manufacture chemicals, such as acetone, butyl alcohol, dextran, sorbose, citric acid, some vitamins, and medicinal preparations. Bacteria are also used to cure vanilla pods, cocoa beans, coffee, and black tea. They are used in the production of vinegar, sauerkraut, and dill pickles. Fibers from linen cloth are separated from flax stems by bacterial action. Green plant material is fermented in silos, providing food for livestock through the action of bacteria. Lastly, bacteria producing the amino acid glutamic acid are used to produce monosodium glutamate (MSG), a common food ingredient.

Plant-Pathogenic True Bacteria

Almost all plants are susceptible to a host of bacterial diseases which cause infections, rotting, and death. Economically, the plant-pathogenic bacteria result in enormous losses of crops and other plant products. It has been estimated that about one-eighth of crops are annual losses to plant diseases.

Plant diseases caused by bacteria include galls, rots, wilts, spots, fascination, blights, and soft rots. *Blights* are caused when bacteria invade plant tissues of stems, leaves, and flowers, producing dead and discolored areas of infection. Fruits and vegetables not completely destroyed are sufficiently discolored to be unmarketable. *Soft rots* typically occur in fleshy storage organs, such as potatoes, eggplants, squashes, and tomatoes. Bacterial infections that cause drooping or wilting of plant tissues are called *wilts*. Wilts occur when bacteria colonize xylem vessels, where they block or interfere with water transport, eventually leading to dysfunction and destruction of the plant. *Galls* are plant swellings produced when bacteria and other organisms invade leaves and stems and lodge in parenchyma tissue. The infected tissue swells to produce a gall that encases the bacterial colony.

Human-Pathogenic Bacteria

Although bacteria do provide some benefits with their feeding habits, certain bacteria have feeding habits that threaten the health of humans. The largest threats stem from bacterial infection. These disease-producing bacteria, which are scientifically referred to as pathogens, synthesize toxic substances that cause disease symptoms. For example, bacteria such as *Clostridium tetani* and *Clostridium botulinium*, which cause, respectively, tetanus and botulism, the latter a deadly form of food poisoning. These bacteria produce toxins that attack the nervous system. Such bacteria are known as anaerobes, and they thrive as spores until they are introduced into a desirable environment. Tetanus enters the body through a deep puncture wound, protecting the bacteria from having contact with oxygen. As the bacteria multiply, they release their poison into the bloodstream.

Bacteria can enter the human body from the air. Every time someone coughs, sneezes, or speaks loudly, they produce an invisible spray of saliva droplets containing bacteria. The fluid around these bacteria quickly evaporates, but the bacteria cling to protein flakes that were also expectorated and enter the lungs during breathing. Once inside the lungs, bacteria access the circulatory system, via which they are transported to tissues and organ systems. Legionnaire's disease is caused by a bacterium that lives in small amounts of water in air conditioning systems. It can be transmitted throughout an entire building by airborne particles that are blown through the air conditioning ducts. In a particularly deadly form of infection, anthrax bacilli can be inhaled, lodge in the lungs, and quickly kill the host.

Bacteria also gain access to the body through the ingestion of contaminated food and water. Bacterial infections caused by eating contaminated food are widespread, especially in the less developed countries of the world. Open sewers and unsanitary toilet conditions increase the risk of waterborne bacterial diseases, such as cholera, dysentery, and food poisoning, such as salmonella. Bacteria may also be ingested via improperly stored foods, such as raw chicken, shellfish, and eggs. Once ingested, the bacteria multiply in the intestinal tract and can be passed with urine.

Some bacteria gain access to the body through direct contact. Most of the sexually transmitted diseases are caused by bacteria. Examples include syphilis and gonorrhea. Other diseases, such as anthrax and brucellosis, enter the body through the skin or mucous membranes. Contact anthrax (less deadly than inhalational anthrax, if treated quickly) is a disease of cattle and other farm animals which occasionally infects humans. It is transmitted to workers in the tanning industry who handle hides and wool. Brucellosis is also a disease from farm animals and is transmitted by contaminated milk. It is sometimes called undulant fever and is characterized by a daily rise and fall of temperature associated with the cyclic release of the toxins by the bacteria.

Other bacteria that live in the soil enter the body through wounds. The tetanus or "lockjaw" bacterium, mentioned above, is a common soil organism. Puncture wounds caused by stepping on dirty nails and other sharp devices introduce the tetanus bacteria deep into the body. Once inside, it produces toxins that are extremely powerful. Tetanus is easily controlled by immunizations that are developed from an attenuated horse serum. Some soil bacteria can cause a disease called gas gangrene. These bacteria respire anaerobically in the body and basically destroy tissues while emitting damaging gases (hence their name). If untreated, a serious infection by gas gangrene bacteria can result in the loss of a limb.

Many bacteria gain access to the human body through the bites of insects and other organisms. If an organism transmits a disease-causing organism to a different host, the first organism is called a *vector*. Many of the most feared and deadly of human diseases are caused by bacteria that are transmitted by vectors. Bubonic plague (black death) and tularemia are transmitted by fleas, deer flies, ticks, or lice. Of these, the most famous—and historically the most deadly—is bubonic plague, which is transmitted by fleas of rats and other rodents. Throughout recorded history, periodic visitation of plagues resulted in catastrophic die-off of thousands and even millions of people. The populations of Thebes, Athens, Rome, Vienna, and other early cities suffered and survived many plague years. The most potent plague years were in the late Middle Ages, when nearly a third of the European population succumbed to the bacterial disease. Bubonic plague is still found today in the United

States in ground squirrel populations and other rodents as well.

Mycoplasmas and Other "Small" Bacteria

The *mycoplasmas*, *rickettsiae*, and *chlamydiae* are small and simple prokaryotes that are sometimes collectively labeled "small bacteria." Of these, the mycoplasmas are the smallest of all bacteria and therefore the smallest of all living organisms, since viruses do not qualify as life. Mycoplasmas are distinctive in that, unlike other bacteria, they lack a cell wall. The relationships and diversity of mycoplasmas are still poorly understood, but the mycoplasmas have the distinction of being the smallest known organisms to cause human disease. One form causes a sexually transmitted disease and another, *Mycoplasma pneumonia*, causes a form of pneumonia commonly called walking pneumonia.

The *rickettsiae* are tiny bacteria that were first described by Howard Ricketts in 1909. *Rickettsiae* species are mostly transmitted by animal vectors, such as ticks and lice, and cause typhus and Rocky Mountain spotted fever. The *chlamydiae* are usually considered to be a subgroup of rickettsiae. Some *chlamydiae* are airborne diseases, among them *Chlamydia psittaci*, which causes parrot fever, or psittacosis. Humans are exposed to parrot fever by inhaling the dried droppings or dust from infected birds. Another airborne chlamydial disease of humans is transmitted by respiratory droplets containing *Chlamydial pneumonia*. This causes a mild form of walking pneumonia in humans. Other chlamydia cause sexual diseases which resemble gonorrhea and can result in serious infections of the urogenital tract if undetected or left untreated.

Prochlorophytes

Also designated as the *prochlorobacteria*, these bacteria were discovered in 1976 by Ralph Lewin of the Scripps Institute of Oceanography. The prochlorophytes are of considerable scientific interest because they have photosynthetic pigments (chlorophyll *a* and *b*) that are found in higher plants, thereby hinting at possible relationships between this group of bacteria and higher plants. In structure and characteristics, the prochlorophytes are closely related to true bacteria, however.

Genetic Engineering with Bacteria

Since they are relatively simple organisms that can easily be cultivated in large numbers, bacteria are one of the most important of all groups of organisms used in scientific experiments. As a result, they have been the subject of much genetic engineering, which is the artificial introduction of DNA into bacteria to change their characteristics. Genetic engineering is also called gene splicing and begins with the isolation of plasmid DNA from a bacterium. The DNA molecule is broken up into separate genes or groups of genes by special enzymes called restriction enzymes. The resulting DNA fragments are then mixed with repair enzymes and injected into another bacterium, which absorbs the new genes and functions in a new way under the influence of the new genes or combination of genes.

Dwight G. Smith

See also: Algae; Anaerobic photosynthesis; *Archaea*; Biotechnology; Chemotaxis; DNA: recombinant technology; Eutrophication; Food chain; Genetically modified bacteria; Halophytes; Nitrogen fixation; Photosynthesis; Prokaryotes.

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BACTERIAL GENETICS

Categories: Bacteria; disciplines; genetics; microorganisms; reproduction and life cycles

Bacterial genetics is the study of the genetic material of bacterial DNA, which can provide valuable insights into the process of mutation because of bacteria's rapid rate of reproduction.

Plants were the original candidates for genetic studies, which began in the late 1800's. Studies with animals soon followed; bacteria did not become candidates for such study until the mid-1940's, when adequate technology for handling bacteria developed. Bacteria have become extremely useful organisms for genetic studies since the early 1950's. Two major features of bacteria make them desirable subjects. First, bacterial cells typically divide every twenty minutes. Their rapid rate of reproduction allows a very large number of bacteria to be produced in a short time. This, in turn, provides the researcher with more opportunity to detect the "rare genetic events" of *mutation* or *recombination*. Even more important, unlike all other organisms, bacteria have a single *chromosome* with a single set of *genes*. Thus, genetic modifications are more likely to result in immediately observable changes. In organisms that have multiple chromosomes, a change in a single gene may go undetected because its effect is masked by genes on other chromosomes.

Bacterial DNA

All bacteria have a single circular chromosome, composed of deoxyribonucleic acid (DNA). The DNA is subdivided into specific message areas known as genes, and the chromosome carries from four thousand to five thousand individual genes. For many bacteria, this constitutes the entirety of its genetic information. A number of bacteria, however, have additional DNA in the form of *plasmids*. A plasmid is a small additional circular piece of DNA, independent of the chromosome, which can hold an additional twenty to one hundred genes. Plasmid-containing cells often have several plasmids.

Many researchers have described the plasmid genes as nonessential to the normal activities of bacteria. Under certain circumstances, however, those genes might provide a survival advantage to the possessor. For example, genes for antibiotic resistance are often carried on a plasmid. Normally, antibiotics are not present in the bacteria's environment; such resistance genes would therefore be unnecessary. If the bacteria later were to come into contact with antibiotics, however, having antibiotic-resistant genes would be to their distinct advantage.

Two major types of plasmids exist: F plasmids, or *fertility plasmids*, and R plasmids, or *resistance plasmids*. Both types can carry resistance genes. Only the F plasmids, however, are able to control the formation of a special cytoplasmic tube known as the sex pilus. Cells with the F plasmids are known as F+, or donor cells. Cells without the F plasmids are called F-, or recipient cells.

Conjugation

The plasmid is a prerequisite to one type of genetic exchange, conjugation. During conjugation, the donor cell copies its plasmids and transfers them to a recipient cell to which it has attached itself by means of a sex pilus. The recipient cell can now take advantage of whatever additional genes it has received. If, in the process, it received an F plasmid, it has also become a potential donor cell. Whenever bacterial cells undergo cell division, any plasmids they possess are typically passed on to their progeny. Originally it was thought that conjugation could occur only between members of the same species, but that is not always true. For example, it is now known that some strains of the bacteria responsible for causing gonorrhea, *Neisseria gonorrhoeae*, have received antibiotic-resistant genes from unrelated species of bacteria.

There is one other type of donor cell, the Hfr+, or high-frequency recombinant, cell. Instead of the plasmid remaining independent of the cell's chromosome, it inserts itself into the chromosome. When that plasmid gets ready to copy itself, the chromosomal genes are the first to be copied. Unless the donor and recipient cells are able to maintain direct contact for a fairly long period of time, which almost never occurs, the recipient cell will not receive the plasmid. It will, however, receive numerous chromosomal genes from the donor. Those genes may later be incorporated into the chromosome of the recipient, causing gene replacement.

Not all species of bacteria participate in conjugation. Some rely on transduction as a means of receiving new genetic information. This is how *Staphylococcus aureus* has developed resistance to many antibiotics.

Transduction

There are two types of transduction: generalized and specialized. In both cases, a donor cell becomes infected with a *bacteriophage*, a virus that attacks bacteria. Upon the death of that donor cell, fragments of donor DNA are transferred as the escaping bacteriophage infects another bacterium.

In generalized transduction, a bacteriophage infects a bacterial cell. Shortly after infection, the bacterial chromosome becomes fragmented, and viral components are produced. Later the viral components are assembled to form a complete virus particle. Occasionally during this assembly process, a particle becomes contaminated with fragments of the bacterial chromosome or plasmids. After assembly is completed, the bacterial cell ruptures, allowing the escape of all virus particles. Eventually these virus particles will invade other bacterial cells. Any cells that are invaded by contaminated bacteriophage particles are said to be transduced, because they have received DNA from another bacterium. The DNA received in this manner is strictly random.

Specialized transduction involves what is known as a *latent bacteriophage*. After the initial invasion of a bacterium, the bacteriophage inserts itself into a specific region of that cell's chromosome. At some later time, the bacteriophage removes itself from the chromosome and accidentally takes a few bacterial genes located near its original insertion point. When the bacterial cell finally begins making new bacteriophage components, it behaves as if those particular genes are part of the bacteriophage and replicates them as such. Therefore, all the newly formed bacteriophage particles will contain those bacterial genes. Transduction then occurs when these bacteriophage particles invade other bacterial cells.

Transformation

The final method of genetic transfer is transformation. An extensively utilized organism for such investigation has been *Streptococcus pneumoniae*. The most famous studies involved converting nondisease-causing strains of *Streptococcus pneumoniae* into disease-causing strains. Transformation also occurs in a wide variety of other bacteria. The process of transformation requires that a population of actively reproducing bacteria come into contact with DNA fragments, often from closely related dead bacteria. These DNA fragments are referred to as either naked or cell-free DNA.

Genetic Modification

A small portion of that DNA can be absorbed and utilized by the growing bacteria. These recipients can then take advantage of any usable genes that the fragments might contain, incorporating them into their chromosome in place of their own copies of these genes by the process of recombination.

Conjugation, transduction, and transformation are all mechanisms of genetic change within a bacterial population. These mechanisms allow a specific characteristic to be spread throughout the population within a few hours. A wide number of bacterial genes have been found to be transferred by these methods, including genes that control a bacterium's ability to cause disease, to produce toxins, and to develop resistance to antibiotics and other drugs as well as genes that control a number of other characteristics. The purpose of these mechanisms, as far as the bacteria are concerned, is to enable the bacteria to adapt to changing environmental conditions so that their survival is ensured. Scientists, however, have found ways to adapt some of these mechanisms for human benefit.

Scientists have used the mechanisms of genetic transfer along with new technology from DNA research to perform *genetic engineering* on bacteria. They can use genes and specially engineered plasmids, called plasmid vectors, to make recombinant DNA in the laboratory. Recombinant plasmids can then be used to transform bacteria such as *Escherichia coli* (*E. coli*). The bacteria will treat these recombinant plasmids just like ordinary plasmids, replicating them and, for expression vectors, expressing any genes included in them. In this manner, bacteria can be used to produce a wide variety of products for medicine, agriculture, and industry. Genetic engineering and the products that result from it would not be possible without the knowledge of genetic transfer gained from studies of bacterial conjugation, transduction, and transformation.

Randy Firstman, updated by Bryan Ness

See also: Bacteria; Bacterial resistance and super bacteria; Bacteriophages.

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BACTERIAL RESISTANCE AND SUPER BACTERIA

Categories: Bacteria; environmental issues; medicine and health; microorganisms

Inappropriate use of antibiotics has caused bacteria to develop resistance to the most common antibiotics. Bacterial pathogens that have developed resistance to multiple antibiotics that previously could be used to control them are referred to as super bacteria.

Bacteria are the most adaptable living organisms on earth, found in virtually all environments—from the lowest ocean depths to the highest mountains. Bacteria can resist extremes of heat, cold, acidity, alkalinity, heavy metals, and radiation that would kill most other organisms. *Deinococcus radiodurans*, for example, grows within nuclear power reactors, and *Thiobacillus thiooxidans* can grow in toxic acid mine drainage. The term "super bacteria" generally refers to bacteria that have either intrinsic (naturally occurring) or acquired resistance to multiple antibiotics. Because many of the bacteria that acquire resistance are pathogens that previously could be controlled by antibiotics, development of antibiotic resistance is regarded as a serious public health crisis, particularly for those individuals who have compromised immune systems.

History of Antibiotic Use

In the early twentieth century German chemist Paul Ehrlich received worldwide fame for discovering Salvarsan, the first relatively specific prophylactic agent against the microorganisms that caused syphilis. Salvarsan had undesirable side effects because it contained arsenic. In addition, secondary infections resulting from hospitalization were still a leading cause of death in the early twentieth century. Scottish bacteriologist Alexander Fleming discovered a soluble antimicrobial compound produced by the fungus *Penicillium*. Two English scientists, Howard Florey and Ernst Chain, took Fleming's fungus and produced purified penicillin just in time for use during World War II.

Antibiotics such as penicillin are low-molecular-weight compounds excreted by bacteria and fungi. Antibiotic-producing microorganisms most often belong to a group of soil bacteria called *actinomycetes*. *Streptomyces* are good examples of antibiotic-producing actinomycetes, and most of the commercially important antibiotics are isolated from *Streptomyces*. It is not entirely clear what ecological role the antibiotics play in natural environments.

The success of penicillin as a therapeutic agent with almost miraculous effects on infection prompted other microbiologists to look for naturally occurring antimicrobial compounds. In 1943 Selman Waksman, an American biochemist born in Ukraine, discovered the antibiotic streptomycin, the first truly effective agent to control *Mycobacterium tuberculosis*, the bacterium that causes tuberculosis. Widespread antibiotic use began shortly after World War II and was regarded as one of the great medical advances in the fight against infectious disease. By the late 1950's and early 1960's, pharmaceutical companies had extensive research and development programs devoted to isolating and producing new antibiotics.

Antibiotics were so effective, and their production ultimately so efficient, they came to be routinely prescribed for all types of infections, particularly to treat upper respiratory tract infections. When it was discovered that low levels of antibiotics also promoted increased growth in domesticated animals, antibiotics began to appear routinely as feed supplements.

Development of Antibiotic Resistance

The widespread use and, ultimately, misuse of antibiotics inevitably caused antibiotic-resistant bacteria to appear, as microorganisms adapted to new selective pressure. There are now many strains of pathogenic organisms on which antibiotics have little or no effect.

Streptococcal infections are the leading bacterial cause of morbidity and mortality in the United States. In the mid-1970's *Streptococcus pneumonia* was uniformly susceptible to penicillin. However, penicillin-resistant strains were being isolated as early as 1967. A study in Denver, Colorado, showed that penicillin-resistant *S. pneumonia* strains increased from 1 percent of the isolates in 1980 to 13 percent of the isolates in 1995. One-half of the resistant strains were also resistant to another antibiotic, cephalosporin.

Tuberculosis was once the leading cause of death in young adults in industrialized countries, so common and feared that it was known as the White Plague. Before 1990 multidrug-resistant tuberculosis was uncommon. However, by the mid-1990's there were increasing outbreaks in hospitals and prisons, in which the death rate ranged from 50 to 80 percent. Likewise, multiple drug resistance in *Streptococcus pyogenes*, the so-called flesh-eating streptococci, was once rare. There are now erythromycin- and clindimycin-resistant strains.

Many old pathogens have become major clinical problems because of increased antibiotic resistance. The number of resistant isolates in England rose from 1.5 percent in 1989 to more than

The Growth of Antibiotic Resistance

Antibiotic	*Enterococcal Species*	*% of Resistant Bacteria*		
		1995	*1996*	*1997*
Ampicillin	*Enterococcus faecium*	69.0	77.0	83.0
	Enterococcus faecalis	0.9	1.6	1.8
Vancomycin	*Enterococcus faecium*	28.0	50.0	52.0
	Enterococcus faecalis	1.3	2.3	1.9

Note: Measurements taken over a three-year period indicate a general rise in enterococcal resistance to two common antibiotics.
Source: U.S. Centers for Disease Control.

34 percent in 1995. Gonorrhea, caused by *Neisseria gonorrhoeae*, is the most common sexually transmitted disease. Physicians began using a class of broad-spectrum cephalosporin antibiotics called fluoroquinolones because *N. gonorrhoeae* had become resistant to penicillin, tetracycline, and streptomycin. There is now real concern in the medical community that exclusive use of fluoroquinolones, the only antibiotics to which *N. gonorrhoeae* are routinely susceptible, has led to rapidly developing resistance. Even newly discovered pathogens such as *Helicobacter pylori*, which is associated with peptic ulcers, are rapidly developing resistance to the antibiotics used to treat them.

The development of resistance to some antibiotics appears to be linked to antimicrobial use in farm animals. Shortly after antibiotics appeared, it was discovered that subtherapeutic levels could promote growth in animals. One such antimicrobial drug, avoparcin, is a glycopeptide (a compound containing sugars and proteins) that is used as a feed additive. Vancomycin-resistant enterococci such as *Enterococcus faecium* were first isolated in 1988 and appeared to be linked to drug use in animals. Antibiotic resistance in enterococci has been more prevalent in farm animals exposed to antimicrobial drugs. Prolonged exposure to oral glycoproteins in tests led to vancomycin-resistant enterococci in 64 percent of the subjects.

Soap and Water

Even the use of household antibacterial agents contributes to bacterial resistance. Following are some everyday ways to deprive harmful bacteria of the chance to build up resistance and become even stronger, from the October, 1998, article "Antibacterial Overkill" in the *Tufts University Health and Nutrition Letter.*

- Use regular soap for hand-washing and regular dishwashing liquid in the kitchen, rather than cleaners containing an antibacterial agent. Soap loosens bacteria from dishes; running water then rinses them away. For the same reason, frequent hand-washing is the best way to get rid of unwanted bacteria.
- Cleaning products that contain bleach and chlorine disinfect (get rid of bacteria on) surfaces in the kitchen and bathroom. Because these cleaners are not antibacterial agents, however, they will not encourage the growth of resistant bacteria.
- Do not insist on antibiotics for a viral infection, such as the flu; they will not work. Antibiotics attack bacteria but not viruses. At a seminar conducted by Dr. Stuart B. Levy of Tufts University, more than 80 percent of the physicians present admitted to having written antibiotic prescriptions against their better judgment because of patient demands.
- Do not share prescription antibiotics with family or friends. Not knowing the dose they may need, or even whether they need any, could encourage the bacteria in their systems to develop resistance they might otherwise not have had.

How Antibiotic Resistance Occurs

Antibiotic resistance occurs because the antibiotics exert a selective pressure on the bacterial pathogens. This pressure eliminates all but a few bacteria that can persist through evasion or mutation. One reason antibiotic treatments may be prescribed for several weeks is to ensure that bacteria that have evaded the initial exposure are killed. Terminating antibiotic treatment early, once symptoms disappear, has the unfortunate effect of stimulating antibiotic resistance without completely eliminating the original cause of infection.

Mutations that promote resistance occur with different frequencies. For example, spontaneous resistance of *Mycobacterium tuberculosis* to cycloserine and viomycin may occur in 1 in 1,000 cells; resistance to kanamycin may occur in only 1 in 1 million cells; and resistance to rifampicin may occur in only 1 in 100 million cells. Consequently, one billion bacterial cells will contain several individuals resistant to at least one antibiotic. Using multiple antibiotics further reduces the likelihood that an individual cell will be resistant to all antibiotics used. However, it can cause multiple antibiotic resistance to develop in bacteria that already have resistance to some of the antibiotics.

Bacterial pathogens may not need to mutate spontaneously to acquire antibiotic resistance. There are several mechanisms by which bacteria can acquire the genes for antibiotic resistance from microorganisms that are already antibiotic-resistant. These mechanisms include *conjugation* (the exchange of genetic information through direct cell-to-cell contact), *transduction* (the exchange of genetic information from one cell to another by means of a virus), *transformation* (acquiring genetic information by taking up deoxyribonucleic acid, or DNA, directly from the environment), and transfer of *plasmids*, small, circular pieces of the genetic material DNA that frequently carry genes for antibiotic resistance.

Genes for antibiotic resistance take many forms. They may make the bacteria impermeable to the antibiotic. They may subtly alter the target of the antibiotic within the cell so that it is no longer affected. The genes may code for production of an enzyme in the bacteria that specifically destroys the antibiotic. For example, fluoroquinolone antibiotics inhibit DNA replication in pathogens by binding to the enzyme required for replication. Resistant bacteria have mutations in the amino acid sequences of this enzyme that prevent the antibiotic from binding to this region.

New Strategies

The increased use of antibiotics has led to increases in morbidity, mortality caused by previously controlled infectious diseases, and health costs. Some of the recommendations to deal with this public health problem include changing antibiotic prescription patterns, changing patient attitudes about the necessity of antibiotics, increasing the worldwide surveillance of drug-resistant bacteria, improving techniques for susceptibility testing, banning the use of antibiotics as animal feed additives, and investing in research and development of new antimicrobial agents.

Gene therapy is regarded as one promising solution to antibiotic resistance. In gene therapy, the genes expressing part of the pathogen's cell are injected into a patient and stimulate a heightened immune response. Some old technologies are also being revisited. There is increasing interest in using serum treatments, in which antibodies raised against a pathogen are injected into a patient to cause an immediate immune response. Previous serum treatment techniques have yielded mixed results. However, with the advent of monoclonal antibodies and the techniques for producing them, serum treatments can now be made much more specific and the antibodies delivered in much higher concentrations.

There have been numerous reports from Russia about virus treatment for pathogenic infections. Viruses attack cells in all living organisms, including bacteria, but are extremely specific, so that they will not infect more than one type of cell. In essence, virus treatments are a form of *biocontrol*. In virus treatments, the patient is injected with viruses raised against specific pathogens. Once injected, the viruses begin specifically attacking the pathogenic bacteria. Although this technology has not been widely used, it is the subject of growing research.

Mark S. Coyne

See also: Bacteria; Biopesticides.

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BACTERIOPHAGES

Categories: Diseases and conditions; genetics; microorganisms

Viruses that attack bacterial cells are known as bacteriophages. Many results gained from studying bacteriophages have universal implications. For example, the physical properties of DNA and RNA are remarkably identical in all organisms, and these are perhaps easiest to study in bacteriophage systems.

Bacteriophages, or phages for short, are viruses that parasitize bacteria. Viruses are an extraordinarily diverse group of ultramicroscopic particles, distinct from all other organisms because of their noncellular organization. Composed of an inert outer protein shell, or *capsid*, and an inner core of nucleic acid—either *deoxyribonucleic acid* (DNA) or *ribonucleic acid* (RNA) but never both—viruses are obligate intracellular parasites, depending to a great extent on host cell functions for the production of new viral particles.

There is considerable variation in size and complexity among viruses. Some have fewer than ten genes and depend almost entirely on host functions. Others are known to contain from thirty to one hundred genes and rely more on proteins encoded by their own DNA. Even the largest viruses are too small to be seen under the light microscope, so studies on viral structure rely heavily on observation with the transmission electron microscope.

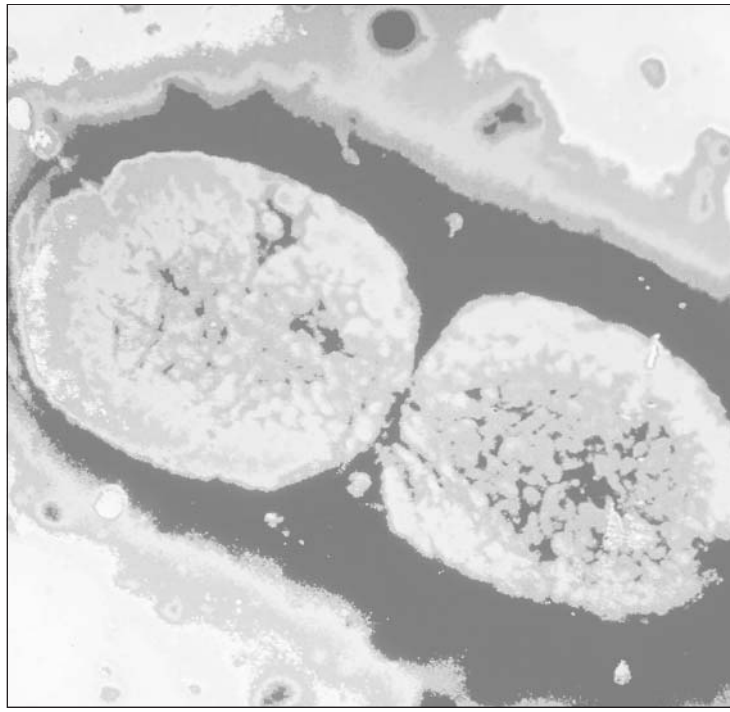
The Study of Bacteriophages

Because scientists know more about the molecular and cell biology of the common bacterium *Escherichia coli* than about any other cell or organism, it is perhaps not surprising that the best-known phages are those that require *E. coli* as a host (*coliphage*). It is not possible to observe phage growth directly (as bacterial growth can be detected by the appearance of colonies on an agar plate), but phage growth can be indirectly observed by the formation of plaques, small clear areas in an otherwise continous lawn of host bacteria growing on a solid growth medium in a petri dish.

Reproductive Cycles

Bacteriophages can multiply by two different mechanisms, termed the *lytic cycle* and the *lysogenic cycle*. Some phages are capable only of lytic growth, while others retain the ability to reproduce by either lytic growth or entry into the lysogenic cycle. In the lytic cycle, phages first attach themselves to specific receptor sites on the host cell wall. The phage nucleic acid (DNA or RNA) is injected inside the host, while the protein capsid of the infecting particle remains outside of the host cell at all times. Once the DNA or RNA is inside, transcription of phage genes begins, and phage-encoded proteins begin to be made. Some of these proteins serve to inactivate and destroy the host cell DNA, ensuring that the cell's energy resources will be directed exclusively toward the production of phage proteins and the replication of phage nucleic acid. Phage DNA or RNA replication ensues quickly and is followed by the packaging of this genetic material into the newly synthesized capsids of the progeny phage particles. The final step is host cell lysis—the bursting of the host cell to release the completed and infective phage progeny. The number of phages released in each burst varies with growth conditions and species, but ideal conditions often result in a burst size of one hundred to two hundred per host cell.

For temperate bacteriophages, those capable of entering the lysogenic cycle, infection of the host cell only rarely causes lysis. Injection of the phage DNA into the host is followed by a brief period of *messenger RNA* (mRNA) synthesis, necessary to direct the production of a phage repressor protein, which inhibits the production of phage proteins involved with lytic functions. A DNA-insertion enzyme is also made, allowing the phage DNA to be physically inserted into the DNA of the host. The cell then can continue to grow and multiply, and new copies of the phage genes are replicated every cell generation as part of the bacterial chromosome. The host cell is said to be lysogenic, for it retains the potential to be lysed if the prophage pops out of the host DNA and enters the lytic cycle. The integrated prophage does confer a useful property on the host cell, however, for the cell will now be immune to further infection from the same phage species.



Tom Broker/Rainbow

Because scientists know more about the molecular and cell biology of the common bacterium Escherichia coli *than about any other cell or organism, it is perhaps not surprising that the best-known bacteriophages are those that require* E. coli *as a host.*

T4 Coliphage

One of the best-known lytic phages, which is often used in genetic studies, is the coliphage T4. Its protein capsid consists of three major sections—the head, the tail, and the tail fibers. The double-stranded circular DNA molecule of T4 is packaged into the icosahedral-shaped head, and during the infection process it is forced through the hollow core of the cylindrical tail and then directly into the host cell. Contact with the cell is established and maintained throughout the infection process by the tail fibers.

Self-assembly of progeny phages occurs in at least three distinct cellular locations, as complete heads, tails, and tail fibers are first assembled separately and then pieced together in one of the last phases of the infection cycle. Packaging of the replicated T4 DNA is an integral part of the head assembly process. Each of the three subassemblies involves a reasonably complex and highly regulated sequence of assembly steps. For example, head assembly is known to require the activity of eighteen genes, even though only eleven different proteins are found as structural components of mature heads. Identification of the number and sequence of genes involved with each subassembly process has been facilitated by the analysis of artificial lysates from t^s mutants.

For those temperate phages capable of entering the lysogenic cycle, many additional strategies for genetic control and regulation have evolved. The most thoroughly studied of the temperate coliphages is phage lambda (λ). Genes controlling phage DNA integration, excision, and recombination, and those involved with repressor functions, have been identified in phage λ as well as structural genes involved with lytic functions that are similar to those studied in T4.

Research Tool

One of the most important conclusions to be drawn from studies on bacteriophages, and viral genetics in general, is that many of the results have universal implications. For example, the physical properties of DNA and RNA are remarkably identical in all organisms, and these are perhaps easiest to study in bacteriophage systems. The experiment that provided the final proof that DNA was the genetic material was performed using a coliphage very similar to T4. Studies on the origin of spontaneous mutations, first performed in phage, have extended to higher forms of life as well. Some of the most basic questions concerning protein-DNA interactions are best addressed in viral systems, and the principles that emerge seem to hold for all other experimental systems. There is every reason to believe that many basic questions in cell and molecular biology will continue to be best studied in viruses such as bacteriophages, and that some of these investigations will spawn applications that can directly benefit humankind.

It is certain that advances in molecular biology that have revolutionized the understanding of cell biology and the molecular architecture of cells will continue to expand the frontiers of knowledge in the study of viral genetics. Applications in human medicine, veterinary medicine, and plant breeding are sure to follow, as scientists continue to unravel the complexities of these simplest of organisms.

Jeffrey A. Knight

See also: Bacterial genetics; Viruses and viroids.

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BASIDIOMYCETES

Categories: Fungi; taxonomic groups

The Basidiomycetes *constitute the largest of the three classes of the* Basidiomycota *(basidiosporic fungi), a very large class of about fourteen thousand species of the most diverse terrestrial fungi.*

The largest fungi belong in the *Basidiomycetes* class, as do some of the most unusual. All members of *Basidiomycetes* produce a *basidium* from hyphal cells and not from spores. (The basidium is a cell produced at the end of a dikaryotic hypha.) The basidium will produce either two or four spores as the result of meiosis. The basidium may be either a nonseptate cell, with two or four sterigmata (the *basidiospore* is produced on the end of the sterigma) at the apex, or it may be septate. The septa can be either horizontal or vertical. When observed from the apex, the vertical septa will produce a crosslike pattern. In either case, septate basidia will have one sterigma per cell. Basidiospores are thin-walled and may be released either actively or passively.

Basidiocarps

The *basidiocarp* is the fruiting body of the fungus. The fungus grows as a dikaryotic mycelium through the substrate. When the fungus has acquired sufficient energy, and environmental conditions are adequate, the fungus will produce a basidiocarp. The basidiocarp often appears overnight and may reach a meter in height. Some basidiocarps are tiny, less than a centimeter in height. The basidiocarp may look like a mushroom or may have the appearance of a golf ball or any variation in between. The basidiocarp may be edible or deadly poisonous. It often serves as food for wild animals and insects.

Classification

The *Basidiomycetes* are divided into two groups based on septa in the sterigma. Those that have a septate sterigma are classified in *Phragmobasidiomycetidae*, while those without septa in the sterigma are classified in *Holobasidiomycetidae*. *Phragmobasidiomycetidae* is a small group that includes some smaller fungi whose basidiocarps often have a gelatinous appearance. *Holobasidiomycetidae* is a large group of fungi and is easily divided into two major groups based on the release of the basidiospore. The hymenomycetes release spores actively, while the gasteromycetes release spores passively.

Hymenomycetes

The *hymenomycetes* are the most familiar fleshy fungi. These are the ones that resemble the common mushroom and can be seen when the weather is warm and damp. These fungi may have gills or pores on the underside of the *pileus* (the cap). The gills or pores are lined with a layer of basidia that produce spores. Some of these fungi are produced on the sides of trees or fallen wood and may be acentric. Many of them appear to arise from the ground. Colors of these fungi can be found anywhere in the rainbow, but most appear in earth tones.

Some of the major orders within the hymenomycetes are the *Agaricales* and the *Boletales*. The *Agaricales* contain the fungi that produce gills on the underside of the pileus. The *Boletales* contains the fungi that produce pores on the underside of the pileus. For the most part, the *Agaricales* are fleshy fungi that are supple at maturity and last for no more than a week or two in nature. The *Boletales* are also fleshy and can be confused with other fungi that have pores and are hard. Some of these hard fungi are common parasites of trees; the "shelves" that they produce can grow for years.

Gasteromycetes

The gasteromycetes are a much more diverse group of fungi. The fungi in this group are often associated with soil or decomposing organic matter, although some may be mycorrhizal (in a symbiotic association with plant roots). There is tremendous diversity in this group, and many scientists believe that this group is artificial (not based on evolutionary relationships).

Some of the more interesting fungi of this group are shaped like balls that lie on the soil. Members of *Lycoperdales* and *Sclerodermatales* produce ball-like basidiocarps that form at the soil line. The size can range from that of a small marble up to that of a soccer ball. These are called *puffballs*, as they release spores in small clouds when kicked. In nature, the upper layers of the basidiocarp crack, and spores are released as drops of water, hitting the outer layer of the basidiocarp. Many of these are edible when properly identified.

Other interesting fungi are found in the order *Nidulariales*. These are called the *bird's nest fungi*, as the basidiocarp resembles a small bowl containing two or three small "eggs," which contain the basidia. When a droplet of water lands in the "nest" the "eggs" are thrown upward and outward. As they are released, a small thread is pulled behind, and the thread sticks onto some part of a plant, such as a blade of grass. The "egg" will then degrade and release the spores to be disseminated in the wind.

Among the most bizarre fungi are the *stinkhorns*. These fungi produce basidiocarps from structures that look like chicken eggs. The elongate structure produces the basidia on the end in a mass of slimy, smelly mucus. Flies are attracted to the smell, land on the mucus, and fly away. The basidiospores adhere to their feet and drop off, thereby disseminating the fungus.

J. J. Muchovej

See also: Ascomycetes; Basidiosporic fungi; Fungi; Mushrooms; Mycorrhizae; Rusts; *Ustomycetes*.

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BASIDIOSPORIC FUNGI

Categories: Economic botany and plant uses; fungi; microorganisms; pests and pest control; taxonomic groups

Basidiosporic fungi (also known as the Basidiomycota *or* Basidiomycotina*) are fungi that produce sexual spores on a specialized cell called a basidium.*

The basidiosporic fungi are the most diverse phylum of the fungi world, with more than 22,300 species described. Some of the fungi in this phylum are microscopic, while the larger members of this group produce fruiting structures that are basketball-sized and weigh in excess of 10 pounds. This phylum contains fungi that fall into three classes: mushroom, rusts, and smuts—and range widely in appearance, from the common mushroom to weblike fungi with an odor that can be detected at several feet.

Taxonomy

The basidiosporic fungi are divided into three classes: *Basidiomycetes* (mushrooms); *Teliomycetes* (rusts); and *Ustomycetes* (smuts). The *Basidiomycetes* are the higher basidiosporic fungi, which are normally fleshy. They produce true basidiocarps, and the only spore formed is the basidiospore. The other two classes both have more than one spore form and do not have extensive mycelium. The *Teliomycetes* are commonly called rusts and are serious biotrophic parasites of plants. The rusts are able to complete their life cycle only in the presence of living plant host tissue. The *Ustomycetes* are commonly called smuts and are mostly minor pathogens of plants, especially monocots. Some smuts have been cultured in axenic culture, where they form a "yeastlike" phase. The yeastlike phase has no true mycelium but rather individual cells.

Basidium

The *basidium* is a single cell on which basidiospores are produced externally. The basidium forms either as the terminal cell of a dikaryotic mycelium or from a resting spore that initially is dikaryotic. The dikaryotic mycelium or spore contains two haploid nuclei, one donated by each of the parent strains. As the basidium begins to form, the two nuclei migrate into the center of the cell and fuse, forming a diploid nucleus. This nucleus then undergoes meiosis, forming four haploid nuclei. As this is occurring, the cell wall of the basidium begins to produce little extensions called *sterigmata*, upon which the basidiospores will form. The tips of the sterigmata then inflate, and one nucleus migrates into each forming basidiospore. The basidiospore is haploid and has a very thin cell wall. The spore is normally transmitted in air currents. Upon germination, the basidiospore produces a haploid mycelium which will fuse with a compatible hyphae, producing a dikaryotic mycelium.

Spore release from the basidium can be either active or passive. Passive release occurs when the junction of the sterigma and basidiospore separates, releasing the spore. Active release is more specialized. When the basidiospore is forming, a small segment of the spore wall at the junction with the sterigma loosens and fills with either gas or liquid. At the time of release, the fluid or gas escapes, propelling the basidiospore away from the basidium. The distance traveled is not great, just enough to make sure that the basidiospore is able to enter into air currents for dissemination.

Hyphal Structure

The hyphae of the *Basidiomycetes* are septate and have special modifications at the septa. When a cell divides, a crosswall forms between the two daughter cells. With the dikaryotic hyphae of the *Basidiomycetes*, as the cell divides, the nuclei migrate toward the apex of the hyphae. The nuclei then undergo mitosis, with one of the nuclei migrating into a small outgrowth of the hyphae and the other migrating backward. Septa form, creating a new dikaryotic cell near the apex and two haploid cells, one in line and the other as the outgrowth. The outgrowth then turns and fuses with the haploid cell, and the nucleus migrates back to form a dikaryotic cell. The outgrowth remains visible with a microscope and is called a clamp connection.

The reproductive structure of the *Ustomycetes* is called a sorus. The sorus is a mass of dikaryotic spores that are normally dark brown or black in color. The sorus is formed in meristematic regions of the plants. The spores are called probasidia, because they form basidia when they germinate.

With the *Teliomycetes*, there are up to five distinct spore forms. The basidiospore lands on a susceptible plant and germinates, producing a haploid mycelium that infects the plant. The infection results in the formation of a haploid spermagonium that produces both spermatia and receptive hyphae. When a compatible spermatia and receptive hypha combine, a dikaryotic hypha is produced, which initiates formation of an aecium. The aecium produces dikaryotic spores that are transmitted by air currents and infect another plant. The resultant infection produces a subcuticular or subepidermal mass of thin-walled spores. These dikaryotic spores are called urediniospores and are formed in the uredinium. The urediniospores are blown by air currents and produce reinfection of the same species of plant. At the end of the growing season, infections by urediniospores will result in the formation of a subcuticular or subepidermal mass of thick-walled spores called teliospores which are formed in the telium. These spores are initially dikaryotic but then become diploid and finally germinate by formation of the basidium.

Basidiocarps

The *basidiocarp* is the fruiting body of the higher *Basidiomycetes*. This structure is multicellular and composed of hyphae. The basidiocarp resembles the familiar image of the mushroom. The *mushroom* consists of a stalk (*stipe*) which has a cap (*pileus*) on top. The stipe can be as tall as a meter (40 inches), and the pileus as long as a meter in diameter. Alternatively, both parts could be less than a centimeter in size. The pileus has pores or gills on the underside, where the basidia are produced. The layer of basidia is called a hymenium or "fertile layer."

Other kinds of basidiocarps may be found in nature. Some are totally enclosed and remain on the ground, looking much like a golf ball. These are called *puffballs*. As the puffball matures, the other layers begin to crack at the apex. When drops of rain fall, the force of the impact causes spores to puff out of the opening. Another kind of puffball is the earthstar. In these unique fungi, the outer layers pull away from central part of the puffball and form a starlike pattern on the ground.

Ecological Importance

The basidiosporic fungi all play important roles in ecosystems. The rusts and the smuts are important plant pathogens, capable of great destruction of crops. These fungi have been known for thousands of years and are some of the most devastating fungi around.

The mushrooms are part of the natural cycle of decay. They are found on the ground or on wood and are the later stages of decay of organic matter. Some mushrooms are found on living plants, where they can be serious pathogens. Others are edible and are excellent sources of digestible protein. Still others are toxic or poisonous and can be fatal when eaten.

Stinkhorns and the *bird's nest fungi* are unique basidiosporic fungi. The stinkhorns are basidiocarps that form on the soil and produce the basidia in a mass of putrid cells. The stench from the cells draws flies, which walk over the spores and then disseminate them. These can be found in wooded areas and can be detected by smell at distances of up to several meters.

The bird's nest fungi look like small birds' nests. The outer part of the basidiocarp resembles a small nest, up to an inch in diameter. On the inside, several small puffball-like structures can be found, with basidia on the inside. These look like small eggs. When a drop of water enters the nest, the force thrusts the "egg" upward and extends a small cord from the back. The small cord catches hold of a plant and suspends the egg in the air. As the egg dries, it turns into a powdery mass, which is blown about by the wind.

J. J. Muchovej

See also: Ascomycetes; *Basidiomycetes*; Fungi; Mushrooms; Mycorrhizae; Rusts; *Ustomycetes*; Yeasts.

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BIOCHEMICAL COEVOLUTION IN ANGIOSPERMS

Categories: Angiosperms; animal-plant interactions; evolution; physiology; *Plantae*; poisonous, toxic, and invasive plants

Flowering plants, or angiosperms, produce many compounds that are not directly related to growth and development. These secondary metabolites arise from primary metabolic pathways and act as antiherbivory mechanisms, allelochemicals, or attractants.

Secondary metabolites are biochemicals produced by plants in response to selection pressures. These pressures may be from herbivory, competition, or the need for pollination. As plants produce compounds to enhance their survival, predators, competitors, and pollinators react and evolve means of adjusting to the plant's efforts. Chemically simple secondary metabolites may be widespread throughout angiosperm (flowering plant) families, whereas more complex chemicals are often restricted to a single species. Secondary metabolites are often under high selection pressures, causing individual compounds to have very limited distributions and making them useful in determining the evolutionary relationships between taxonomic groups. Presence of secondary compounds influences the activities of organisms interacting with the plants and, over long periods of time, influences evolution of those species.

Antiherbivory Mechanisms

Antiherbivory chemicals may have a wide range of effects on herbivores (plant-eating animals). Many compounds merely deter grazing. Crystals produced from calcium oxalate (raphides) may be ejected from the vacuoles of cells along with proteinaceous toxins, causing tissue swelling in the mouth of an offending herbivore. Many monocotyledonous plant families, such as *Liliaceae*, *Heliconiaceae*, *Rubiaceae*, and *Arecaceae*, produce this type of antiforaging device. This type of defense is especially notable in young tissues that have not developed the toughness found in mature leaves as a herbivory deterrent. Red oaks produce tannins in response to gypsy moth attacks, reducing further herbivory. Continued feeding on plants containing tannins would lead to slow starvation of a herbivore, as its digestive system could not absorb proteins. The same tannins are not deterrents to squirrels. Squirrels harvest acorns and bury them for later consumption, providing a food source for the squirrel and a dispersal mechanism for the acorn.

Beavers provide another example of the interaction between plant and animal evolution. Some of the beaver's preferred foods include species that are unpalatable or toxic to other mammals, such as bracken fern, nettles, thistles, and skunk cabbage. This gives the beaver a largely uncontested food source that may involve a metabolic "cost" to the animal.

Other antiherbivory chemicals result in effects more severe than mere deterrence of feeding. Alkaloids such as caffeine, nicotine, and strychnine are potent antiherbivory mechanisms, causing convulsions, comas, and even death in herbivores. These effects may not occur in all herbivores. Strychnine, for example, is produced by the fruit of some plants that may be eaten by birds without ill effects, but in mammals the same fruit causes failure of the central nervous system and induces seizures. The plant reduces herbivory by mammals, and the seeds get dispersed by birds that are able to detoxify the strychnine. Grains and seed crops, such as wheat and peanuts, which are particularly attractive to animal and insect herbivores, often produce cyanogenic glycosides that release hydrogen cyanide as the tissues are digested. This compound inhibits cellular respiration, thus killing the herbivore. In each case members of a plant population are consumed by the herbivore, but future generations are spared by the loss.

Allelochemicals

Allelochemicals are compounds produced by an organism that interfere with the growth or development of another organism. Many phenolic acids act as allelochemicals, inhibiting root growth of competing species. Many grains are known to release ferulic acid and caffeic acid into the soil, thus inhibiting the germination of weed species. Phenolics may also act as antifungal compounds, increasing in concentration with fungal infection, thus protecting the plant from further attack. Phenolic compounds produced in tobacco and tomato leaves reduce the growth of these plants' natural predator, tobacco hornworm, without affecting the growth or activity of the hornworm's natural predator.

Allelochemicals produced in response to injury by herbivores may also attract predators of the herbivore. Wastes from many species of caterpillars induce the release of terpenoids from green leaves that attract parasitoid insects. Production of specific combinations of volatiles on the part of the plant signals the predator, which will then reduce further herbivory. The plants have evolved the signal in response to herbivory, and the predators have evolved the ability to detect the signal indicating the location of their host.

Lectins are widely distributed carbohydrate-binding proteins, most commonly found in the *Leguminoseae* (legume) family. When found in the seeds, these compounds act as broad-spectrum insecticides, whereas in the roots of legumes they maintain bacterial relationships in nitrogen-fixing nodules, providing the plant with a source of nitrogen unavailable to plants not producing nodules.

Attractants

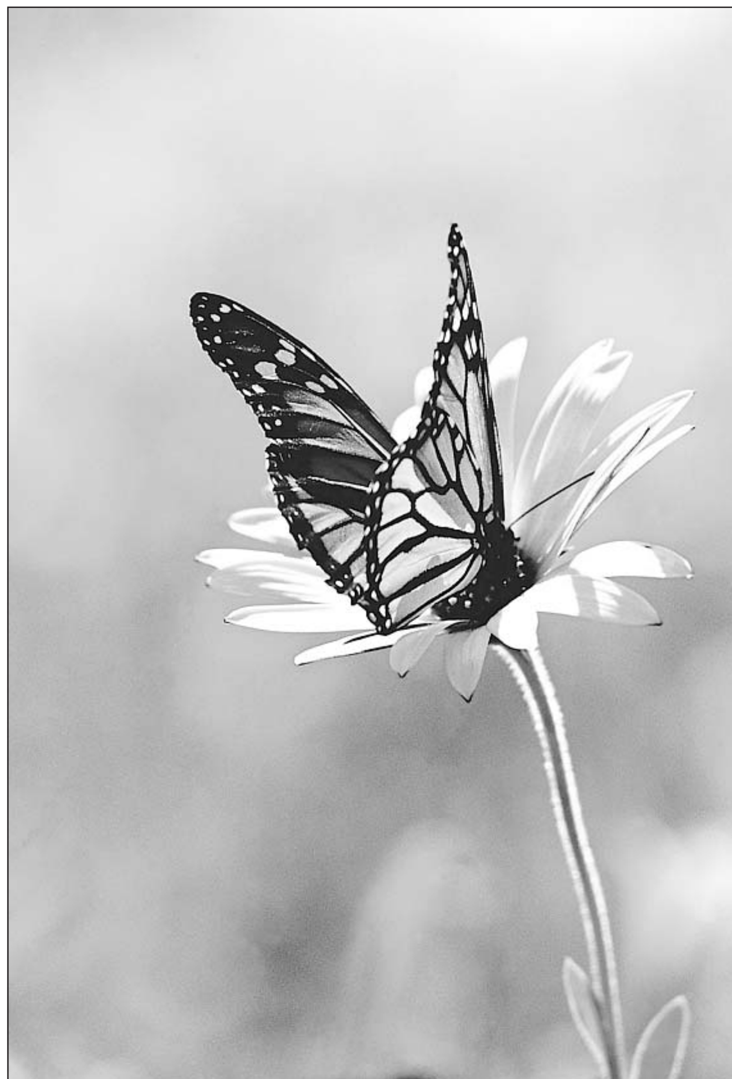
Terpenoids and aliphatic compounds are often the components of essential oils of plants. The volatile nature of these compounds produces a distinctive odor that attracts pollinators. Composition of the volatile compounds often closely matches the natural pheromones produced by the pollinator, mimicking the chemical scent of a female insect in an attempt to attract male pollinators. Pheromone mimicry is found primarily in members of the *Orchidaceae*, which are often dependent on single species of wasp for pollination. Other plants may mimic the odor of food. The smell of rotting flesh, attractive to flies, is produced via ammonia and alkylamines, such as cadaverine and putrescine. Methylesters may attract moth pollinators by mimicking the sweet smell of fruit.

Flavonoids often provide color to fruits and flowers and act as visual cues for pollination. Reds, blues, or yellows in varying patterns stand out against a background of green leaves, helping pollinators locate the flower. Species may have minor chemical differences in their flavonoids that allow for the determination of identity, hybridization between species, and possible coevolution with pollinators. For example, tropical flowers tend to have a more intense red color from anthocyanins than do temperate flowers. This difference correlates with differences in pollinator preferences, indicating a role by natural selection. Birds, such as hummingbirds, prefer red to yellow, whereas bees are not able to discern reds but are attracted to yellows. Carotenoids, such as xanthophyll and beta-carotene, give fruits and flowers distinctive yellow and orange colors.

Color patterns are also important in attracting pollinators. Butterflies are attracted to red/yellow color patterns. Flavonoid compounds not only impart color but also may modify color patterns by absorbing ultraviolet (UV) light. Bees are capable of seeing in the UV range, so the presence of flavonoids may alter the bees' perception of the flower. The patterns may also create cues as to the location of nectaries within the flower, guiding the pollinator to its reward.

Cheryld L. Emmons

See also: Allelopathy; Angiosperm evolution; Animal-plant interactions; Coevolution; Flowering regulation; Hormones; Pheromones; Metabolites: primary vs. secondary; Pigments in plants; Pollination.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Color patterns are important in attracting pollinators; for example, butterflies are attracted to red and yellow colors. Flavonoids not only provide color to fruits and flowers but also may modify color patterns by absorbing ultraviolet light.

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BIOFERTILIZERS

Categories: Agriculture; bacteria; biotechnology; economic botany and plant uses; nutrients and nutrition; soil

The use of biofertilizers, biological systems that supply plant nutrients such as nitrogen to agricultural crops, could reduce agriculture's dependency on chemical fertilizers, which are often detrimental to the environment.

Plants require an adequate supply of the thirteen mineral nutrients necessary for normal growth and reproduction. These nutrients, which must be supplied by the soil, include both *macronutrients* (nutrients required in large quantities) and *micronutrients* (nutrients required in smaller quantities). As plants grow and develop, they remove these essential mineral nutrients from the soil. Because normal crop production usually requires the removal of plants or plant parts, the nutrients are continuously removed from the soil. Therefore, the long-term agricultural utilization of any soil requires periodic fertilization to replace lost nutrients.

Nitrogen is the plant nutrient that is most often depleted in agricultural soils, and most crops respond to the addition of nitrogen fertilizer by increasing their growth and yield. Therefore, more nitrogen is applied to cropland than any other fertilizer component. In the past, nitrogen fertilizers have been limited to either *manures*, which have low levels of nitrogen, or *chemical fertilizers*, which usually have high levels of nitrogen. However, the excess nitrogen in chemical fertilizers often runs off into nearby waterways, causing a variety of environmental problems.

Less Harmful Alternatives

Biofertilizers offer a potential alternative: They supply sufficient amounts of nitrogen for maximum yields yet have a positive impact on the environment. Biofertilizers generally consist of either naturally occurring or *genetically modified* microorganisms that improve the physical condition of soil, aid plant growth, or increase crop yield. Biofertilizers provide an environmentally friendly way to increase plant health and yields with reduced input costs, new products and additional revenues for the agricultural biotechnology industry, and cheaper products for consumers.

Nitrogen Fixing

While biofertilizers could potentially be used to supply a number of different nutrients, most of the interest is focused on nitrogen. The relatively small amounts of nitrogen found in soil come from a variety of sources. Some nitrogen is present in all organic matter in soil; as this organic matter is de-

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graded by microorganisms, it can be used by plants. A second source of nitrogen is *nitrogen fixation*, the chemical or biological process of taking nitrogen from the atmosphere and converting it to a form that can be used by plants. Bacteria such as members of *Rhizobium* can live symbiotically in the roots of certain plants, such as legumes. Rhizobia and plant root tissue form root nodules, which house the nitrogen-fixing bacteria; once inside the nodules, the bacteria use energy supplied by the plant to convert atmospheric nitrogen to ammonia, which nourishes the plant. Natural nitrogen can also be supplied by free-living microorganisms, which can fix nitrogen without forming a symbiotic relationship with plants. The primary objective of biofertilizers is to enhance any one or all of these processes.

One of the major goals for the genetic engineering of biofertilizers is to transfer the ability to form nodules and establish effective symbiosis to nonlegume plants. The formation of nodules in which the *Rhizobia* live requires plant cells to synthesize many new proteins, and many of the genes required for the expression of these proteins are not found in the root cells of plants outside the legume family (*Fabaceae*). If transfer of the appropriate genes could be accomplished, *Rhizobia* could be used as a biofertilizer for a variety of plants.

There is also much interest in using the free-living, soil-borne organisms that fix atmospheric nitrogen as biofertilizers. These organisms, including types bacteria and algae, live in the *rhizosphere* (the region of soil in immediate contact with plant roots) or thrive on the surface of the soil. Because the exudates from these microorganisms contain nitrogen that can be used by plants, increasing their abundance in the soil could reduce the dependency on chemical fertilizers. Numerous research efforts have been designed to identify and enhance the abundance of nitrogen-fixing bacteria in the rhizosphere. Soil microorganisms primarily depend on soluble root exudates and decomposed organic matter to supply the energy necessary for fixing nitrogen. Hence, there is also an interest in enhancing the *biodegradation* of organic matter in the soil. This research has primarily centered on inoculating the soil with cellulose-degrading fungi and nitrogen-fixing bacteria or applying organic matter, such as straw that has been treated with a combination of the fungi and bacteria to the soil.

D. R. Gossett

See also: Fertilizers; Nitrogen cycle; Nitrogen fixation.

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BIOLOGICAL INVASIONS

Categories: Ecology; ecosystems; environmental issues; poisonous, toxic, and invasive plants

Biological invasions are the entry of a type of organism into an ecosystem outside its historic range. In a biological invasion, the "invading" organism may be an infectious virus, a bacterium, a plant, an insect, or an animal.

Species introduced to an area from somewhere else are referred to as alien or exotic species or as invaders. Because an exotic species is not native to the new area, it is often unsuccessful in establishing a viable population and disappears. The fossil record, as well as historical documentation, indicates that this is the fate of many species in new environments as they move from their native habitats. Occasionally, however, an invading species finds the new environment to its liking. In this case, the invader may become so successful in exploiting its new habitat that it can completely alter the ecological balance of an ecosystem, decreasing *biodiversity* and altering the local *biological hierarchy*. Because of this ability to alter *ecosystems*, exotic invaders are considered major agents in driving native species to extinction.

Biological invasions by notorious species constitute a significant component of earth's history. In general, large-scale climatic changes and geological crises are at the origin of massive exchanges of flora and fauna. On a geologic time scale, migrations of invading species from one continent to another are true evolutionary processes, just as speciation and extinction are. On a smaller scale, physical barriers such as oceans, mountains, and deserts can be over-

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come by many organisms as their populations expand. Organisms can be carried by water in rivers or ocean currents, transported by wind, or carried by other species as they migrate seasonally or to escape environmental pressures. Humans have transplanted plants since the beginning of plant cultivation in pre-Columbian times. The geological and historical records of the earth suggest that biological invasions contribute substantially to an increase in the rate of extinction within ecosystems.

Invasive Plants

In modern times, most people are not aware of the distinction between *native plants* and exotic species growing in their region. Recent increases in intercontinental invasion rates by exotic species, brought about primarily by human activity, create important ecological problems for the recipient lands. Invasive plants in North America include eucalyptus trees, morning glory, and pampas grass.

It would seem logical to assume that invading species might add to the biodiversity of a region, but many invaders have the opposite effect. In all ecosystems the new species are often opportunistic, driving out native species by competing with them for resources. For example, *Pueraria lobata*, or kudzu, is a vine native to Japan. Introduced in the United States at the 1876 Philadelphia Exposition, kudzu was planted to control erosion on hillsides and for livestock forage. By the end of the twentieth century, it could be found from Connecticut to Missouri, extending south to Texas and Florida. Kudzu covers everything in its path and grows as much as 1 foot (0.3 meter) per day. Similarly, English ivy (*Hedera helix*), a native of Eurasia, is considered a serious problem in West Coast states. It forms "ivy deserts" in forests and crowds out native trees and shrubs that make up essential wildlife habitat.

The invasion of an ecosystem by an exotic species can effectively alter ecosystem processes. An invading species does not simply consume or compete with native species but can actually change the rules of existence within the ecosystem by altering processes such as primary productivity, decomposition, hydrology, geomorphology, nutrient cycling, and natural disturbance regimes.

Invasive Insects and Microorganisms

The invasion of native forests alone by nonnative insects and microorganisms has been devastating on many continents. The white pine blister rust and the balsam woolly adelgid have invaded both commercial and preserved forest lands in North America. Both exotics were brought to North America in the late 1800's on nursery stock from Europe. The balsam woolly adelgid attacks fir trees and causes their death within two to seven years from chemical damage and by feeding on the trees' vascular tissue. The adelgid has killed nearly every adult cone-bearing fir tree in the southern Appalachian Mountains. The white pine blister rust attacks five-needle pines; in the western United States fewer than 10 pine trees in 100,000 are resistant. Because white pine seeds are an essential food source for bears and other animals, the loss of the trees is having severe consequences across the food chain.

Since the 1800's the deciduous trees of eastern North America have been attacked numerous times by waves of invading exotic species and diseases. One of the most notable invaders is the gypsy moth, which consumes a variety of tree species. Other invaders have virtually eliminated the once-dominant American chestnut and the American elm. Tree species that continue to decline because of new invaders include the American beech, mountain ash, white birch, butternut, sugar maple, flowering dogwood, and eastern hemlock. It is widely accepted that the invasion of exotic species is the single greatest threat to the diversity of deciduous forests in North America.

Effects on Humans and Humans as Invaders

Some introduced exotic species are beneficial to humanity. It would be impossible to support the present world human population entirely on species native to their regions. Humans, the ultimate biological invaders, have been responsible for the extinction of many species and will continue to be in the future. At the beginning of the twenty-first century, the United States was spending $4 billion annually to eradicate invasive plant species, a figure that does not take into account loss of biodiversity or wildlife habitat.

Randall L. Milstein, updated by Elizabeth Slocum

See also: Food chain; Invasive plants.

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BIOLOGICAL WEAPONS

Categories: Economic botany and plant uses; medicine and health; microorganisms; poisonous, toxic, and invasive plants

Biological weapons are biological agents that can be used to destroy living organisms. This general definition includes the use of virtually any kind of microorganism (bacterium or fungus) or biological agent (mycoplasmalike organism, virus, viroid, or prion) to destroy any biologically important plant or animal.

There are two basic ways of using biological weapons against humanity. The first is to attack the food or water supply. This would produce hardship and the possible death from starvation of many individuals. In developed countries such as the United States, total devastation due to such an attack would likely be avoided, as there are considerable stores of food, in dispersed locations, that would mitigate against crop failure of moderate proportions. In addition, most experts agree that the amount of biological contaminant required to overcome the effects of dilution and time in most water reservoirs makes poisoning of water supplies impractical, although not impossible.

The other way of using biological weapons against humanity is to attack individuals directly, using pathogens. Numerous known pathogens could be used, but the most effective biological weapons would creep upon the population with stealth. Naturally occurring agents that have promise as biological weapons are pathogens, which can infect and colonize a host. A pathogen causes *disease*, an alteration in the metabolism of a host.

In order for disease to occur, it is necessary to have a *virulent pathogen*, that is, one that is capable of causing disease; a *susceptible host*, able to be infected; and an environment that is favorable to both the host and the pathogen. When these occur together, disease occurs. For the disease cycle to begin, it is necessary for *propagules* of the pathogen to come in contact with the susceptible host. Propagules include those that cause initial infections, called the *primary inoculum*. As the disease cycle progresses, the host may release other propagules, considered the *secondary inoculum*. When only one progression of disease occurs during a prolonged span of time, the disease is termed *monocyclic*. When more than one cycle of disease takes place in a growing season, the disease is called *polycyclic*.

Monocyclic Diseases

An example of the monocyclic disease cycle occurs with corn smut. The primary inoculum is released in the spring, as the tassel and silk of the corn appear. Infection occurs, symptoms of large black galls develop on the ears, and new inoculum is produced for the following growing season. This kind of disease produces a single cycle during a growing season. The potential for problems depends on the amount of inoculum present at the beginning of the disease cycle. In order to use corn smut as a biological weapon, the initial amount of inoculum must be sufficient to reach all of the plants that are targeted.

This is the same general case as with *anthrax*. Anthrax is a disease of animals that is caused by the bacterium *Bacillus anthracis*. The bacterium is able to survive in nature as small spores that are able to resist extremes of climate and time. These microscopic spores are produced at any time when environmental conditions are unfavorable for growth of the bacterium. The spores are less than 2 microns in diameter, and if they become suspended in the air, they will hang indefinitely. Such small particles are called PM10 (particulate matter less than 10 microns in size). These particles are of extreme importance, as they are not filtered out by common filters and must be removed by HEPA (high-efficiency particulate-arresting) filters, which can remove particles smaller than a micron. When these particles are inhaled, they cause disease of the lung tissue, which will result in destruction of the lungs and the resultant death of the host.

The reasons that *Bacillus anthracis* could be a biological weapon are that it is easily concealed and disseminates quickly as an invisible, airborne powder. The small particle size allows it to be inhaled, after which it lodges in the lungs and begins the process of infection. The infection begins like that of a common chest cold. By the time the host determines that anthrax might have been contracted, the condition is normally fatal. One of the features of anthrax as a biological weapon is that it is not contagious. Spores are not produced until the host is dead, at which time the spores are not placed back into the air currents. This permits anthrax to be used against a specific target.

Polycyclic Diseases

Some kinds of biological weapons can be termed *weapons of mass destruction*. These biological weap-

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ons are able to self-perpetuate and thereby create great amounts of destruction. They are polycyclic in nature.

A plant-based example of this is the epidemic of *potato late blight*, which caused the Irish Potato Famine of the mid-1840's. Most of the people living in Ireland at that time depended on their own harvests for food. During a two-year period, the climate became especially cool and damp, conditions favorable for the spread of potato late blight. Because potatoes are planted from vegetative parts, there was genetic uniformity of the crop, which was highly susceptible. The pathogen is extremely virulent, with the capacity to destroy a single plant overnight. Total crop failure resulted in the reduction of Ireland's population from about six million to about two million people. About one-third of the people emigrated to other lands, and about one-third of the population died from starvation. All of this destruction could have started from a single fungal propagule that infected a plant and then spread. This fungus is still problematic worldwide. However, regular sprays with fungicide reduce the risk of crop destruction.

Pathogens that occur at low levels in any given area are called *endemic* and may, when conditions are favorable, produce a widespread surge of disease in that area. This is called an *epidemic*. Epidemics that occur over wide geographic ranges, such as two or more continents, are called *pandemics*. The endemic potato late blight fungus caused an epidemic, and because it also spread into Europe and North America, the situation could be called a pandemic.

A similar concern is expressed with regard to the disease *smallpox*. Smallpox is caused by a virus that is easily passed from an infected individual to a healthy one. The smallpox virus no longer occurs in nature (is not endemic) anywhere in the world. The last reported case of smallpox in nature occurred in the late 1970's. As a result of a concerted vaccination effort among many nations, this normally fatal disease was eradicated. The last stores of smallpox virus are housed at the Centers for Disease Control (CDC) in Atlanta, the U.S. Army Biological Weapons Research Unit in Fort Detrick, Maryland, and the Russian Academy of Sciences in Moscow. Some people fear some of the inoculum from one of these storehouses could be transported into unconfined areas of the outside world. As such, smallpox would become a very formidable biological weapon.

Smallpox is highly contagious and spreads easily from person to person. Should an infected person walk the streets of a highly populated urban area, it would be possible to infect millions of people within the span of a week or two. Within several weeks, especially in this age of global travel, the infection could spread around the world.

Vectors

One method of spreading disease is through the use of vectors. *Vectors* are arthropods or other invertebrates that have the ability to transmit a pathogen from one host to another. The most famous vector is the mosquito, which can transmit malaria, dengue fever, West Nile virus, and many other diseases. The corresponding vector in plants is the aphid, which can transmit a host of viruses and mycoplasmas (bacteria that lack cell walls). In order for transmission to occur, it is necessary for a vector to first come in contact with an infected host, feed upon that host, and then pass the pathogen to an uninfected host. The most notable vector-borne disease is plague, which is passed from infected animals to humans by fleas. This disease, which was once responsible for hundreds of thousands of deaths, is now readily controlled by the use of insecticides to kill off the vector.

Designer Weapons

With twentieth century advances in technology, the manipulation of the genetics of a pathogen to make it a "super pathogen" is possible. The creation of a genetic code which could be pathogenic is also possible. So-called designer weapons are those that may be envisioned by someone who feels he or she has a need to make a more destructive or more "targeted" weapon. These weapons could then be used on a specific population or area. The creator of the designer weapon would have an advantage, as he or she would also be able to create a vaccine against the designer weapon, which could be administered to a specific group of individuals. Designer weapons, like all biological weapons, work best when there is an abundant supply of susceptible hosts and when the genetics of these hosts do not vary greatly.

Pathogen Dispersal

There is considerable opportunity for the use of any pathogen as a biological weapon. Most pathogens can be cultured with standard laboratory equipment; however, the difficulty is in creating a system of *dispersal* that will effectively spread the inoculum over an area of susceptible hosts. There are innumerable systems that could be used; these include spraying particles into the air, mailing them in an envelope, or placing them into a bomb. One of the less sophisticated methods of dissemination is the use of aircraft that are used for agricultural spraying. These aircraft could spray inoculum over large areas, with the potential of infecting large populations.

J. J. Muchovej

See also: Bacteria; Biological invasions; Genetically modified bacteria; Viruses and viroids.

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BIOLUMINESCENCE

Categories: Algae; cellular biology; fungi; physiology; water-related life

Bioluminesence is the production of light by living organisms, including algae and phytoplankton in the oceans and fungi on land.

Bioluminescence is a specific form of chemiluminescence in which the chemical energy that is produced in a chemical reaction is converted into radiant energy. In bioluminescence the reaction originates in a wide variety of living organisms, including a small number of plants. It should not be confused with fluorescence or phosphorescence, both of which do not involve a chemical reaction. In either of the former cases the energy from a source of light, not from a chemical reaction, is basically absorbed and then re-emitted in some form of another photon. The chemical reactions that lead to bioluminescence release energy in the form of light. Unlike the light bulb, in which electrical energy is converted into light, with some of this energy lost in the form of heat, a bioluminescent reaction is 100 percent efficient and converts all the emitted energy into light. Because there is no heat released, bioluminescence is also known as "cold light."

Species and Habitats

Bioluminescence is primarily marine in nature and is the only source of light in the deep ocean, which is the largest habitable biome of the earth. The phenomenon rarely occurs in any source of fresh water. Bioluminescent organisms include ctenophores, annelid worms, mollusks, insects, and fish. The most common manifestation of this phenomenon on land is seen as a glowing fungus on wood or in the few families of luminous insects. This property can be used as a means of species recognition in the darkness as well as for courtship, preying, and mating.

There are several bioluminescent fungi that are not marine in nature, occurring primarily in the tropics. These fungi appear in different colors. The most common is *Panellus stiptucus*, which is a small decay fungus that is mostly restricted to North America. The jack-o'-lantern mushroom (*Omphalotus olearius*) glows brightly, especially when fresh. A few *Armillaria* species are also reported to glow mildly. No luminous tree or plant is known, however.

Mechanisms of Bioluminescence

Bioluminescence occurs only when two different species are in contact and, almost exclusively, when oxygen is present. The two species are *luciferin*, which produces the light, and *luciferase*, a protein that triggers and catalyzes the reaction. The mechanism involves the loss of two electrons, also known as *oxidation*, by luciferin, a process achieved only through the intervention of luciferase to yield oxyluciferin. Occasionally luciferin, luciferase, and a cofactor such as oxygen are bound together in a single moiety called *photoprotein*, which leads to light formation upon contact with a positively charged species, such as the calcium cation. The mechanism appears to involve a peroxide decomposition with free radical intervention.

Dinoflagellates

Dinoflagellates known as *Pyrrhophyta*, or fire plants, are the most common sources of bioluminescence at the surface of the ocean. They are a group of marine algae that produce light upon mechanical, chemical, or temperature changes. The phenomenon was first observed in the genus *Noctiluca* in the nineteenth century and has since been observed to occur within other species.

Generally, three types of stimuli can cause bioluminescence in dinoflagellates: mechanical, chemical, and temperature stimulation.

Mechanical forms of stimulation, such as the stirring of water from a moving boat, a swimming fish, or a breaking wave, are prevalent in many *Pyrrhophyta*. The light appears to serve as a "burglar alarm" against grazing predators, which are then being seen through the flash by a larger second predator. For example, as a copepod approaches the dinoflagellate, agitation of the seawater stimulates light flashes which a small fish, the secondary predator, uses to pinpoint the position of the copepod and eventually consume it. It appears that the mechanical stimulation deforms the cell membrane to create a short flash as little as one one-hundredth of a second.

Dinoflagellate luciferin is thought to derive from the similarly structured chlorophyll, which is found in most plants. The molecule is protected from luciferase at slightly basic medium by a luciferin-binding protein. However, once the acidity increases, the free luciferin reacts, and light is emitted. The light produced by a single dinoflagellate is only six to eight photons in energy, and the flashing may last only one-tenth of a second. Larger organisms, such as jellyfish, provide flashes that may last up to tens of seconds. Temperature lowering in some dinoflagellate species also creates bioluminescence.

Purpose and Applications

The disappearance of the flash, once oxygen is consumed, has suggested that the bioluminescent reaction was originally used to remove toxic oxygen from primitive types of bacteria that developed at a time when oxygen was not available. Bioluminescence has also played a crucial role in the direct studies of several cellular and biochemical processes, such as in the formation of ultimate carcinogens from benzoapyrene. The phenomenon has served scientists in many ways. Calcium levels are monitored via the jellyfish biochemical system, adenosine triphosphate (ATP) measurements are achieved through the firefly, and the gene activity of organisms can be detected by splicing known bioluminescent proteins.

Soraya Ghayourmanesh

See also: Dinoflagellates; Phytoplankton.

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BIOMASS RELATED TO ENERGY

Categories: Ecology; ecosystems; environmental issues

The relationship between the accumulation of living matter resulting from the primary production of plants or the secondary production of animals (biomass) and the energy potentially available to other organisms in an ecosystem forms the basis of the study of biomass related to energy.

Biomass is the amount of organic matter, such as animal and plant tissue, found at a particular time and place. The rate of accumulation of biomass is termed *productivity*. *Primary production* is the rate at which plants produce new organic matter through photosynthesis. *Secondary production* is the rate at which animals produce their organic matter by feeding on other organisms. Biomass is an instantaneous measure of the amount of organic matter, while primary and secondary production give measures of the rates at which biomass increases. Plant and animal biomass consists mostly of carbon-rich molecules, such as sugars, starches, proteins, and lipids, and other substances, such as minerals, bone, and shell. The carbon-rich organic molecules are not only the building blocks of life but also the energy-rich molecules used by organisms to fuel their activities.

Solar Energy and Photosynthesis

Ultimately, all energy used by organisms to produce the building blocks of life and to drive life processes originated as solar energy captured by plants. Only a small fraction, less than 2 percent, of the total solar light energy received by a plant is absorbed and transformed by photosynthesis into energy-containing organic molecules. The rest of the sun's energy passes out of the plant as heat. The rate at which plants capture light energy and transform it into chemical energy is called primary production. Because plants do not rely on other organisms to provide their energy needs, they are referred to as primary producers, or *autotrophs* (meaning "self-feeding"). In addition to light energy, plants must absorb water, carbon dioxide gas, and simple nutrients, such as nitrate and phosphate, to produce various organic molecules during photosynthesis. Oxygen gas is also produced.

Sugars are the first energy-containing organic molecules produced in photosynthesis, and they can be changed to other, more complex, molecules, such as starches, proteins, and fats. The energy in the sugar molecules can be used immediately by the plants to maintain their own respiration needs, stored as starches and fats, or can be converted to new plant tissue. It is the stored organic matter plus new tissue that contributes to the growth of plants and to biomass.

Because the energy-containing products of photosynthesis can be used either immediately in respiration or in the formation of new plant biomass, two types of primary production can be distinguished. *Gross production* refers to the total amount of energy produced by photosynthesis. It includes both the energy used by the plant for respiration and the energy that goes into new biomass. *Net production* refers only to the amount of energy that accumulates as new biomass. It is only the energy in net production that is potentially available to animal consumers as food.

The rate of primary production varies directly with the rate of photosynthesis; therefore, factors in the environment that affect the rate of photosynthesis affect the rate of primary production. These factors most often include light intensity, temperature, nutrient concentrations, and moisture conditions. Each species of plant has a specific combination of these factors that promotes maximum rates of primary production. If one or more of these factors is in excess or is in short supply, then the rate of primary production is slowed.

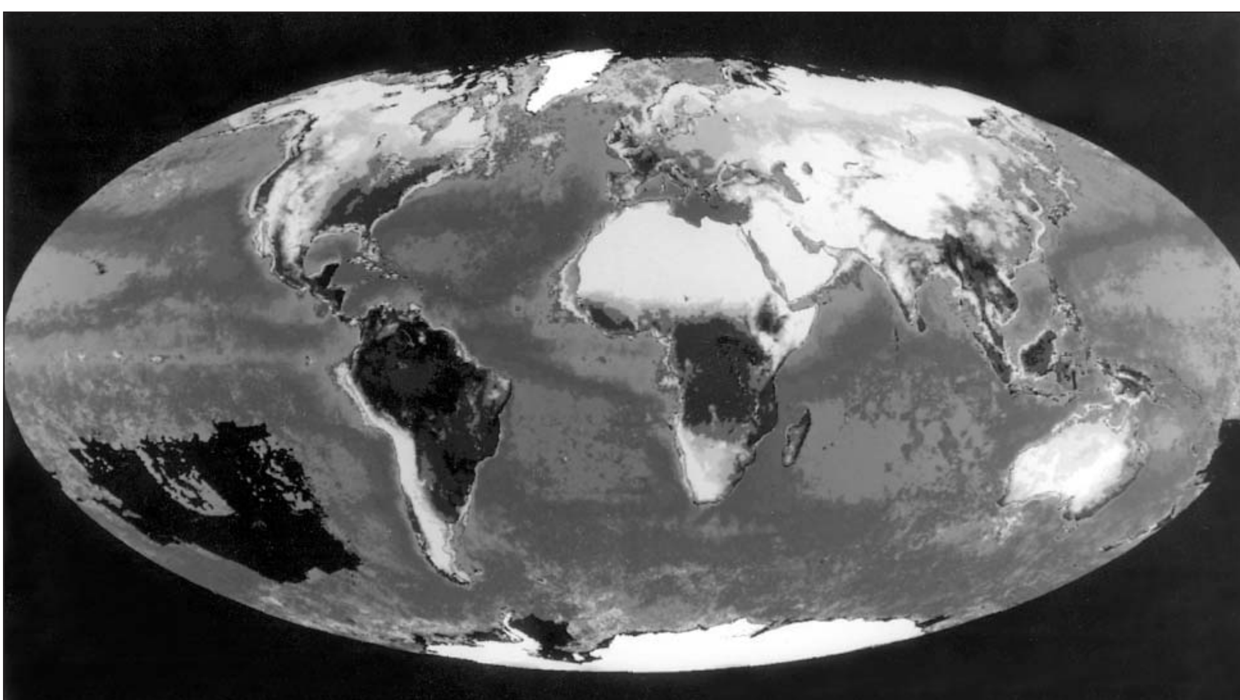
Primary Production

On land, the rate of primary production by plants is determined largely by light, temperature, and rainfall. The favorable combination of intense sunlight for twelve hours per day, warm temperatures throughout the year, and considerable rainfall make the tropical rain forests the most productive ecosystems on land. In contrast, Arctic tundra vegetation is exposed to reduced light intensity, very cold winters, and cool summers. Primary production there is very low. In deserts, the lack of water severely limits primary production even though light and temperature are otherwise favorable.

In aquatic habitats, rates of primary production by algae, such as phytoplankton, are determined by nutrient concentration and light intensity. As sunlight penetrates water, it is quickly absorbed by the water molecules and by small suspended particles. Thus, all primary production occurs near the surface, as long as nutrients are available. Although the waters of the open ocean are very clear, and sunlight can penetrate to great depths, the scarcity of nutrients reduces the rate of primary production to less than one-tenth that of coastal bays.

Secondary Production

The energy and material needs of some organisms are met by consuming the organic materials produced by others. These consumer organisms are called *heterotrophs*; there are two types. Those that obtain their food from other living organisms are called *consumers* and include all animals. Those that obtain their energy from dead organisms are called *decomposers* and include mostly the fungi and bacteria.



NASA

This composite image of the earth's biosphere shows the planet's heaviest vegetative biomass in the dark sections, known to be rain forests. The combination of intense sunlight for twelve hours per day, warm temperatures throughout the year, and considerable rainfall makes tropical rain forests the most productive ecosystems on land.

The energy available to each type of consumer becomes progressively less at each level of the *food chain*. Each consumer level uses most of its food energy, about 90 percent, to fuel its respiratory activities. In this energy-releasing process, most of the food energy is actually converted to heat and is lost to the environment. Only 10 percent or less of the original food energy is used to form new biomass. It is only this small amount of energy that is available for the next consumer level. The result is that food chains are limited in their number of links or levels by the reduced amount of energy available at each higher level.

Generally, the greater the amount of primary production, the larger the number of consumer organisms and the longer the food chain. Most food chains consist of three levels; rarely are there examples of up to five levels. It should be noted that the food chain concept is a simplified view of a more complex network of energy pathways, known as *food webs*, that occur in nature. Another outcome of the reduction in energy flow up the food chain is a progressive decrease in production and biomass. The most productive level, and the one with the greatest biomass, is therefore the primary producers, or plants.

Human Threats to Primary Production

The total natural primary production of the earth is limited, and human efforts to increase total world primary production much beyond its present levels may be futile. One reason for this is that much of the earth's surface lacks optimal conditions for plant growth. The open ocean, which covers about 71 percent of the earth's surface, has very little plant growth. On land, the Arctic, subarctic, and Antarctic regions are very unproductive most of the year. Human attempts to increase primary production in the form of food or fuel crops usually involve changing the characteristics of the land, converting forests into croplands, for example, and adding large quantities of nutrients and water. It has been estimated that humans are currently utilizing most of the easily workable croplands and that the development of additional lands for agriculture would require major changes to currently unworkable habitats, changes that would be expensive and demand much fuel energy.

The study of production processes is vitally important in understanding the ecology of natural ecosystems. Such information is necessary to manage and conserve *habitats* and their organisms in the face of human pressures. These processes provide insight into the general health of ecosystems. Pollutants, such as acid rain or industrial toxic wastes, are known to reduce the primary and secondary productivity of forests and lakes.

Throughout the world, humans are reducing the biomass of the world's primary producers through *deforestation*. This is particularly true in the tropics, where high population pressures have necessitated that land be cleared for agriculture and development. There is a worldwide demand for lumber. One obvious consequence is the dramatic reduction in the primary and secondary production of these areas. The *clear-cutting* (removal of all the trees) of tropical forests allows unprotected soils to wash away quickly during the heavy tropical rains. It will take hundreds of years for new soils to develop and for the forest to return—if it can return at all.

Deforestation is also harmful in that tropical forests form a major part of the world's life-support system. For millions of years these forests have buffered the earth's atmosphere by producing the oxygen gas needed by animals and by removing carbon dioxide and other toxic gases. The low level of carbon dioxide in the atmosphere is believed to have moderated the earth's temperature, counteracting the so-called *greenhouse effect*. It is therefore of great importance to understand and preserve these forests and other primary producers of the world.

Ray P. Gerber

See also: Deforestation; Food chain; Trophic levels and ecological niches.

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BIOMES: DEFINITIONS AND DETERMINANTS

Categories: Biomes; ecology; ecosystems

The concept of biomes is similar to plant ecologists' classification of plant formations and classification of life zones. However, the biomes usually refer to ecological communities of both plants and animals, whereas plant formations concern plant communities only. Worldwide, there are six major types of biomes on land: forest, grassland, woodland, shrubland, semidesert scrub, and desert.

One who travels latitudinally from the equator to the Arctic will cross tropical forests, deserts, grasslands, temperate forests, coniferous forest, tundra, and ice fields. Those major types of natural vegetation at regional scales are called biomes. A biome occurs wherever a particular set of climatic and edaphic (soil-related) conditions prevail with similar physiognomy. For example, prairies and other grasslands in the North American Middle West and West form a biome of temperate grasslands, where moderately dry climate prevails. Tropical rain forests in the humid tropical areas of South and Central America, Africa, and Southeast Asia create a biome where rainfall is abundant and well-distributed through the year.

In general, biomes are delineated by both physiognomy and environment. There are six major physiognomic types on land: *forest*, *grassland*, *woodland*, *shrubland*, *semidesert scrub*, and *desert*. Each of the six types occurs in a wide range of environments. Therefore, more than one biome may be defined within each physiognomic type according to major differences in climate. Tropical forests, temperate deciduous forests, and coniferous forests are, for example, separate biomes, although forests dominate all of them. On the other hand, some

Biomes and Their Features

Biome	*Annual Mean Rainfall*[1]	*Climate and Temperature*[2]
Desert	250 mm or less	Arid, with extremes of heat and cold
Grasslands	250-750 mm	Cold winters, warm summers; dry periods
Mediterranean scrub	Low to moderate	Cool winters, hot summers; latitudes 30° to 45°; includes chaparral, maquis
Rain forest (tropical)	2,500-4,500 mm	20-30°
Savanna, deciduous tropics	1,500-2,500 mm	Hot summers; 3-6 months dry; seasonal fires
Taiga (boreal forest)	1,000 mm	Cold, long winters; mild, short summers; seasonal fires
Tundra	Very low year-round	Very cold (3° or less); soil characterized by permafrost; Arctic tundra occurs in Arctic Circle; alpine tundra in other high elevations

1. In millimeters
2. Degrees Celsius

biome types, such as the tundra, are dominated by a range of physiognomic types and are in one prevailing environmental region.

Classification of Biomes

There are many ways to classify biomes. One system, which designates a small number of broadly defined biomes, divides global vegetation into nine major terrestrial biomes: tundra, taiga, temperate forest, temperate rain forest, tropical rain forest, savanna, temperate grasslands, chaparral, and desert. Other systems more narrowly define biomes, designating a larger total number. In those cases, some of the broadly defined biomes are divided into two or more biomes. For example, the biome called temperate forest in a broad classification may be separated into temperature deciduous forest and temperate evergreen forest in a fine classification. The biome of desert in the broad classification may be broken into warm semidesert, cool semidesert, Arctic-alpine semidesert, Arctic-pine desert, and true desert in the fine classification.

Description of Biome Distributions

Naturalists, geographers, and ecologists have tried to correlate world major types of biomes to climatic patterns in both descriptive and quantitative approaches. For example, in northern North America, the tundra and boreal forests are two broad belts of vegetation that stretch from east to west. The distribution of the two biomes is primarily influenced by temperature. South of those two belts are biome types that are mostly controlled by precipitation and evaporation. From east to west in North America, available moisture decreases, influencing biome distribution. Humid regions along the East Coast support forest biomes, including temperate coniferous forests and temperate deciduous forest. West of the eastern forests is a biome type of grasslands, including tall-grass prairie and short-grass steppe. In this zone, there is less precipitation than evaporation. The ratio of precipitation to evaporation is about 0.6 to 0.8 in the land that supports a tall-grass prairie and 0.2 to 0.4 farther west, where a short-grass steppe is supported. Beyond the short-grass steppe are shrubland and the deserts of the West. Western North America is a mountainous country in which vegetation zones reflect climatic changes on an altitudinal gradient. The vegetation in the lowlands is characteristic of the regions (short-grass steppe on the east side of Rocky Mountains, sagebrush cold semideserts in the Great Basin between the Rocky Mountains and the Sierra Nevada, and grasslands in California's Central Valley west of the Sierra Nevada). Above the base regions, the vegetation changes from shrub, woodland, or deciduous forest to montane coniferous forest or alpine tundra. In Central America, from Mexico to Panama where precipitation becomes ample and temperatures are high, tropical rain forests and tropical seasonal forests occur.

Similar distributions of biomes along latitude and altitude can be found in South America, Africa, and Eurasia. In general, the climate-induced patterns of vegetation are influenced by latitude; the location of regions within a continent, which affects the amount of moisture they receive; and altitude, in which mountains modify the climate patterns. In addition, other factors, such as fire and human disturbance, may influence distributions of biomes. For example, most grasslands require periodic fires for maintenance, renewal, and elimination of incoming woody growth. Grasslands at one time covered about 42 percent of the land surface of the world. Humans have converted much of that area into croplands.

Quantitative Relationships

Descriptive relationships can provide pictures of world vegetation distributions along latitudinal and altitudinal gradients of temperature and moisture. Ecologists in the past several decades have also sought quantitative relationships between distributions of biomes and environmental factors. For example, when R. H. Whittaker plotted various types of biomes on gradients of mean annual temperature and mean annual precipitation in 1975, a global pattern emerged relating biomes to climatic variables. It was shown that tropical rain-forest biomes are distributed in regions with annual mean precipitation of 2,500 to 4,500 millimeters and annual mean temperatures of 20 to 30 degrees Celsius. Tropical seasonal forest and savannas also occur in warm regions with precipitation of 1,500-2,500 millimeters and 500-1,500 millimeters per year, respectively. Temperate forests occupy regions with annual temperature of 5 to 20 degrees Celsius and precipitation exceeding 1,000 millimeters per year.

PhotoDisc

Humid regions along the East Coast of North America support forest biomes, including temperate coniferous forests and temperate deciduous forests.

This thermal zone can support temperate rain forest when annual precipitation is more than 2,500 millimeters and temperate grassland when annual precipitation is below 750 millimeters. Temperate woodland occurs between temperate forests and grasslands. Tundra and taiga are distributed in regions with an annual mean temperature below 3 degrees Celsius, whereas deserts occupy areas with annual precipitation below 250 millimeters.

These relationships between climatic variables and biomes provide a reasonable approximation of global vegetation patterns. Many types of biomes intergrade with one another. Soil, exposure to fire, and regional climate can influence distributions of biomes in a given area.

Yiqi Luo

See also: Biomes: types; Climate and resources; Ecology: concept; Ecology: history; Ecosystems: overview; Ecosystems: studies.

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BIOMES: TYPES

Categories: Biomes; ecology; ecosystems

The major recognizable life zones of the continents are divided into biomes, characterized by their plant communities.

Temperature, precipitation, soil, and length of day affect the survival and distribution of biome species. Species diversity within a biome may increase its stability and capability to deliver natural services, including enhancing the quality of the atmosphere, forming and protecting the soil, controlling pests, and providing clean water, fuel, food, and drugs. Major biomes include the *temperate*, *tropical*, and *boreal forests*; *tundra*; *deserts*; *grasslands*; *chaparral*; and *oceans*.

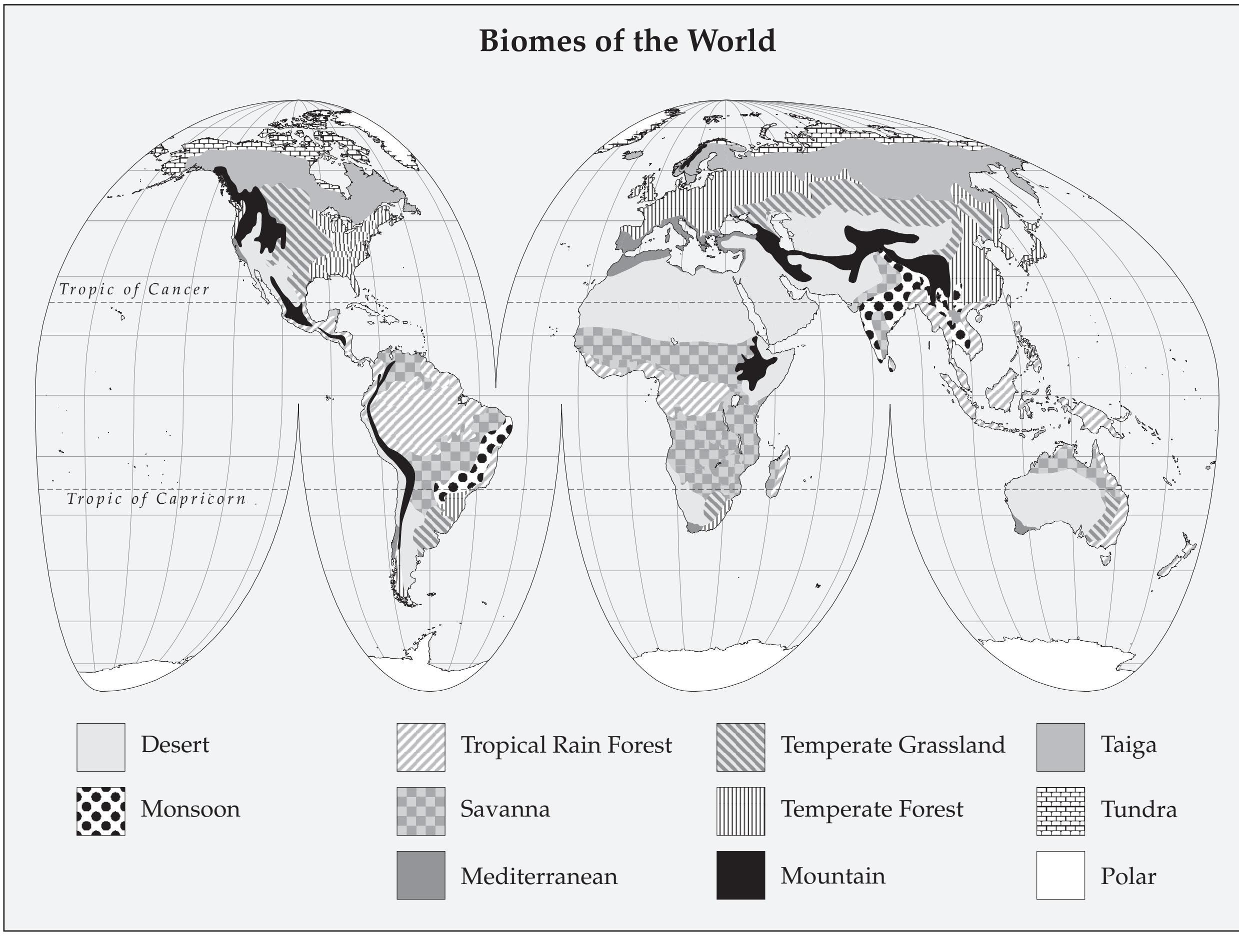
Temperate Forests

The temperate forest biome occupies the so-called temperate zones in the midlatitudes (from about 30 to 60 degrees north and south of the equator). Temperate forests are found mainly in Europe, eastern North America, and eastern China, and in narrow zones on the coasts of Australia, New Zealand, Tasmania, and the Pacific coasts of North and South America. Their climates are characterized by high rainfall and temperatures that vary from cold to mild.

Temperate forests contain primarily *deciduous* trees—including maple, oak, hickory, and beechwood—and, secondarily, *evergreen* trees—including pine, spruce, fir, and hemlock. Evergreen forests in some parts of the Southern Hemisphere contain eucalyptus trees. The root systems of forest trees help keep the soil rich. The soil quality and color are due to the action of earthworms. Where these forests are frequently logged, soil runoff pollutes streams, which reduces spawning habitat for fish. Raccoons, opossums, bats, and squirrels are found in the trees. Deer and black bears roam forest floors. During winter, small animals such as marmots and squirrels burrow in the ground.

Tropical Forests

Tropical forests exist in frost-free areas between the Tropic of Cancer and the Tropic of Capricorn.



Temperatures range from warm to hot year-round. These forests are found in northern Australia, the East Indies, Southeast Asia, equatorial Africa, and parts of Central America and northern South America.

Tropical forests have high biological diversity and contain about 15 percent of the world's plant species. Animal life thrives at each layer of tropical forests. Nuts and fruits on the trees provide food for birds, monkeys, squirrels, and bats. Monkeys and sloths feed on tree leaves. Roots, seeds, leaves, and fruit on the forest floor feed larger animals. Tropical forest trees produce rubber and hardwood, such as mahogany and rosewood. Deforestation for agriculture and pastures has caused reduction in plant and animal diversity in these forests.

Boreal Forests

The boreal forest is a circumpolar Northern Hemisphere biome spread across Russia, Scandinavia, Canada, and Alaska. The region is very cold. Evergreen trees such as white spruce and black spruce dominate this zone, which also contains larch, balsam, pine, fir, and some deciduous hardwoods such as birch and aspen. The acidic needles from the evergreens make the leaf litter that is changed into soil humus. The acidic soil limits the plants that develop.

Animals in boreal forests include deer, bears, and wolves. Birds in this zone include red-tailed hawks, sapsuckers, grouse, and nuthatches. Relatively few animals emigrate from this habitat during winter. Conifer seeds are the basic winter food.

Tundra

About 5 percent of the earth's surface is covered with *Arctic tundra* and 3 percent with *alpine tundra*. The Arctic tundra is the area of Europe, Asia, and North America north of the boreal coniferous forest zone, where the soils remain frozen most of the year. Arctic tundra has a permanent frozen subsoil, called *permafrost*. Deep snow and low temperatures slow the soil-forming process. The area is bounded by a 50 degrees Fahrenheit (122 degrees Celsius) circumpolar *isotherm*, known as the summer isotherm. The cold temperature north of this line prevents normal tree growth.

The tundra landscape is covered by mosses, lichens, and low shrubs, which are eaten by caribou, reindeer, and musk oxen. Wolves eat these herbivores. Bears, foxes, and lemmings also live there. The most common Arctic bird is the old squaw duck. Ptarmigans and eider ducks are also very common. Geese, falcons, and loons are some of the nesting birds of the area.

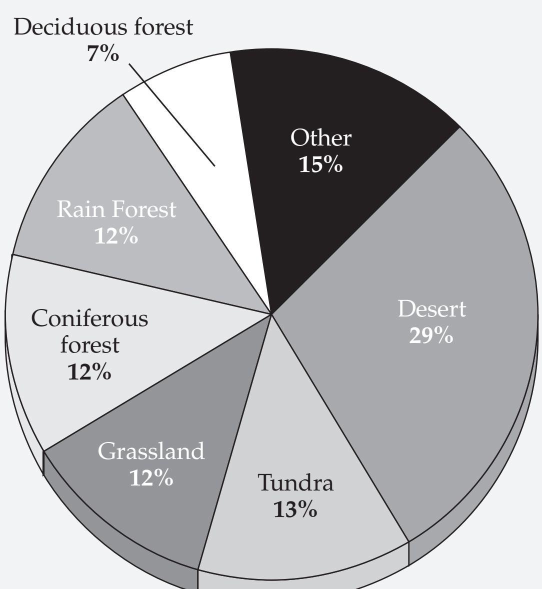
The alpine tundra, which exists at high altitude in all latitudes, is acted upon by winds, cold temperatures, and snow. The plant growth is mostly cushion- and mat-forming plants.

Deserts

The desert biome covers about one-seventh of the earth's surface. Deserts typically receive no more than 10 inches (25 centimeters) of rainfall per year, and evaporation generally exceeds rainfall. Deserts are found around the Tropic of Cancer and the Tropic of Capricorn. As warm air rises over the equator, it cools and loses its water content. The dry air descends in the two subtropical zones on each side of the equator; as it warms, it picks up moisture, resulting in drying the land.

Rainfall is a key agent in shaping the desert. The lack of sufficient plant cover contributes to soil *erosion* during wind- and rainstorms. Some desert plants—for example, the mesquite tree, which has roots that grow 40 feet (13 meters) deep—obtain water from deep below the earth's surface. Other plants, such as the barrel cactus, store large amounts of water in their leaves, roots, or stems. Some plants slow the loss of water by having tiny leaves or shedding their leaves. Desert plants have very short growth periods, because they cannot grow during the long drought periods.

Terrestrial Biomes (percentages)



Grasslands

Grasslands cover about one-quarter of the earth's surface and can be found between forests and deserts. Treeless grasslands exist in parts of central North America, Central America, and eastern South America that have between 10 and 40 inches (250-1,000 millimeters) of erratic rainfall per year. The climate has a high rate of evaporation and periodic major droughts. Grasslands are subject to fire.

Some grassland plants survive droughts by growing deep roots, while others survive by being dormant. Grass seeds feed the lizards and rodents that become the food for hawks and eagles. Large animals in this biome include bison, coyotes, mule deer, and wolves. The grasslands produce more food than any other biome. Overgrazing, inefficient agricultural practices, and mining destroy the natural stability and fertility of these lands, resulting in reduced carrying capacity, water pollution, and soil erosion. Diverse natural grasslands appear to be more capable of surviving drought than are simplified manipulated grass systems. This may be due to slower soil mineralization and nitrogen turnover of plant residues in the simplified system.

Savannas are open grasslands containing deciduous trees and shrubs. They are near the equator and are associated with deserts. Grasses there grow in clumps and do not form a continuous layer.

Chaparral

The chaparral, or *mediterranean*, biome is found in the Mediterranean Basin, California, parts of

Australia, middle Chile, and the Cape Province of South America. This region has a climate of wet winters and summer drought. The plants have tough, leathery leaves and may have thorns. Regional fires clear the area of dense and dead vegetation. The seeds from some plants, such as the California manzanita and South African fire lily, are protected by the soil during a fire and later germinate and rapidly grow to form new plants. Vegetation *dwarfing* occurs as a result of the severe summer drought and extreme climate changes.

Oceans

The ocean biome covers more than 70 percent of the earth's surface and includes 90 percent of its volume. Oceans have four zones. The *intertidal zone* is shallow and lies at the land's edge. The *continental shelf*, which begins where the intertidal zone ends, is a plain that slopes gently seaward. The *neritic zone* (*continental slope*) begins at a depth of about 600 feet (180 meters), where the gradual slant of the continental shelf becomes a sharp tilt toward the ocean floor, plunging about 12,000 feet (3,660 meters) to the ocean bottom, which is known as the abyss. The *abyssal zone* is so deep that it does not have light.

Plankton are animals that float in the ocean. They include algae and copepods, which are microscopic crustaceans. Jellyfish and animal larva are also considered plankton. The nekton are animals that move freely through the water by means of their muscles. These include fish, whales, and squid. The benthos are animals that are attached to or crawl along the ocean's floor. Clams are examples of benthos. Bacteria decompose the dead organic materials on the ocean floor.

The circulation of materials from the ocean's floor to the surface is caused by winds and water temperature. Runoff from the land contains pollutants such as pesticides, nitrogen fertilizers, and animal wastes. Rivers carry loose soil to the ocean, where it builds up the bottom areas. Overfishing has caused fisheries to collapse in every world sector.

Human Impact on Biomes

Human interaction with biomes has increased *biological invasions*, reduced species *biodiversity*, changed the quality of land and water resources, and caused the proliferation of toxic compounds. Managed care of biomes may not be capable of undoing these problems.

Ronald J. Raven

See also: Arctic tundra; Biological invasions; Biomes: definitions and determinants; Deserts; Ecosystems: overview; Forests; Grasslands; Marine plants; Mediterranean scrub; Rain-forest biomes; Taiga; Tundra and high-altitude biomes; Wetlands.

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BIOPESTICIDES

Categories: Agriculture; bacteria; biotechnology; economic botany and plant uses; environmental issues; microorganisms; pests and pest control

Biopesticides are biological agents, such as viruses, bacteria, fungi, mites, and other organisms used to control insect and weed pests in an environmentally and ecologically friendly manner.

Biopesticides allow biologically based, rather than chemically based, control of pests. A pest is any unwanted animal, plant, or microorganism. When the environment provides no natural resistance to a pest and when no natural antagonists are present, pests can run rampant. For example, spread of the fungus *Endothia parasitica*, which entered New York in 1904, caused the nearly complete destruction of the American chestnut tree because no natural control was present. Viruses, bacteria, fungi, protozoa, mites, insects, and flowers have all been used as biopesticides.

Image Not Available

Advantages of Biopesticides

Many plants and animals are protected from pests by passive means. For example, plant rotation is a traditional method of insect and disease protection that is achieved by removing the host plant long enough to reduce a region's pathogen and pest populations. Biopesticides have several significant advantages over commercial pesticides. They appear to be ecologically safer than commercial pesticides because they do not accumulate in the food chain. Some biopesticides provide persistent control, as more than a single mutation is required to adapt to them and because they can become an integral part of a pest's life cycle. In addition, biopesticides have slight effects on ecological balances because they do not affect nontarget species. Finally, biopesticides are compatible with other control agents. The major drawbacks to using biopesticides are the time required for them to kill their targets and the inefficiency with which they work; also, if the organism being used as a biopesticide is a nonnative species, it may cause unforeseen damage to the local ecosystem.

Viruses and Bacteria

Viruses have been developed against insect pests such as *Lepidoptera* (butterflies and moths), *Hymenoptera* (bees, wasps, and ants), and *Dipterans* (flies). Gypsy moths and tent caterpillars, for example, periodically suffer from epidemic virus infestations, which could be exploited and encouraged.

Many *commensal* microorganisms (microorganisms that live on or in other organisms causing no direct benefit or harm) that occur on plant roots and leaves can passively protect plants against microbial pests by *competitive exclusion* (that is, simply crowding them out). *Bacillus cereus* has been used as an inoculum on soybean seeds to prevent infection by fungal pathogens in the genus *Cercospora*. Some microorganisms used as biopesticides produce antibiotics, but the major mechanism in most cases seems to be competitive exclusion. For example, *Agrobacterium radiobacter* antagonizes *Agrobacterium tumefaciens*, which causes the disease crown gall. Species of two bacterial genera—*Bacillus* and *Streptomyces*—when added as biopesticides to soil help control the damping-off disease of cucumbers, peas, and lettuce caused by *Rhizoctonia solani*. *Bacillus subtilis* added to plant tissue also controls stem rot and wilt rot caused by species of the fungus *Fusarium*. *Mycobacteria* species produce cellulose-degrading enzymes, and their addition to young seedlings helps control fungal infection by species of *Pythium*, *Rhizoctonia*, and *Fusarium*. Species of *Bacillus* and *Pseudomonas* produce enzymes that dissolve fungal cell walls.

Bacillus thuringiensis and *Bacillus popilliae* as Microbial Biocontrol Agents

	Bacillus thuringiensis	*Bacillus popilliae*
Pest controlled	*Lepidoptera* (many)	*Coleoptera* (few)
Pathogenicity	low	high
Response time	immediate	slow
Formulation	spores and toxin crystals	spores
Production	in vitro	in vivo
Persistence	low	high
Resistance in pests	developing	reported

Source: Data adapted from J. W. Deacon, *Microbial Control of Plant Pests and Diseases* (1983).

***Bacillus thuringiensis* Toxins**

The best examples of microbial insecticides are *Bacillus thuringiensis* (*B.t.*) toxins, which were first used in 1901. They have had widespread commercial production and use since the 1960's and have been successfully tested on 140 insects, including mosquitoes. Insecticidal endotoxins are produced by *B.t.* during sporulation, and exotoxins are contained in crystalline parasporal protein bodies. These protein crystals are insoluble in water but readily dissolve in an insect's gut. Once dissolved, the proteolytic enzymes paralyze the gut. Spores that have been consumed germinate and kill the insect. *Bacillus popilliae* is a related bacterium that produces an insecticidal spore that has been used to control Japanese beetles, a corn pest.

The gene for the *B.t.* toxin has also been inserted into the genomes of cotton and corn, producing genetically modified, or GM, plants that produce their own *B.t.* toxin. GM cotton and *B.t.* corn both express the gene in their roots, which provides them with protection from root worms. Ecologists and environmentalists have expressed concern that constantly exposing pests to *B.t.* will cause insects to develop resistance to the toxin. In such a scenario, the effectiveness of traditionally applied *B.t.* would decrease.

Fungi and Protozoa

Saprophytic fungi can compete with pathogenic fungi. There are several examples of fungi used as biopesticides, such as *Gliocladium virens*, *Trichoderma hamatum*, *Trichoderma harzianum*, *Trichoderma viride*, and *Talaromyces flavus*. For example, *Trichoderma* species compete with pathogenic species of *Verticillium* and *Fusarium*. *Peniophora gigantea* antagonizes the pine pathogen *Heterobasidion annosum* by three mechanisms: It prevents the pathogen from colonizing stumps and traveling down into the root zone, it prevents the pathogen from traveling between infected and uninfected trees along interconnected roots, and it prevents the pathogen from growing up to stump surfaces and sporulating.

Nematodes are pests that interfere with commercial button mushroom (*Agaricus bisporus*) production. Several types of nematode-trapping fungi can be used as biopesticides to trap, kill, and digest the nematode pests. The fungi produce constricting and nonconstricting rings, sticky appendages, and spores, which attach to the nematodes. The most common nematode-trapping fungi are *Arthrobotrys oligospora*, *Arthrobotrys conoides*, *Dactylaria candida*, and *Meria coniospora*.

Protozoa have occasionally been used as biopesticide agents, but their use has suffered because of slow growth and the complex culture conditions associated with their commercial production.

Mites, Insects, and Flowers

Well-known "terminator" bugs include praying mantis and ladybugs as well as decollate snails, which eat the common brown garden snail. Fleas, grubs, beetles, and grasshoppers often have natural nematode species that prey on them, which can be used as biocontrol agents. Predaceous mites are used as a biopesticide to protect cotton from other insect pests such as the boll weevil. Parasitic wasps of the genus *Encarsia*, especially *E. formosa*, prey on whiteflies, as does *Delphastus pusillus*, a small, black ladybird beetle.

Dalmatian and Persian insect powders contain pyrethrins, which are a toxic insecticidal compounds produced in *Chrysanthemum* flowers. Synthetic versions of these naturally occurring compounds are found in products used to control head lice.

Mark S. Coyne, updated by Elizabeth Slocum

See also: Bacterial resistance and super bacteria; Herbicides; Pesticides.

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BIOSPHERE CONCEPT

Categories: Ecology; ecosystems; environmental issues

The term "biosphere" was coined in the nineteenth century by Austrian geologist Eduard Suess in reference to the 20-kilometer-thick zone extending from the floor of the oceans to the top of mountains, within which all life on earth exists. Thought to be more than 3.5 billion years old, the biosphere supports nearly one dozen biomes, regions of climatic conditions within which distinct biotic communities reside.

Compounds of hydrogen, oxygen, carbon, nitrogen, potassium, and sulfur are cycled among the four major spheres, one of which is the biosphere, to make the materials that are essential to the existence of life. The other spheres are the *lithosphere*, the outer part of the earth; the *atmosphere*, the whole mass of air surrounding the earth; and the *hydrosphere*, the aqueous vapor of the atmosphere, sometimes defined as including the earth's bodies of water.

The Water Cycle

The most critical of these compounds is water, and its movement among the spheres is called the *hydrologic cycle*. Dissolved water in the atmosphere condenses to form clouds, rain, and snow. The annual precipitation for any region is one of the major factors in determining the terrestrial biome that can exist. The precipitation takes various paths leading to the formation of lakes and rivers. These flowing waters interact with the lithosphere (the outer part of the earth's crust) to dissolve chemicals as they flow to the oceans. Evaporation of water from the oceans then supplies most of the moisture in the atmosphere. This cycle continually moves water among the various terrestrial and oceanic biomes.

Solar Energy

The biosphere is also dependent upon the energy that is transferred from the various spheres. Solar energy is the basis for almost all life. Light enters the biosphere as the essential energy source for photosynthesis. Plants take in carbon dioxide, water, and light energy, which is converted via *photosynthesis* into chemical energy in the form of sugars and other organic molecules. Oxygen is generated as a by-product. Most animal life reverses this process during *respiration*, as chemical energy is released to do work by the oxidation of organic molecules to produce carbon dioxide and water.

Incoming solar energy also interacts dramatically with the water cycle and the worldwide distribution of biomes. Because of the earth's curvature, the equatorial regions receive a greater amount of solar heat than the polar regions. Convective movements in the atmosphere—such as winds, high- and low-pressure systems, and weather fronts—and the hydrosphere—such as water currents—are generated during the redistribution of this heat. The weather patterns and climates of earth are a response to these energy shifts. Earth's various climates are defined by the mean annual temperature and the mean annual precipitation.

Toby R. Stewart and Dion Stewart

See also: Biomes: types; Carbon cycle.

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BIOTECHNOLOGY

Categories: Agriculture; bacteria; biotechnology; disciplines; economic botany and plant uses; environmental issues; genetics; history of plant science

Biotechnology is the use of living organisms, or substances obtained from those organisms, to produce processes or products of value to humanity, such as foods, high-yield crops, and medicines.

Modern biotechnological advances have provided the ability to tap into a natural resource, the world gene pool, with such great potential that its full magnitude is only beginning to be appreciated. Theoretically, it should be possible to transfer one or more genes from any organism in the world into any other organism. Because genes ultimately control how any organism functions, gene transfer can have a dramatic impact on agricultural resources and human health in the future.

History of Biotechnology

Although the term "biotechnology" is relatively new, the practice of biotechnology is at least as old as civilization. Civilization did not evolve until humankind learned to produce food crops and domestic livestock through the controlled breeding of selected plants and animals. Eventually humans began to utilize microorganisms in the production of foods such as cheese and alcoholic beverages. During the twentieth century, the pace of modification of various organisms accelerated. Through carefully controlled breeding programs, plant architecture and fruit characteristics of crops have been modified to facilitate mechanical harvesting. Plants have been developed to produce specific drugs or spices, and microorganisms have been selected to produce antibiotics and other medicinal or food products.

Developments in Biotechnology

Since the mid-twentieth century, the ability to utilize artificial media to propagate plants has led to the development of a technology called tissue culture. The earliest form of tissue culture involved using the culture of meristem tissue to produce numerous tiny shoots that can be grown into full-size plants, referred to as clones because each plant is genetically identical. More than one thousand plant species have been propagated by tissue culture techniques. Plants have been propagated via the culture of other tissues, including the stems and roots. In some of these techniques, the plant tissue is treated with hormones to produce callus tissue, masses of undifferentiated cells. The callus tissue can be separated into single cells to establish a cell suspension culture. Callus tissue and cell suspensions can be used to produce specific drugs and other chemicals. Entire plants can also be generated from the callus tissue or from single cells by addition of specific combinations of hormones.

A far more complex method of cloning of plants and animals from the deoxyribonucleic acid (DNA) of a single cell is a more recent development. Proponents of this method of producing copies of organisms have suggested that cloning technology might be used to improve agricultural stock and to regenerate endangered species. These ideas have had their detractors, however, as critics have noted the potential dangers of narrowing a species' gene pool. The July, 1996, birth in Scotland of Dolly, a sheep cloned and raised to adulthood, demonstrated that the cloning of animals had left the realm of science fiction and become a matter of scientific fact.

Recombinant DNA Technology

In practice, recombinant DNA methodology is complex, but in concept, it is fairly easy to comprehend. The genes in all living cells are composed of the same chemical, DNA. The DNA of all cells, whether from bacteria, plants, or animals including humans, is very similar. When DNA from a foreign species is transferred into a different cell, it functions exactly as the native DNA functions; that is, it "codes" for protein.

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The easiest way to manipulate genes is using bacterial cells (most often *Escherichia coli*) and a *vector*, an agent that can be used to pass the gene from one cell to another. *Plasmids*, small extra circular DNA molecules found in many bacterial cells, are commonly used for this purpose. Plasmids are replicated along with the bacterial cell's own DNA every time the cell reproduces. Plasmids can be easily isolated from bacterial cells. When a specific gene has been isolated, it can be fused, using *restriction endonucleases*, with a plasmid to produce a recombinant plasmid. These *recombinant plasmids* can then be put into bacterial cells by a process called *transformation*. Special plasmids called *expression vectors* allow expression of inserted genes once they are inside a bacterial cell.

Although expressing foreign genes in bacterial cells is relatively simple, inserting them into plants and getting them expressed is more complicated. The *Ti plasmid* is a widely used vector that works well in dicots but has never worked for monocots. Consequently, the first successful transgenic plants were dicots, while success with the most important food crops, monocots such as rice and corn, took more time and effort.

Many alternative methods for inserting genes into plant cells have been developed that work on both monocots and dicots. *Microinjection* can be used to insert a gene into individual cells. A less laborious method is called *biolistic*, for biological ballistic, where millions of copies of the gene are attached to tiny projectiles that are then fired into groups of plant cells. Using these and other methods, genetic modification of plants is becoming more routine.

Future of Biotechnology in Agriculture

This new technology could have a tremendous impact on agriculture. As the human population grows, biotechnology will most likely play an important role in producing an increase in food production. Such an increase will require developments such as crop plants that will produce higher yields under normal conditions and crops that will produce higher yields when grown in marginal environments. Biotechnology provides a means of developing higher-yielding crops in much less time than it takes to develop them though traditional plant-breeding programs. Genes for the desired characteristics can be inserted directly into the plant without having to go through repeated controlled selection and breeding cycles to establish the trait.

There are also economic advantages in diversifying agriculture production in a given area. A producer might wish to grow a particular high-value cash crop in an area where soil or climate conditions would prevent such a crop from thriving. Biotechnology can help solve these types of problems. For example, high value crops can be developed to grow in areas that heretofore would not have supported such crops. Plants also can be developed to produce new products such as antibiotics, drugs, hormones, and other pharmaceuticals. Crop plants bioengineered to produce novel products mean that pharmaceuticals and other valuable products could be grown in farm environments rather than in laboratories.

While there will be a growing pressure for agriculture to produce more food in the future, there will also be pressure for crop production to be more friendly to the environment. Biotechnology has the potential to play a major role in the development of a long-term, sustainable, environmentally friendly agricultural system. For example, the development of crop varieties with improved resistance to pests will reduce the reliance on pesticides. Methods of crop production and harvest with less environmental impact will also have to be developed. Because agriculture will continue to have an impact on the environment, the need to remediate polluting agents will continue to exist. Hence biotechnology will play an important role in the development of bioremediation systems for agriculture as well as other industrial pollutants.

Ownership Issues

There will be many difficult ethical and economic issues surrounding the use of this new biotechnology. One of the major questions concerns ownership. Patent laws in the United States read that ownership over an organism can be granted if the organism has been intentionally genetically modified through the use of recombinant DNA techniques. In addition, processes that utilize genetically modified organisms can be patented. Therefore one biotechnology firm may own the patent to an engineered organism, but another firm may own the rights to the process used to produce it.

D. R. Gossett, updated by Bryan Ness

See also: Microbial nutrition and metabolism.

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BOTANY

Categories: Disciplines; history of plant science

Botany is the branch of science that studies plant life.

Botany is a very old branch of science that began with early people's interest in the plants around them. Plant science now extends from that interest to cutting-edge biotechnology. Any topic dealing with plants, from the level of their *cellular biology* to the level of their economic production, is considered part of the field of botany.

History and Subdisciplines

The origins of this branch of biology are rooted in human beings' attempts to improve their lot by raising better food crops around 5000 B.C.E. This practical effort developed into intellectual curiosity about plants in general, and the science of botany was born. Some of the earliest botanical records are included with the writings of Greek philosophers, who were often physicians and who used plant materials as curative agents. In the second century B.C.E. Aristotle had a botanical garden and an associated library.

As more details became known about plants and their functions, particularly after the discovery of the microscope, a number of subdisciplines arose. Plant *anatomy* is concerned chiefly with the internal structure of plants. Plant *physiology* delves into the living functions of plants. Plant *taxonomy* has as its interest the discovery and systematic classification of plants. Plant geography, also known as geobotany or *phytogeography*, deals with the global distribution of plants. Plant *ecology* studies the interactions between plants and their surroundings. Plant *morphology* studies the form and structure of plants. Plant *genetics* attempts to understand and work with the way that plant traits are inherited. Plant *cytology*, often called cell biology, is the science of cell structure and function. *Economic botany*, which traces its interest back to the origins of botany, studies those plants that play important economic roles. These include major crops such as wheat, rice, corn, and cotton.

Ethnobotany is a rapidly developing subarea in which scientists communicate with indigenous peoples to explore the knowledge that exists as a part of their folk medicine. Several new drugs and the promise of others have developed from this search.

At the forefront of botany today is the field of *genetic engineering*, including the *cloning* of organisms. New or better crops have long been developed by the technique of *crossbreeding*, but genetic engineering offers a much more direct course. Using its techniques, scientists can introduce a gene carrying a desirable trait directly from one organism to another. In this way scientists hope to protect crops from frost damage, to inhibit the growth of weeds, to provide insect repulsion as a part of the plant's own system, and to increase the yield of food and fiber crops.

The role that plants play in the energy system of the earth (and may someday play in space stations or other closed systems) is also a major area of study. Plants, through photosynthesis, convert sunlight into other useful forms of energy upon which humans have become dependent. During the same process carbon dioxide is removed from the air, and oxygen is delivered. Optimization of this process and discovering new applications for it are goals for botanists.

Kenneth H. Brown

See also: History of plant science; Plant science.

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BROMELIACEAE

Categories: Angiosperms; economic botany and plant uses; *Plantae*; taxonomic groups

The family Bromeliaceae *comprises a group of perennial, monocotyledon herbs or trees that often age slowly.*

Important ornamentals (called bromeliads) as well as sources of food and medicines, *Bromeliaceae* have substantial economic value and are widely cultivated. The colors of the leaves offer decorative foliage, and the flowers are of astonishing hues due to the rich content of pigment-forming substances known as anthocyanins. Based on ovary position, habit, and floral and pollen morphology, the family *Bromeliaceae* has been split into three subfamilies: subfamily *Pitcairnioideae*, subfamily *Tillandsioideae*, and subfamily *Bromelioideae*. There are fifty-six genera and approximately twenty-six hundred species, growing mostly in the neotropical regions of the world, from Virginia to southern Argentina. One species, *Pitcairnia feliciana*, originated in Africa. This interesting family can nevertheless occupy a variety of ecologically diverse environments, ranging from the dry deserts in Peru to the highest montane forest in the Andes Mountains.

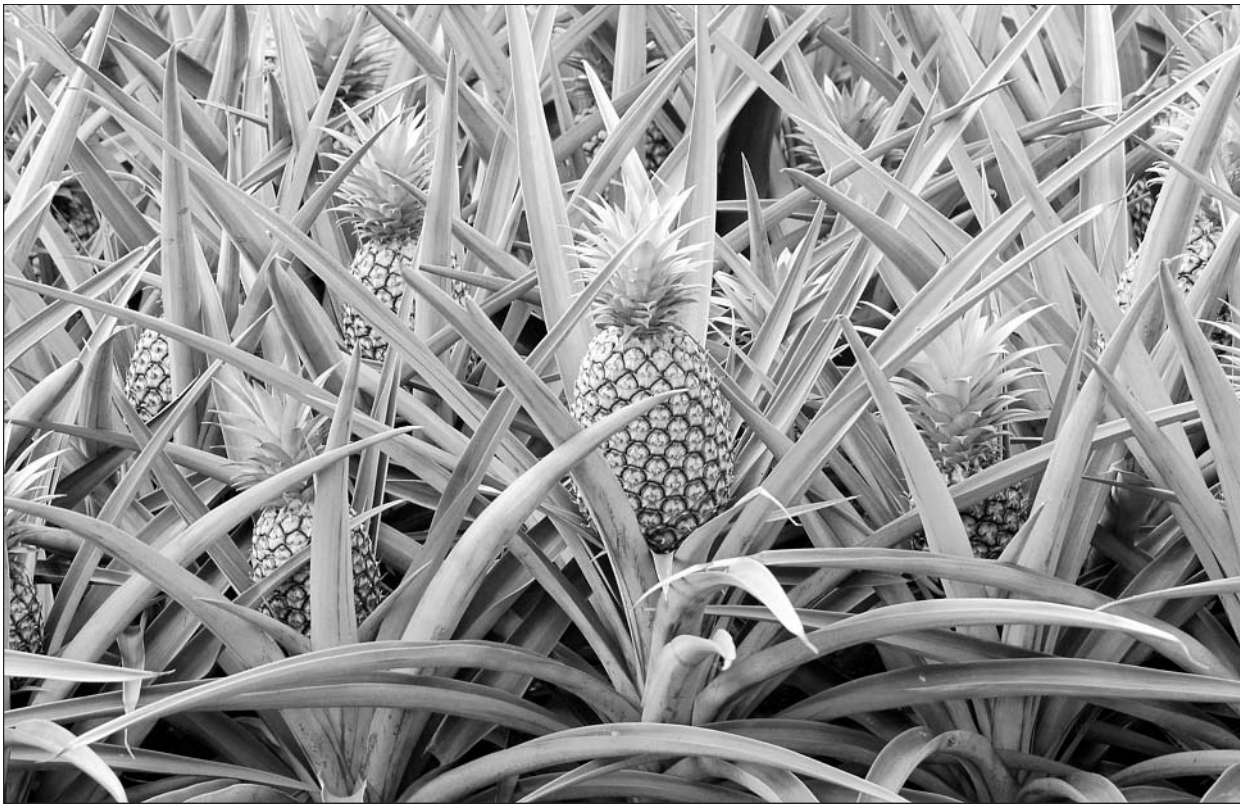
Appearance and Structure

The *Bromeliaceae* family shares a basic ground plan of construction that consists of branches (ramets) and an inflorescence that follows a repetitive pattern when growing. However, modifications, in the form of reductions, of this basic plan have evolved in different subfamilies. The basic pattern consists of sympodial branching, a rhythmic type of growth in which the axis is built up by a linear series of shoot units, each distal unit developing from an axillary bud located on the previous shoot unit. This pattern of development leads to a series of condensed ramets with terminal flowers. Roots, when present, usually emerge from the lower half of each ramet.

Growing Habit

Bromeliaceae range from small plants, such as some miniature *Tillandsia*, to very tall individuals, such as *Puya raimomndii*, reaching up to 32 feet (10 meters) in height. They can be epiphytes, that is, plants that use other species as support without harming them, or terrestrial. Some grow on top of rocks, and some are carnivorous.

Those species whose leaves are born from a common place in the stem (in a rosulate shape) can develop the tank form, also known as *phytotelma*, that is common in genera such as *Aechmea* and *Brocchinia*. These phytotelma harbor a variety of insects and small vertebrates that grow in small pools



The pineapple, Ananas comosus, *is the species of bromeliad most widely used as food.*

of water and old leaves that collect at the bottom of the "tank." The tanks accumulate water and partially dissolved organic matter, creating a nutrient-rich substrate as a continuous supply of moisture. Other *Bromeliaceae* do not form tanks; instead, they have fully functional roots and specialized hairs for water absorption.

Scales

Physiological adaptations to different environments among some species correlate with the presence of a highly evolved type of foliar hair (or trichome) known as a *scale*. The scales may cover the entire surface of the leaf, sometimes appearing in different locations and patterns; they absorb atmospheric water through capillary action, like blotting paper, and the water is later transported to the leaf tissue, where it is stored in the parenchyma. Division of the scale in two parts—known as the shield, or *trichome covering*, and the water absorption cells—is what makes *Bromeliaceae* unique. When water is scarce the scale shrinks, and when water is present the shield cells expand. Scales protect the leaves against transpiration and reduce water evaporation during the dry periods.

Flowers and Pollination

The flowers of *Bromeliaceae* are generally hermaphroditic (functionally unisexual). Their shape can be radial or slightly asymmetric, and the number of floral parts known as sepals and petals is always three. The stamen arrangement is in two whorls, with three stamens in each one. The ovary can be superior or inferior, and the placentation (position of the ovules) is mostly axial. Septal nectaries are always present at the base of the flower. The sepals are distinguished from the petals by their color and size. The petals show bright colors, while the sepals may remain mostly in green hues. Fruits are usually a capsule or a berry, and the seeds are winged.

The bloom of *Bromeliaceae* flowers is usually odorless, although some species may have scented flowers, indicating pollination by nocturnal moths or butterflies. However, their abundant secretion of nectar indicates that the plants are pollinated primarily by birds.

Uses

The main uses of *Bromeliaceae* are as textile fiber, food, medicine, and ornamental plantings. In the food category the pineapple, *Ananas comosus*, is the most widely used species. The medicinal properties of pineapple are based on the presence of bromelain, a proteolitic (protein-breaking) enzyme that is widely used to treat inflammation and pain. Serotonin, a neurotransmitter, is also present, and steroids from the leaves possess estrogenic activity. Thirteen species of *Bromeliaceae* are used as a source of textile fibers; for example, hammocks are made from the fibers of *Aechmea bracteata* and of pineapple.

Miriam Colella

See also: South American flora.

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BROWN ALGAE

Categories: Algae; *Protista*; taxonomic groups; water-related life

Seaweeds that are brown to olive-green in color belong to the phylum Phaeophyta*, or brown algae, which includes between fifteen hundred and two thousand species.*

Brown algae (phylum *Phaeophyta*) are familiar to most people as brown or dark green seaweeds. Some brown algae are microscopic in size, but many are relatively large: One giant kelp measured 710 feet in length. All brown algae are multicellular.

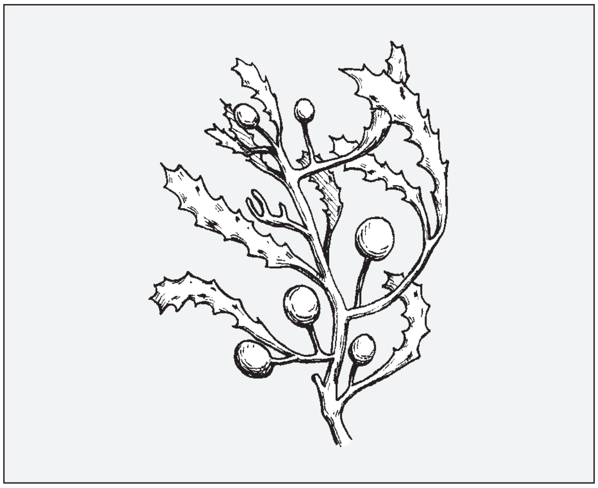
Appearance and Distribution

Brown algae have a body, called a *thallus*, which is a fairly simple, undifferentiated structure. Some thalli consist of simple branched filaments. Some brown algae have more complex structures called *pseudoparenchyma* because they superficially resemble the more complex tissues of higher plants.

Giant kelp have a thallus that is differentiated into a *holdfast*, a *stipe*, and one or more flattened, leaflike *blades*. The holdfast functions as the name implies, and holds the rest of the organism to the substrate. It is a tough, sinewy structure resembling a mass of intertwined roots. The stalk that constitutes the stipe is often hollow, with a meristem (a zone of growing tissue) either at its base or at the blade junctions. Because the meristem produces new tissue at the base, the oldest parts of the blades are at the tips.

The blades, which, like most of the rest of the giant kelp body, are photosynthetic, may have gas-filled floats called bladders toward their bases, which may contain carbon monoxide gas. The function of this particular gas has not yet been determined.

The vast majority of species are marine, living in cold, shallow ocean waters, and may be the dominant plant life on rocky coastlines. The giant kelp can be found in waters around 100 feet deep. Only 4 of the 260 identified genera occur in fresh water. Brown algae of the order *Fucales* are commonly



Brown algae, which range in color from olive green to golden, are among the largest algae, including the giant kelps, and often have a thallus (body) that is differentiated into a holdfast, a stipe (stalk), and one or more flattened, leaflike blades.

called rockweeds; kelp belong to the order *Laminariales*.

Brown algae are less common in tropical and subtropical areas. However, in the Caribbean region, *sargassum* (large masses of brown algae having a branching thallus with lateral outgrowths differentiated into leafy segments, air bladders, or spore-bearing structures) make up large floating mats; they gave their name to the Sargasso Sea.

Pigments and Food Reserves

The color of the brown algae can vary from light yellow-brown to almost black. Its color reflects the presence of varying amounts of the brown xanthophyll pigment fucoxanthin, a carotenoid pigment, in addition to chlorophylls *a* and *c*. The main food reserve is a carbohydrate called laminarin, although giant kelp can also translocate mannitol. Algin (alginic acid) can be found in or on the cell walls and may comprise as much as 40 percent of the dry weight of some kelps.

Reproduction

Reproductive cells of brown algae are unusual in that their two flagella are located laterally, instead of at the ends. The only motile cells in the brown algae are the gametes or reproductive cells. In the common genus *Fucus*, separate male and female thalli are produced. Fertile areas called *receptacles* develop at the tips of the lobes of the thallus. Each receptacle has pores on the surface. These pores open into special spherical, hollow chambers called *conceptacles*, in which the gametes are formed. Eight eggs are produced in the female structure, while sixty-four sperm cells are produced in the male structure. Eventually, both eggs and sperm are released into the water, where fertilization takes place and the resulting zygotes develop into mature thalli.

Economic Uses

Brown algae have several uses and applications for humans. Giant kelp is eaten, and one species found in the Pacific Ocean has been used, in chopped-up form, as a poultice applied to cuts. Algin, a colloidal substance produced by brown algae, is used as a thickener or stabilizer in commercially produced ice cream, salad dressing, beer, jelly beans, latex paint, penicillin suspensions, paper, textiles, toothpastes, and floor polish. Brown algae, with its high concentration of the element iodine, has been used to treat goiter, an iodine-deficiency disease. Kelp, also high in nitrogen and potassium, has been used as fertilizer and as livestock feed.

Some types of brown algae, such as *Fucus*, contain either phenols or terpenes. Botanists believe these substances may discourage herbivory. These substances also have been shown to possess microbe- and cancer-fighting properties. Brown algae is the subject of continuing research in these areas of medicine.

Carol S. Radford

See also: Agriculture: marine; Algae; Marine plants; Medicinal plants; Red algae.

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BRYOPHYTES

Categories: Nonvascular plants; paleobotany; *Plantae*; taxonomic groups

Bryophytes comprise three phyla of nonvascular plants, which generally lack the specialized conductive tissues (xylem and phloem) that are found in the vascular plants, are small in size, and are distributed worldwide in moist, shady habitats.

Bryophytes (from the Greek word *bryon*, meaning "moss") were once grouped together into one large phylum. Many botanists today recognize that these organisms belong to at least three distinct phyla: phylum *Hepatophyta* (the liverworts), phylum *Anthocerophyta* (the hornworts), and phylum *Bryophyta* (the mosses).

Origin and Relationships

Bryophytes are thought to have originated more than 430 million years ago, during the Silurian period. Many botanists speculate that bryophytes arose from an ancestor in the green algal order *Charales* or *Coleochaetales* based on biochemical, morphological, and life history comparisons. For example, *Chara* has a flavonoid biosynthesis pathway that is similar to that of higher plants, while *Coleochaete* retains its zygote inside parental tissue, similar to higher plants. These characteristics, along with similarities in cell division patterns, photosynthetic pigment contents, and the use of starch as a storage material, all suggest ancestry in the *Charales* or *Coleochaetales* orders.

Historically, bryophytes were thought to represent a group that formed a separate lineage from that of vascular plants. By the late 1990's a growing body of evidence suggested that bryophytes and vascular plants were derived from a common green algal ancestor. Some botanists suggest that the earliest land plants may have been members of the phylum *Anthocerophyta*. One of the key arguments in this theory is that the structure of some hornwort chloroplasts is virtually identical to the chloroplast structure of the presumed algal ancestors.

Studies conducted in the 1990's involving the presence or absence of certain portions of noncoding deoxyribonucleic acid (DNA) called *introns* in the genetic information of several groups of algae, bryophytes, and vascular plants revealed that members of the *Hepatophyta*, the liverworts, were likely among the first land plants. Like the algae, they lack the introns that are found in groups that are presumed to be more derived. Thus, based on the assumption that introns are derived characters, ancestors of modern liverworts may have given rise to vascular plants.

Anatomy

The dominant phase of the bryophyte life cycle is the haploid gametophyte phase. The gametophyte is photosynthetic and is usually small because of the lack of efficient vascular tissues.

Bryophytes possess rootlike *rhizoids* that anchor the plant to the soil and aid in nutrient uptake. A waxy *cuticle*, which helps prevent water loss, covers the body. Liverworts have pores for gas exchange, while hornworts and mosses have stomata to regulate gas movement. Some liverworts and hornworts have a thalloid body type, which is not differentiated into leaf and stem. The *thallus* may be simple, composed of a ribbonlike, flattened body of relatively undifferentiated tissues, or complex, in which there is a distinct differentiation of tissues. The flat body may aid in the uptake of water and minerals and in gas exchange. The bodies of some liverworts and the mosses are divided into leaf and stem. These terms are used for convenience even though xylem and phloem are not present.

Some mosses possess tissues that have functions similar to xylem and phloem. *Hydroids* are water-conducting cells that make up a tissue called hadrom. *Leptoids* are food-conducting cells that make up a tissue called leptom. These tissues appear similar to the conducting tissues in a group of fossil plants called *protracheophytes*, which are thought to be an intermediate group between the bryophytes and the vascular plants.

The diploid sporophyte of liverworts and mosses consists of a *foot*, which is attached to a stalklike *seta*. The seta connects the foot to the spore-producing organ called the *sporangium*, or *capsule*. The hornwort sporophyte, however, lacks a seta and possesses a long, cylindrical sporangium. The foot of the bryophyte sporophyte contains specialized transfer cells, which bring materials from the maternal gametophyte to the sporophyte. The sporophyte is totally dependent on the maternal gametophyte for its survival. A layer of sterile tissue called the *calyptra* covers the capsules of liverworts and mosses. When the spores are mature, the sporophyte may die, allowing the release of spores as the capsule decays (as in some thalloid liverworts). Alternatively, the capsule may rupture, allowing spores to be released through pores (as in mosses and leafy liverworts), or the capsule may split along the side to release the spores (as in the hornworts). Liverworts and hornworts often have specialized structures in the capsules called *elaters* that aid in dispersing spores from the capsules.

Reproduction and Life Cycle

Bryophytes may reproduce either asexually or sexually. Asexual reproduction primarily occurs by *fragmentation*. Some of the liverworts also repro-

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duce asexually by the production of small masses of vegetative tissue called *gemmae* in special structures called *gemma cups*. Water drops disperse the gemmae.

Bryophytes exhibit a typical plant life-cycle pattern called *alternation of generations*. There are distinct male and female gametophytes in some species, while other species produce both male and female organs in one plant. The reproductive organs are all multicellular. Male organs are called *antheridia*. Special cells within an antheridium undergo mitotic cell division to produce flagellated haploid sperm cells. The sperm cells are the only flagellated cells produced by bryophytes. As with many other plant groups, the presence of flagella on the sperm indicates that these cells require liquid water to swim to the egg.

The female organs are called *archegonia*. The archegonium is composed of a slender neck, within which is a canal. The base of the archegonium has a swollen region called the venter, which contains the egg. Special cells within an archegonium undergo mitotic cell division to produce a haploid egg.

If one gametophyte produces both antheridia and archegonia, the organs usually develop at different times, to reduce to likelihood of self-fertilization. When the sperm and eggs are mature, sperm are released from the antheridia in the presence of liquid water. Water drops transfer sperm from an antheridium to an archegonium. Sperm cells swim through the neck canal of the archegonium where fertilization occurs in the venter. The resulting zygote develops into an embryo, which then grows into the diploid sporophyte.

Sporogenous tissues in the sporangium undergo meiosis to produce haploid *spores*. The spore walls contain a substance called *sporopollenin*, which is resistant to chemicals and decay. After release, spores germinate and grow into new haploid gametophytes. The early threadlike stage of mosses and some liverworts is called the *protonema*. Protonemata are very similar to the body form of some algae.

Phylum *Hepatophyta*

There are between six thousand and eight thousand species of *hepatophytes* (from the Greek word *hepar*, meaning "liver"), which are commonly called liverworts. Hepatophytes are divided into three general groups: the simple thalloid liverworts, the complex thalloid liverworts, and the leafy liverworts. More than 85 percent of all hepatophyte species are leafy. Liverworts are usually terrestrial, although some species may be semiaquatic. Thalloid types are found worldwide. Leafy liverworts, which are often similar in appearance to mosses, are abundant in tropical jungles and fog belts. However, they are typically found in habitats that are more moist than those preferred by mosses.

Phylum *Anthocerophyta*

This phylum, the hornworts, consists of some one hundred species and represents the smallest group of bryophytes. The best-known genus, *Anthoceros* (from the Greek words *anthos*, meaning "flower" and *keras*, meaning "horn"), is found in temperate regions. The gametophyte is similar to thalloid liverworts. The cavities of the gametophyte body are filled with *mucilage*, a slimy secretion, in which grow nitrogen-fixing cyanobacteria, such as the genus *Nostoc*.

Phylum *Bryophyta*

Phylum *Bryophyta*, the mosses, consists of more than ninety-five hundred species. There are three important classes: class *Sphagnidae*, which includes the globally distributed, and economically as well as ecologically important genus *Sphagnum*; class *Andreaeidae*, which consists of a small group of blackish green to reddish brown tufted rock mosses growing on granitic or calcareous rocks in northern latitudes; and the class *Bryidae*, which consists of true mosses.

Economic Uses

Bryophytes are ecologically important members of terrestrial ecosystems. They are primary producers, providing food and habitat for animals. Humans have used bryophytes for many purposes. For example, *Sphagnum* deposits in peat bogs have been used for centuries as fuel for heating and cooking. Dried *Sphagnum* also has the ability to absorb large amounts of liquid, which makes it ideal to act as a soil conditioner for planting. American Indians used mosses as compresses to dress wounds. The antiseptic quality of *Sphagnum*, along with its absorptive properties, made its use attractive as bandage material for the British when cotton supplies were low during World War I.

Darrell L. Ray

See also: Hornworts; Liverworts; Mosses.

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BULBS AND RHIZOMES

Categories: Anatomy; physiology; reproduction and life cycles

Bulbs and rhizomes are modified stems, stem bases, or other underground organs used by plants for food (or energy) storage and in asexual reproduction.

Plants reproduce both sexually and asexually. Although sexual reproduction is part of the typical life cycle of plants, for a variety of reasons a plant may reproduce asexually. Exact duplicates of a plant, called *clones*, are formed by asexual reproduction.

Asexual Reproduction

Asexual reproduction involves the production of offspring through the formation of *propagules* by mitosis (the process of nuclear cell division). Because genetic recombination does not occur in mitosis, the offspring are genetically identical to the parent plant. Asexual reproduction does not occur in all plants; some reproduce asexually only when humans intervene. Asexual reproduction occurs when a single plant produces a vegetative propagule that develops into a separate free-living plant. Many of the propagules that support asexual reproduction are actually highly modified branches. Others are modified roots. In rare instances, the tissues of leaves may be modified by nature to support asexual reproduction. The propagules of asexual reproduction vary enormously. They are often found in catalogs describing "bulbs," but technically they include *true bulbs*, *corms*, *stolons*, *tubers*, *rhizomes*, *turions*, *pseudobulbs*, and *fleshy roots*.

True Bulbs

Bulbs, corms, stolons, tubers, rhizomes, and turions are all modified stems. Bulbs are modified stem bases that develop underground. The stem is shortened and thickened to produce a mass of tissue shaped like a coin or like a child's toy top. Scalelike leaves with thickened bases are attached to the base of the bulb. Starch is stored in the thickened bases, a food supply that allows the bulb to survive through a dormant season and to produce adventitious roots. Roots are often absent when the bulb is dormant. The starch can also support a period of rapid stem and leaf growth in the growing season and may support the flowering and fruiting of the plant.

In *tunicate* bulbs, a cloak of dried leaves surrounds the outside of the bulb. These dried leaves provide a barrier to desiccation and allow the tunicate bulbs to be stored aboveground for weeks or even months. Onions (*Allium cepa*) and daffodils (*Narcissus*) are examples of tunicate bulbs. Other bulbs have no cloak and usually have shorter, less cylindrical leaves. These scaly bulbs dry quickly when kept aboveground and usually develop flowers only after a more normal, aerial branch system forms. Lilies (*Lilium*) have scaly bulbs.

Stems of both tunicate and scaly bulbs can branch. Belowground, branches appear at first as

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miniature bulbs (*bulbils* or *bulblets*). Bulblets take their energy from the parent bulb but eventually produce aerial stems or leaves and can be separated from the parent. Profuse branching can be stimulated by wounding the stem of the parent bulb. All the bulbs produced by this technique are clones, identical to the parent in their genetic makeup and physical characteristics.

Corms and Tubers

Corms are similar to bulbs in many ways. They have a disk-shaped or top-shaped stem mass that is shorter and wider than most typical stems. They are often cloaked in a tunic of dried leaves that are thinner and smaller than those on bulbs. Corms do not store significant amounts of starch; it is instead stored primarily in the basal plate of the stem. Branches of the corm stem produce new, miniature corms (*cormels*). Wounding the parent stem stimulates greater branching. Gladiolus and crocus are two common garden plants that produce corms.

Tubers are thick, starchy stems that form usually at the tip of a stolon, runner, or tiller. Tubers may form on the soil surface or belowground. A familiar example is the white or Irish potato (*Solanum tuberosum*). The leaves on most tubers are much smaller than the leaves on other parts of the stem, but above each leaf on the tuber is a well-developed axillary bud, commonly called an *eye*. The axillary bud has the potential to elongate, forming a complete and fully developed branch. If the stolon connecting the tuber to the parent plant dies, the branch from the eye of the tuber becomes an independent clone of the parent plant.

Most tubers contain many eyes. If the tuber is cut into smaller pieces, each containing an eye, each piece develops a rhizome, which in turn develops a new tuber. By this technique, a significant increase in the number of plants can be obtained. The cut pieces of tuber are initially prone to decay, but after they have dried for a few days, they heal over with a layer of callus which protects them like a skin. Cutting tubers into small “seed” pieces is a common method for propagating tuber-forming species.

Rhizomes, Stolons, and Fleshy Roots

Rhizomes are specialized, underground stems. Unlike most areal stems, the rhizomes are normally oriented horizontally. Just as pieces of tuber can provide the tissue and energy source for the formation of a new plant, so too can pieces of a rhizome. Many ferns and fern allies propagate naturally by rhizomes. Large stands of these plants can form from a single individual as the rhizomes grow and branch. Eventually, older pieces of the rhizome die, leaving a population of individuals that all have identical genetic characteristics.

Stolons are long, thin, horizontal stems, also called *runners* or *tillers*, which grow along the surface of the ground. When the stolon has grown far enough from the parent plant, the growth pattern changes, and a *crown*, or tuber, forms. A crown is a compressed stem mass with leaves arranged close to one another, also called a *rosette*. Within the crown, roots form at the points of attachment of the leaves to the stems. If the stolon is broken or dies, the crown becomes an independent clone of the parent plant. In this way, a large number of offspring can be produced from a single plant. This is a mechanism of reproduction of the strawberry (*Fragaria*) and is also a common reproductive mechanism for grasses, including crab grass (*Digitaria sanguinalis*) and quack grass (*Agropyron repens*).

Fleshy roots store energy that can be useful for asexual propagation. Most require at least a small amount of stem tissue to support cell growth and differentiation. The true yam (*Dioscorea*) is a tuber, but the sweet potato (*Ipomoea batatas*) is a fleshy root which can easily be propagated asexually. Many buttercups (*Ranunculus*) are also propagated by breaking up the clumps of their fleshy roots.

Craig R. Landgren, updated by Bryan Ness

See also: Roots; Stems.

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C_4 AND CAM PHOTOSYNTHESIS

Categories: Photosynthesis and respiration; physiology

Alternative forms of photosynthesis are used by specific types of plants, called C_4 and CAM plants, to alleviate problems of photorespiration and excess water loss.

Photosynthesis is the physiological process whereby plants use the sun's radiant energy to produce organic molecules. The backbone of all such organic compounds is a skeleton composed of carbon atoms. Plants use carbon dioxide from the atmosphere as their carbon source.

The overwhelming majority of plants use a single chemical reaction to attach carbon dioxide from the atmosphere onto an organic compound, a process referred to as *carbon fixation*. This process takes place inside specialized structures within the cells of green plants known as *chloroplasts*. The enzyme that catalyzes this fixation is ribulose bisphosphate carboxylase (Rubisco), and the first stable organic product is a three-carbon molecule. This three-carbon compound is involved in the biochemical pathway known as the *Calvin cycle*. Plants using carbon fixation are referred to as *C_3* plants because the first product made with carbon dioxide is a three-carbon molecule.

C_4 Photosynthesis

For many years scientists thought that the only way photosynthesis occurred was through C_3 photosynthesis. In the early 1960's, however, researchers studying the sugarcane plant discovered a biochemical pathway that involved incorporation of carbon dioxide into organic products at two different stages. First, carbon dioxide from the atmosphere enters the sugarcane leaf, and fixation is accomplished by the enzyme phosphoenolpyruvate carboxylase (PEP carboxylase). This step takes place within the cytoplasm, not inside the chloroplasts. The first stable product is a four-carbon organic compound that is an acid, usually malate. Sugarcane and other plants with this photosynthetic pathway are known as *C_4* plants.

In C_4 plants, this photosynthetic pathway is tied to a unique leaf anatomy known as *Kranz anatomy*. This term refers to the fact that in C_4 plants the cells that surround the water- and carbohydrate-conducting system (known as the *vascular system*) are packed very tightly together and are called *bundle sheath cells*. Surrounding the bundle sheath is a densely packed layer of *mesophyll* cells. The densely packed mesophyll cells are in contact with air spaces in the leaf, and because of their dense packing they keep the bundle sheath cells from contact with air. This Kranz anatomy plays a major role in C_4 photosynthesis.

In C_4 plants the initial fixation of carbon dioxide from the atmosphere takes place in the densely packed mesophyll cells. After the carbon dioxide is fixed into a four-carbon organic acid, the malate is transferred through tiny tubes from these cells to the specialized bundle sheath cells. Inside the bundle sheath cells, the malate is chemically broken down into a smaller organic molecule, and carbon dioxide is released. This carbon dioxide then enters the chloroplast of the bundle sheath cell and is fixed a second time with the enzyme Rubisco and continues through the C_3 pathway.

Advantages of Double-Carbon Fixation

The double-carbon fixation pathway confers a greater photosynthetic efficiency on C_4 plants over C_3 plants, because the C_3 enzyme Rubisco is highly inefficient in the presence of elevated levels of oxygen. In order for the enzyme to operate, carbon dioxide must first attach to the enzyme at a particular location known as the *active site*. However, oxygen is also able to attach to this active site and prevent carbon dioxide from attaching, a process known as *photorespiration*. As a consequence, there is an ongoing competition between these two gases for attachment at the active site of the Rubisco enzyme. Not only does the oxygen outcompete carbon dioxide; when oxygen binds to Rubisco, it also destroys some of the molecules in the Calvin cycle.

At any given time, the winner of this competition is largely dictated by the relative concentrations of these two gases. When a plant opens its *stomata* (the pores in its leaves), the air that diffuses in will be at equilibrium with the atmosphere, which is 21 percent oxygen and 0.04 percent carbon dioxide. During hot, dry weather, excess water vapor diffuses out, and under these conditions plants face certain desiccation if the stomata are left open continuously. When these pores are closed, the concentration of gases will change. As photosynthesis proceeds, carbon dioxide will be consumed and oxygen generated.

When the concentration of carbon dioxide drops below 0.01 percent, oxygen will outcompete carbon dioxide at the active site, and no net photosynthesis occurs. C_4 plants, however, are able to prevent photorespiration, because the PEP carboxylase enzyme is not inhibited by oxygen. Thus, when the stomata are closed, this enzyme continues to fix carbon inside the leaf until it is consumed. Because the bundle sheath is isolated from the leaf's air spaces, it is not affected by the rising oxygen levels, and the C_3 cycle functions without interference. C_4 photosynthesis is found in at least nineteen families of flowering plants. No family is exclusively composed of C_4 plants. Because C_4 photosynthesis is an adaptation to hot, dry environments, especially climates found in tropical regions, C_4 plants are often able to outcompete C_3 plants in those areas. In more temperate regions, they have less of an advantage and are therefore less common.

CAM Photosynthesis

A second alternative photosynthetic pathway, known as *crassulacean acid metabolism* (CAM), exists in succulents such as cacti and other desert plants. These plants have the same two carbon-fixing steps as are present in C_4 plants, but rather than being spatially separated between the mesophyll and bundle sheath cells, CAM plants have both carbon dioxide-fixing enzymes within the same cell. These enzymes are active at different times, PEP carboxylase during the day and Rubisco at night. Just as Kranz anatomy is unique to C_4 plants, CAM plants are unique in that the stomata are open at night and largely closed during the day.

The biochemical pathway of photosynthesis in CAM plants begins at night. With the stomata open, carbon dioxide diffuses into the leaf and into mesophyll cells, where it is fixed by the C_4 enzyme PEP carboxylase. The product is malate, as in C_4 photosynthesis, but it is transformed into malic acid (a nonionic form of malate) and is stored in the cell's *vacuoles* (cavities within the cytoplasm) until the next day.

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Although the malic acid will be used as a carbon dioxide source for the C_3 cycle, just as in C_4 photosynthesis, it is stored until daylight because the C_3 cycle requires light as an energy source. The vacuoles will accumulate malic acid through most of the night. A few hours before daylight, the vacuole will fill up, and malic acid will begin to accumulate in the cytoplasm outside the vacuole. As it does, the pH of the cytoplasm will become acidic, causing the enzyme to stop functioning for the rest of the night.

When the sun rises the stomata will close, and photosynthesis by the C_3 cycle will quickly deplete the atmosphere within the leaf of all carbon dioxide. At this time, the malic acid will be transported out of the vacuole to the cytoplasm of the cell. There it will be broken down, and the carbon dioxide will enter the chloroplast and be used by the C_3 cycle; thus, photosynthesis is able to continue with closed stomata.

Crassulacean acid metabolism derives its name from the fact that it involves a daily fluctuation in the level of acid within the plant and that it was first discovered to be common in species within the stonecrop family, *Crassulaceae*. The discovery of this photosynthetic pathway dates back to the 1960's. The observation that succulent plants become very acidic at night, however, dates back to at least the seventeenth century, when it was noted that cactus tastes sour in the morning and bitter in the afternoon.

CAM Plant Ecosystems

There are two distinctly different ecological environments where CAM plants may be found. Most are terrestrial plants typical of deserts or other harsh, dry sites. In these environments, the pattern of stomatal opening and closing provides an important advantage for surviving arid conditions: When the stomata are open, water is lost; however, the rate of loss decreases as the air temperature decreases. By restricting the time period of stomatal opening to the nighttime, CAM plants are extremely good at conserving water.

The other ecological setting where CAM plants are found is in certain aquatic habitats. When this environment was first discovered, it seemed quite odd, because in these environments conserving water would be of little value to a plant. It was found, however, that there are aspects of the aquatic environment which make CAM photosynthesis advantageous. In shallow bodies of water, the photosynthetic consumption of carbon dioxide may proceed at a rate in excess of the rate of diffusion of carbon dioxide from the atmosphere into the water, largely because gases diffuse several times more slowly in water than in air. Consequently, pools of water may be completely without carbon dioxide for large parts of the day. Overnight, carbon dioxide is replenished, and aquatic CAM plants take advantage of this condition to fix the plentiful supply of carbon dioxide available at night and store it as malic acid. Hence, during the day, when the ambient carbon dioxide concentration is zero, these plants have their own internal supply of carbon dioxide for photosynthesis. Thus, two very different ecological conditions have selected for the identical biochemical pathway.

These two modified photosynthetic pathways adequately describe what happens in most terrestrial plants, although there is much variation. For example, there are species that appear in many respects to have photosynthetic characteristics intermediate to C_3 and C_4 plants. Other plants are capable of switching from exclusively C_3 photosynthesis to CAM photosynthesis at different times of the year. Photosynthesis by aquatic plants appears to present even more variation. C_3-C_4 intermediate plants seem to be relatively common compared to the terrestrial flora, and several species have C_4 photosynthesis but lack Kranz anatomy.

Jon E. Keeley, updated by Bryan Ness

See also: Cacti and succulents; Carbon 13/carbon 12 ratios; Vacuoles.

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CACTI AND SUCCULENTS

Categories: Angiosperms; *Plantae*

Succulents are fleshy plants that store water in natural reservoirs such as stems or leaves. Cacti are a group of flowering plants; all cacti are succulents.

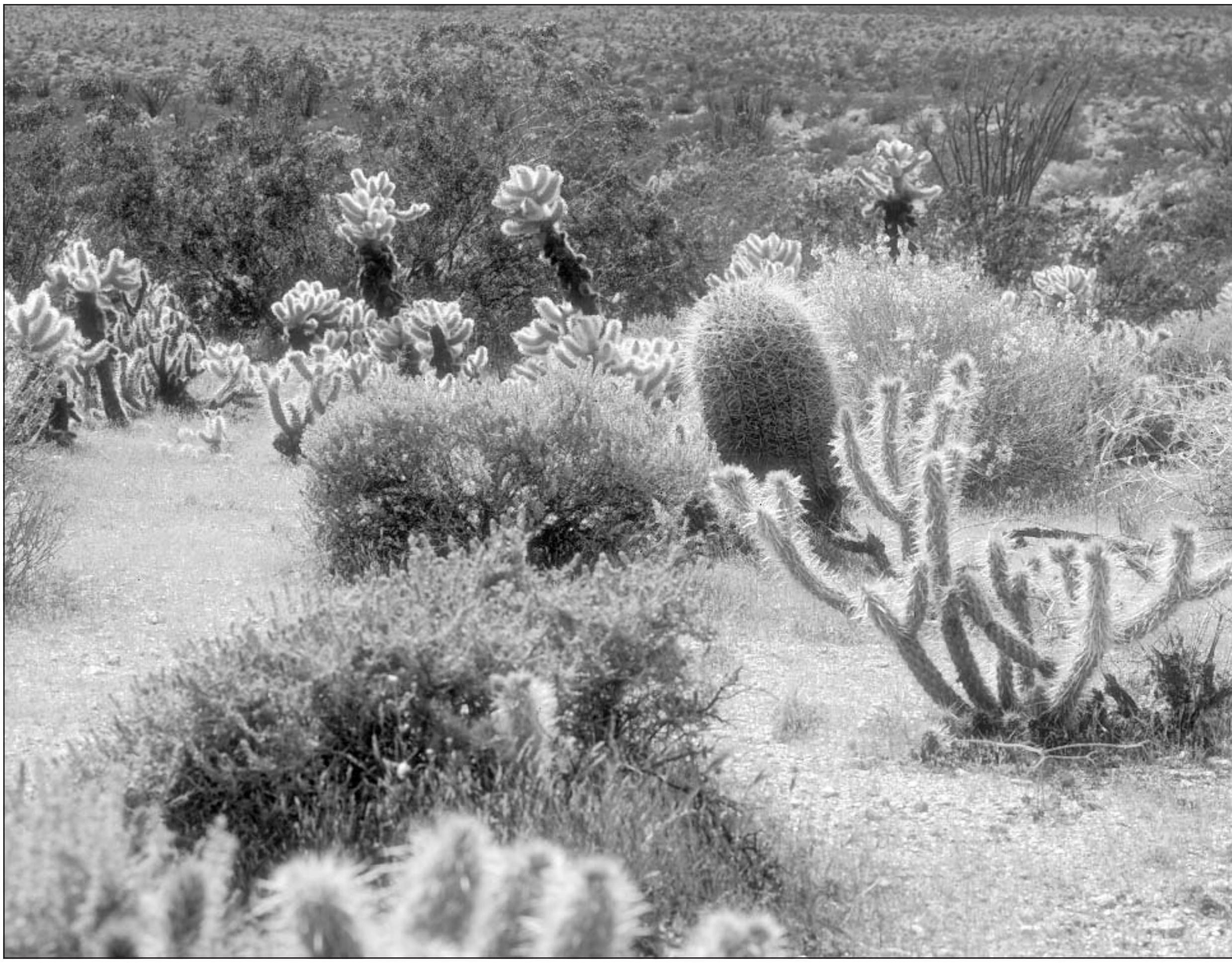
The *Cactaceae* family includes about 1,650 to 3,500 species of *cacti* and *succulents* classified in 130 genera. Because they live in harsh, arid environments, these fleshy, spiny perennial plants have developed a variety of unique characteristics for protection and to retain water, reduce evaporation, and resist heat.

Cacti

The word "succulent" is derived from the Latin term *sucus*, meaning sap. All cacti are succulents. The word "cactus" is derived from the Greek term *kaktos*, describing thistles. Botanists estimate cacti first existed during the Mesozoic era, about 130 million years ago. Limited cacti fossil evidence exists (the earliest known specimen is about forty thousand years old).

Cacti vary in size. The *Copiapoa laui* is a spherical plant several millimeters in diameter, while the *Pachycereus weberi* is cylindrical, stands more than 20 meters tall, and can weigh more than 25 tons. Cacti often develop bizarre shapes to cope with arid conditions. Some stems are flat, and others are puffy. Many consist of jointed segments, while others have one round stem. Cacti stems swell when storing water. Surface ridges and grooves gather water. Roots extend in a wide area near the soil surface, to capture any moisture. The pincushion, barrel, saguaro, prickly pear, night-blooming cereus, and Christmas cactus are some of the most familiar cacti.

Unlike other plants, cacti have *areolas* on stems where branches, spines, *glochids* (bristles), leaves, and flowers grow. Spines protect and shade the plant and its seedlings from predators and ultraviolet radiation and serve as condensation sites. Known as *crassulacean acid metabolism* (CAM), photosynthesis in cacti is reversed from the process in other plants. Stems have chlorophyll because leaves are either absent or tiny. At night, instead of day, cacti open the stomata on their stems to collect carbon dioxide and expel oxygen. The carbon diox-



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Cacti often develop bizarre shapes to cope with arid conditions. Stems of these plants swell when storing water, surface ridges and grooves gather water, and roots extend in a wide area near the soil surface to capture any available moisture.

ide is stored as organic acids for conversion to sugar during the day. Because the temperature is cooler when the stomata are opened, less water is lost. During the day, the closed stomata prevent evaporation from occurring.

Life Cycles of Cacti

Cacti grow slowly and can live more than a century. Flowers usually bloom in late spring and vary in color, size, and shape. Seeds are inside the fruits that blossoms produce. Some cacti grow from seeds if they are shaded and not consumed by predators. Other cacti emerge from stems and take root where they fall. Artificially, cacti can also take root from cuttings. Diverse insects and animals are attracted to the flowers and assist in their pollination. Some birds nest in holes in cacti stems.

Distribution of Cacti

Cacti grow in deserts, prairies, mountains, and tropical climates and have developed a tolerance for extreme conditions. Cacti are indigenous to North, Central, and South America. The *Epiphyllum* species live in tropical trees. Other cacti grow in rocky places. Some Chilean cacti in the Atacama Desert secure water from sea fog. The largest and most diverse population of cacti is in Mexico. The prickly pear is the most widely distributed cactus, ranging from near the Arctic circle to southern South America.

Uses of Cacti

Cactus fruits are edible by humans and animals and used as livestock forage, as a water source, for fuel, and to erect organic barriers. Spines are used as needles and fishhooks, and fibers are twisted into rope. Historically, peyote is a ceremonial hallucinogenic, and other cacti have medicinal purposes. While no cacti are poisonous, some species have unpleasant chemicals that discourage predators.

Some hybrids have naturally occurred, and cactus segments can be detached at joints to graft to artificially unique plants. Because of poaching, cacti are considered endangered plants, with some species threatened by extinction, and are federally protected at Saguaro National Park (in Arizona's Tucson Basin) and Organ Pipe Cactus National Monument (in Arizona's Sonoran Desert).

Succulents

Although they share many traits with their close relatives the cacti, other succulents do not have areolas. Succulents vary in shape and size. Some are as tiny as peas, while others are large as livestock. Succulents take many forms, including that of the string of beads (*Senecio rowleyanus*). Yucca and jade plants are two of the most familiar succulents.

Because of evolutionary adaptation to endure climatic extremes, succulents have small leaves and spongy tissues that keep water for prolonged durations. Succulents retain water to withstand such environmental stresses as drought, scorching wind, shallow or salty topsoil, steep locations, and overcrowding by other plants. Succulents keep flower stalks and fruit until all the water is depleted from them. They have a thick skin, which is waxy, and sometimes alter their shape while adjusting to differences of light and moisture. Most succulents are gray, although a few are colored lilac, pink, light green, beige, or ivory, often in patterns that may serve as camouflage.

The greatest quantity and most diverse succulents can be found in Mexico and South Africa, which have thousands of species. New species are still being discovered because of variations arising from environmentally triggered adaptations. Some succulents, such as the *Argyroderma*, are abundant, growing in thick clumps. The rarer succulents include *Conophytum burgeri*, which lives on only one South African hill. Succulents are threatened by overgrazing and industrial and agricultural development of habitats. Some succulents, particularly aloe, have healing juices to soothe burns.

Elizabeth D. Schafer

See also: Angiosperm evolution; C_4 and CAM photosynthesis; Culturally significant plants; Deserts; Drought; Endangered species; Evolution of plants; Growth habits; Hybridization; Leaf anatomy; Liquid transport systems; Photosynthesis; Plant fibers; Water and solute movement in plants.

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CALVIN CYCLE

Categories: Biogeochemical cycles; photosynthesis and respiration; physiology

The Calvin cycle is the principal mechanism that leads to the conversion of carbon dioxide into sugars by plants, algae, photosynthetic bacteria, and certain other bacteria that use chemicals as an energy source instead of light.

The Calvin cycle, also known as the Calvin-Benson cycle, is an integral part of the process of *photosynthesis* in plants, algae, and photosynthetic bacteria. Named after its discoverer, Melvin Calvin of the University of California at Berkeley, its principal product is a three-carbon compound called *glyceraldehyde 3-phosphate*, or PGAL. Sugars are synthesized using PGAL as a starting material. Light, absorbed by *chlorophyll*, is used to synthesize the high-energy compounds *adenosine triphosphate* (ATP) and reduced *nicotinamide adenine dinucleotide phosphate* (NADPH). Chlorophyll and the enzymes that are used for synthesis of ATP and NADPH are associated with internal membranes in all photosynthetic cells. The ATP and NADPH, once formed, are released from the membrane-bound enzymes and diffuse into the surrounding solution inside the cell. The Calvin cycle takes place in this solution, using the ATP and NADPH molecules as a source of energy to drive the conversion of carbon dioxide into PGAL.

Enzymes

All the steps in the Calvin cycle and sugar biosynthesis are catalyzed by specific enzyme molecules. The carbon dioxide molecules react with a five-carbon sugar-phosphate molecule called *ribulose bisphosphate* (RuBP) to form a six-carbon intermediate. The reaction is catalyzed by the enzyme *ribulose bisphosphate carboxylase/oxygenase* (Rubisco). The six-carbon intermediate reacts with water and decomposes into two identical three-carbon molecules called phosphoglycerate. These, in turn, react with ATP and NADPH to produce PGAL molecules. Some of these leave the Calvin cycle and are used for the formation of sugars. The ADP and NADP molecules, produced when PGAL is formed, diffuse back to the chlorophyll-containing membranes, where they can be used to regenerate a supply of ATP and NADPH for the next round of the Calvin cycle. The remaining PGAL molecules are used for the regeneration of sufficient amounts of RuBP to permit the reactions of the Calvin cycle to be repeated.

The regeneration of RuBP from PGAL involves the rearrangement of the carbon atoms in three-carbon containing molecules to form five-carbon molecules. For example, if there are ten three-carbon molecules remaining after two three-carbon molecules have been removed from the cycle, then six five-carbon molecules are synthesized by the Calvin cycle. This is accomplished by no less than nine separate enzyme-catalyzed steps, involving intermediate compounds containing two, three, four, five, or seven carbon atoms derived from the PGAL molecules. At the end of this complex process, ATP is used to add another phosphate group to each five-carbon molecule, thus regenerating the required amount of RuBP, the original organic starting material for the cycle. A continuous supply of phosphate must be made available in order to continue running the Calvin cycle. Ultimately, all this phosphate must be supplied to the organism from the environment; in the short term, however, it is gleaned from other biochemical reactions, such as sugar biosynthesis.

PGAL

The principal product of the Calvin cycle is not sugar but PGAL. In higher plants, the Calvin cycle takes place inside *chloroplasts*, and the PGAL molecules are transported across the membranes of the chloroplasts and released into the solution between the chloroplast membranes and the cell's outer membrane. In this solution, called the *cytosol*, the PGAL molecules react to form six-carbon sugar phosphates. These six-carbon sugar phosphates then react to form *sucrose*, a twelve-carbon molecule (ordinary table sugar).

A sucrose molecule consists of one molecule each of the six-carbon sugars *fructose* and *glucose*.

Phosphate is released from the sugar phosphates during the formation of sucrose. The phosphate can then be returned to the chloroplast, where it is needed for the formation of ATP. Most of the sucrose is transported out of the cell and flows to various parts of the plant, such as the fruits or the roots. The transport of sucrose out of the cell requires energy derived from ATP. The accumulation of sucrose in the water outside the cell causes the hydrostatic pressure to rise. This pressure drives the flow of the water and sucrose (sap) through the phloem away from the leaves and toward the fruit or roots. The accumulation of sucrose in the fruit accounts for a large part of the nutritional value of plants.

When conditions do not favor the formation of sucrose, the triose phosphates may remain inside the chloroplast. These can react to form six-carbon sugar bisphosphates that, in turn, can react in several steps to form an insoluble carbohydrate storage compound called *starch*. The conversion of six-carbon sugar bisphosphate into starch releases phosphate. The phosphate released can then participate in the synthesis of more ATP, permitting continued operation of the Calvin cycle even when sucrose is not being formed. The accumulation of starch is another major source of nutritional value in plants.

In the morning, when plants begin receiving light, the amounts of phosphoglycerate and six-carbon sugar phosphates increase dramatically. The amounts of other intermediates in the cycle do not change as much. This suggests that some (but not all) steps in the Calvin cycle shut down in the dark and are activated in the light. The Calvin cycle also operates in nonphotosynthetic bacteria that use environmental chemicals as an energy source for the synthesis of ATP and other high-energy molecules. Although these organisms are responsible only for a minor proportion of the total carbon dioxide converted to organic form every year, their existence is interesting because it suggests that the Calvin cycle evolved before the origin of photosynthesis. The starch that builds up in the chloroplasts during the day is converted to sucrose at night and is then exported from the leaf.

Photorespiration

A significant complication must be taken into account when discussing the Calvin cycle: Oxygen can also react with RuBP, because the active site of Rubisco has affinity for both oxygen and carbon dioxide. Under normal conditions in many higher plants, three out of ten RuBP molecules react with oxygen instead of reacting with carbon dioxide. Under conditions where carbon dioxide levels are lower than normal and oxygen levels are higher than normal, oxygen may even react more frequently than carbon dioxide. This has deleterious consequences, because each RuBP molecule that reacts with oxygen is cleaved into two parts. One part is PGA, identical to that produced by the reaction of RuBP with carbon dioxide. The other part, however, is a two-carbon compound called phosphoglycolate. The latter molecule subsequently is cleaved to produce carbon dioxide; only one of the two carbons in phosphoglycolate is salvaged by the cell in a complex series of reactions called *photorespiration*. Because the photorespiratory reactions use energy, the chlorophyll-containing membranes must produce more ATP and NADPH than would otherwise be needed for the Calvin cycle.

Evolution of the Cycle

The Calvin cycle is believed to have originated more than 3.5 billion years ago in marine bacteria that were using very simple carbon compounds as an energy source. Some of the descendants of these bacteria later acquired the ability to synthesize ATP and NADPH (or their equivalents), using light as an energy source. As long as one billion years ago, some of these photosynthetic bacteria are believed to have established mutually beneficial, or *symbiotic*, relationships with other cells. These symbiotic relationships became stabilized and led to the evolution of algae and higher plants. The photosynthetic organelles of plants and algae, the chloroplasts, are thought to be the direct descendants of the symbiotic photosynthetic bacteria.

The early atmosphere of the earth probably had significantly less oxygen than it does now, so the existence of the oxygenase activity of Rubisco would not have been a problem. When the oxygen concentration in the atmosphere rose to its present level about 1.7 billion years ago, however, the losses of energy caused by the oxygenase reaction became significant. Some organisms evolved mechanisms to prevent these losses: In algae, for example, there are molecular pumps which, in effect, concentrate carbon dioxide in the cell so that the oxygenase reaction is inhibited. In sugarcane, corn, and certain other plants that are specialized to live in hot, dry climates, a similar effect is achieved by C_4 photosynthesis.

Not content with the results of evolution, biotechnologists are interested in altering Rubisco. They reason that if this enzyme can be genetically engineered to lower its oxygenase activity, the net photosynthetic rates of some plants could be improved. Possibly a 30 percent increase in plant productivity could be expected if such strategies prove successful, provided other materials (nitrogen, phosphorus, and other nutrients) are present in sufficient supply to permit the extra growth. Thus, although the Calvin cycle is the major route of entry of inorganic carbon into the biosphere, it is also something of a bottleneck. It remains to be seen whether the Calvin cycle can be made to function more efficiently.

Harry Roy, updated by Bryan Ness

See also: ATP and other energetic molecules; C_4 and CAM photosynthesis; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions.

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CARBOHYDRATES

Categories: Cellular biology; nutrients and nutrition

Common organic chemicals found in all living organisms, important in energy metabolism and structural polymers, carbohydrate molecules are made up of carbon, hydrogen, and oxygen.

Carbohydrates are made of carbon, hydrogen, and oxygen molecules in a 1:2:1 ratio, respectively. This is often simplified using the formula nCH_2O, where n represents the number of CH_2O subunits in a carbohydrate. This formula should make it clear how the name carbohydrate was derived, as nCH_2O is essentially carbon and water. The simplest carbohydrates are the *monosaccharides*, or simple sugars. Individual monosaccharides can be joined together to make *disaccharides* (composed of two monosaccharides), *oligosaccharides* (short polymers composed of two to several monosaccharides), and *polysaccharides* (longer polymers composed of numerous monosaccharides).

Monosaccharides

The common monosaccharides found in plants have from three to six carbon atoms in a straight chain with one oxygen atom. Most of the oxygen atoms also have a hydrogen atom attached, making them hydroxyl groups (^{-}OH). One of the oxygen atoms is connected to a carbon by a double covalent bond, while the hydroxyl groups are attached to carbon atoms by single covalent bonds. If the double-bonded oxygen is on a terminal carbon (as an aldehyde group), the monosaccharide is called an *aldose*. If the double-bonded oxygen is on an internal carbon, the monosaccharide is called a *ketose*.

The simplest monosaccharides are the three-carbon sugars, or *trioses*. *Pentoses*, with five carbons, are also important in plants. *Ribose* and *deoxyribose* are found in RNA (ribonucleic acid) and DNA (deoxyribonucleic acid), respectively. *Ribulose bisphosphate* is an important intermediate in the incorporation of carbon dioxide into carbohydrates during photosynthesis. *Xylose* and *arabinose* are found as components of some plant polysaccharides.

Hexoses, six-carbon monosaccharides such as *glucose*, *fructose*, and *galactose*, are the most common monosaccharides in plants. These sugars all have the same formula, $C_6H_{12}O_6$ (note the 1:2:1 ratio of C:H:O), but their atoms are arranged differently. Glucose is the primary carbon-containing product of photosynthesis and reverse glycolysis and later can be metabolized through glycolysis and the Krebs cycle to release energy or can be converted to other carbohydrates needed by the plant.

Oligosaccharides

Oligosaccharides are made by joining two or more monosaccharides. The smallest are the disaccharides, formed from two monosaccharides that are joined together by a condensation reaction. Condensation reactions get their name from the fact that when the two monosaccharides are joined together, a molecule of water is released. *Sucrose* (glucose-fructose) is the most common plant disaccharide and is the principal molecule of short-term energy storage and of translocation (transport) in the phloem. Many plants, including sugarcane (*Saccharum officinarum*) and sugar beets (*Beta saccharifera*), have high concentrations of sucrose, which can be extracted and refined for use as table sugar.

Other disaccharides found in plants are *maltose*, which is a glucose disaccharide formed from the hydrolysis (the reverse of a condensation reaction, wherein water is used to "split" the bond between the monosaccharides) of starch, and *trehalose*, also a glucose disaccharide, which is the primary molecule of translocation in species of *Selaginella* and is seen in cyanobacteria (blue-green algae or blue-green bacteria), red algae, and fungi. *Cellobiose*, another glucose disaccharide, is formed by the hydrolysis of cellulose.

The trisaccharide *raffinose* (galactose-glucose-fructose) is a storage molecule in sugar beets and in cotton and legume seeds. *Stachyose* (galactose-galactose-glucose-fructose) and *verbascose* (galactose-galactose-galactose-glucose-fructose) are also storage oligosaccharides, seen mainly in *Fabaceae* (the legume or pea family).

Polysaccharides

The two main functions of polysaccharides in plants are long-term energy storage and structure. Glucose is the most common subunit in plant polysaccharides. The glucose molecules in these polymers are joined together in different ways. The carbon atoms in glucose molecules are numbered from one to six. In some, the 1-carbon of a glucose is attached to the 4-carbon of the next, and this linkage is repeated throughout the molecule. At other times, an additional bond is formed between the 1-carbon and the 6-carbon of adjacent glucoses, which results in a branched polysaccharide.

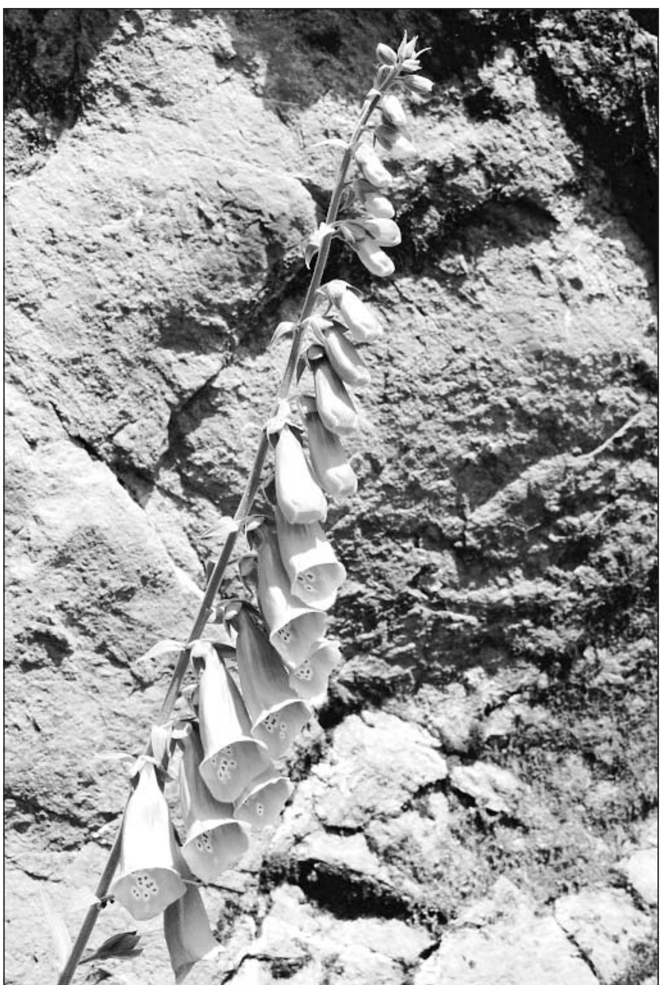
Starch is the most common storage polysaccharide of plants. Two forms of this glucose polymer exist. *Amylose* is a linear polymer made up of between one hundred and several thousand glucose units. *Amylopectin* is very similar, but it is a branched polymer. In most plants, starch is 15-25 percent amylose and 75-85 percent amylopectin. However, starch in some waxy varieties of corn is nearly 100 percent amylopectin and in some wrinkled varieties of peas is as high as 80 percent amylose. Phytoglycogen found on corn (*Zea mays*) is an even more branched glucose polymer.

Fructosans are another type of storage polysaccharide in plants. They are branched or unbranched fructose polymers with a terminal glucose subunit. *Inulin* is found in the tubers or rhizomes of plants in *Campanulaceae* (the bellflower family) and *Asteraceae* (the sunflower or aster family) and usually has thirty to fifty fructose subunits. *Levans*, used for temporary storage by several monocots, especially in *Poaceae* (the grass family), range from seven to eight fructose subunits in the unbranched levans to seventy-two fructose subunits in some highly branched ones.

Structural Polysaccharides

Structural polysaccharides form the fibrous material in plant cell walls. *Cellulose*, an unbranched glucose polymer that averages about eight thousand glucose subunits per molecule, is the main cell wall component of plants, a few fungi, and some algae. Cellulose molecules form microfibrils, many individual cellulose molecules held together by hydrogen bonds. Other microfibrillar cell wall polysaccharides are sometimes called the hemicelluloses. Examples are *mannans* and *glucomannans*, found in the primary cell walls of several green algae and simple vascular plants and in the secondary cell walls of some conifers; *xylans* are found in other algae and in the secondary cell walls of many hardwoods. *Chitin*, a polymer of N-acetylglucosamine, is the main substance forming the cell walls of fungi. (Chitin is the same substance that forms the exoskeletons of most insects.)

Pectins are matrix polysaccharides found in plant cell walls. The most common pectin in higher plants is unbranched polygalacturonic acid (galacturan). Branched and unbranched rhamnogalacturans and arabinans are also present in smaller quantities. Pectin is commercially important as a gelling agent in the production of jams and jellies. A similar pectinlike polysaccharide found in brown algae is alginic acid, a mixture of mannuronic and guluronic acids. It is used as a thickener and a stabilizer in many prepared foods.



PhotoDisc

*Glycosides are formed when carbohydrates are attached to various plant chemicals and include the cardiac glycosides of the foxglove plant (*Digitalis purpurea*), which has strong physiological effects on heart muscle.*

Other Plant Carbohydrates

Carbohydrates are often found attached to other cell components. In both cell membranes and cell walls, there are many glycoproteins, proteins with short oligosaccharides attached. *Glycosides* are interesting carbohydrate-containing secondary metabolites found in many plants. Glycosides are formed when carbohydrates are attached to various plant chemicals. Anthocyanins, which give red to blue color to flowers, fruits, and autumn leaves, are glycosides. Other glycosides include the cardiac glycosides of the foxglove (*Digitalis purpurea*) and milkweed (*Asclepias*) species, which have strong physiological effects on heart muscle, and the cyanogenic glycosides of the almond (*Prunus amygdalus*), which liberate cyanide.

Richard W. Cheney, Jr.

See also: Algae; Calvin cycle; Cell wall; Fungi; Glycolysis and fermentation; Krebs cycle; Metabolites: primary vs. secondary; Photosynthesis; Sugars.

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CARBON CYCLE

Categories: Biogeochemical cycles; ecology; environmental issues; photosynthesis and respiration

The carbon cycle is the movement of the element carbon through the earth's rock and sediment, the aquatic environment, land environments, and the atmosphere. Large amounts of organic carbon can be found in both living organisms and dead organic material.

An enormous reservoir of carbon, on the order of 20×10^{15} tons, may be found on the surface of the earth. Most of this reservoir is found in rock and sediment. The carbon cycle therefore represents the movement of this element through the biosphere in a process mediated by photosynthetic plants on land and in the sea. The process involves the fixation of carbon dioxide (CO_2) into organic molecules, a process called *photosynthesis*. Energy used in the process is stored in chemical form, such as that in carbohydrates (sugars such as glucose). The organic material is eventually oxidized, as occurs when a photosynthetic organism dies. Through the process of respiration, the carbon is returned to the atmosphere in the form of carbon dioxide. Because the "turnover" time of such forms of carbon is so slow (on the order of thousands of years), the entrance of this material into the carbon cycle is insignificant on the human scale.

Photosynthesis

Organisms that use carbon dioxide as their source of carbon are known as *autotrophs*. Many of these organisms also use sunlight as the source of energy for reduction of carbon dioxide; hence, they are frequently referred to as *photoautotrophs*. This process of carbon dioxide fixation is carried out by phytoplankton in the seas, by land plants (particularly trees), and by many microorganisms. Most of the process is carried out by the land plants.

The process of photosynthesis can be summarized by the following equation:

$$CO_2 + \text{water} + \text{energy} \rightarrow \text{carbohydrates} + \text{oxygen}$$

The process requires energy from sunlight, which is stored in the form of the chemical energy in carbohydrates. While most plants produce oxygen in the process—the source of the oxygen in the earth's atmosphere—some bacteria may produce products other than oxygen. Organisms that carry out carbon dioxide fixation, using photosynthesis to synthesize carbohydrates, are often referred to as *producers*. Approximately 20 billion to 30 billion tons of carbon are fixed each year by the process—clearly a large amount but only a small proportion of the total carbon found on the earth. Approximately 450 billion tons of carbon are contained within the earth's forests; some 700 billion tons exist in the form of atmospheric carbon dioxide.

Much of the organic carbon on the earth is found in the form of land plants, including forests and grasslands. When these plants or plant materials die, as when leaves fall to the earth in autumn, the dead organic material becomes *humus*. Much of the carbon initially bound during photosynthesis is in the form of humus. Degradation of humus is a slow process, on the order of decades. However, it is the decomposition of humus, particularly through the process called respiration, that returns much of the carbon dioxide to the atmosphere. Thus, the carbon cycle represents a dynamic equilibrium between the carbon in the atmosphere and carbon fixed in the form of organic material.

Respiration

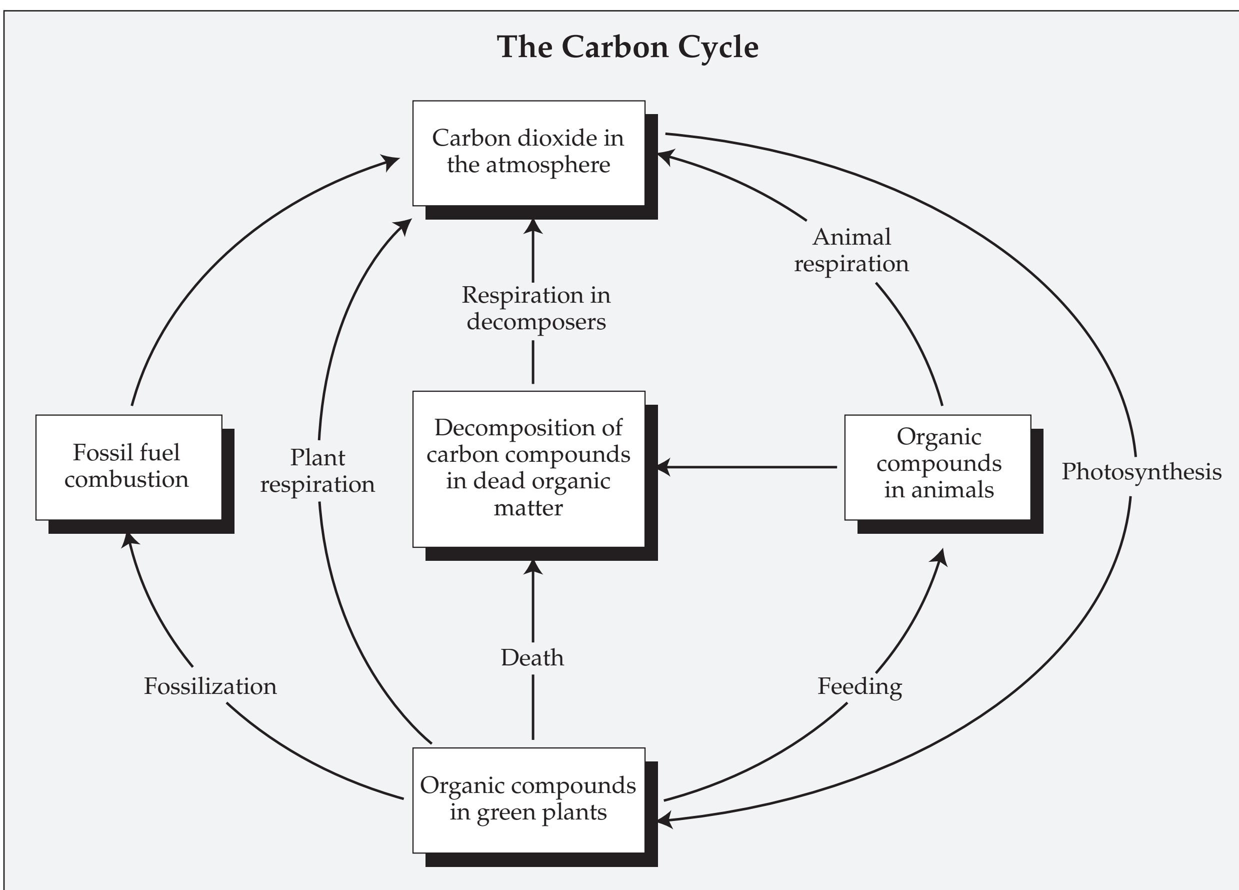
Respiration represents the reverse of photosynthesis. All organisms that use oxygen, including humans, carry out the process. However, it is primarily humic decomposition by microorganisms that returns most of the carbon to the atmosphere. Depending on the particular microorganism, the carbon is in the form of either carbon dioxide or methane (CH_4). Respiration is generally represented by the equation:

$$\text{Carbohydrate} + \text{oxygen} \rightarrow \text{carbon dioxide} + \text{water} + \text{energy}$$

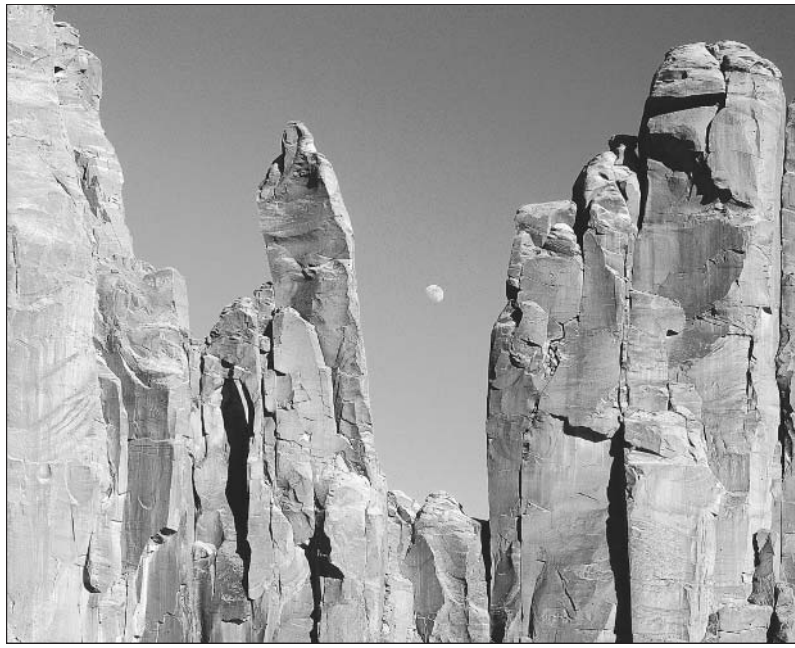
Energy released by the reaction is used by the organism (that is, the consumer) to carry out its own metabolic processes.

Carbon Sediment

Despite the enormous levels of carbon cycled between the atmosphere and living organisms, most carbon is found within carbonate deposits on land and in ocean sediments. Some of this originates in marine ecosystems, where organisms use dissolved carbon dioxide to produce carbonate shells (calcium carbonate). As these organisms die, the shells sink and become part of the ocean sediment. Other organic deposits, such as oil and coal, originate from



fossil deposits of dead organic material. The recycling time for such sediments and deposits is generally on the order of thousands of years; hence their contribution to the carbon cycle is negligible on a human time scale. Some of the sediment is recycled naturally, as when sediment dissolves or when acid rain falls on carbonate rock (limestone), releasing carbon dioxide. However, when such deposits are burned as fossil fuels, the levels of carbon dioxide in the atmosphere may increase at a rapid rate.



PhotoDisc

The biogeochemical carbon cycle is the movement of carbon through the earth's ecosystems. An enormous reservoir of carbon may be found on the surface of the earth, mostly within rock and sediment.

Environmental Impact of Human Activities

Carbon dioxide gas is only a small proportion (0.036 percent) of the volume of the atmosphere. However, because of its ability to trap heat from the earth, carbon dioxide acts much like a thermostat, and even small changes in levels of this gas can significantly alter environmental temperatures. Around 1850, humans began burning large quantities of fossil fuels; the use of such fuels accelerated significantly after the invention of the automobile. By the end of the twentieth century, between 5 billion and 6 billion tons of carbon were being released into the atmosphere every year from the burning of fossil carbon. Some of the released carbon probably returns to the earth through biological carbon fixation, with a possible increase in the land biomass of trees or other plants. (Whether this is so remains a matter of dispute.) Indeed, large-scale deforestation could potentially remove this means by which levels of atmospheric carbon dioxide could be naturally controlled.

Richard Adler

See also: Greenhouse effect; Photosynthesis; Respiration; Trophic levels and ecological niches.

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CARBON 13/CARBON 12 RATIOS

Categories: Cellular biology; photosynthesis and respiration; physiology

The carbon 13 to carbon 12 ratio is the ratio of two stable carbon isotopes in a given organic sample, often used to determine the photosynthetic pathway being used by a plant.

Although the atom is the smallest unit having the properties of its element, atoms are composed of subatomic particles, of which protons, neutrons, and electrons are the most important. All atoms of a given element (in their non-ionic form) have the same number of protons and electrons, but some atoms may have more neutrons than other atoms of the same element. These different atomic forms are called *isotopes* of the element, and in nature there is a mixture of isotopes for most elements.

Carbon Isotopes

Carbon has an atomic number of 6, meaning that it has six protons. Most carbon atoms also have six neutrons. Because the atomic weight is largely determined by the mass of the protons plus neutrons, this isotope is called carbon 12 (^{12}C); it is the most common form of carbon, accounting for about 99 percent of the carbon in nature. Most of the remaining 1 percent of carbon consists of atoms of the isotope carbon 13 (^{13}C), with seven rather than six neutrons; thus, this isotope is heavier than ^{12}C. A third isotope, carbon 14 (^{14}C), is present in the environment in minute quantities but is not very stable. Consequently, ^{14}C decays spontaneously, giving off radiation, and thus it is a *radioactive isotope*. Both ^{12}C and ^{13}C are considered stable isotopes.

Stable isotopes are measured using a mass spectrometer, an instrument that separates atoms on the basis of their mass differences. Initially when plant material is combusted, the carbon dioxide (CO_2) given off is analyzed by the mass spectrometer for the ratio of carbon 13 to carbon 12 isotopes. This ratio is compared to the ratio of carbon 13 to carbon 12 in an internationally accepted standard of known ^{13}C to ^{12}C ratio and is expressed as the difference between the sample and the standard, minus one. This number is multiplied by one thousand and expressed as a "per mil" (per million parts). In plant matter, this number is always negative. The more negative the ratio of carbon 13 to carbon 12, the less carbon 13 there is present.

C_3, C_4, and CAM Plants

There are three biochemical pathways of carbon acquisition used by different plant species, and the ratio of carbon 13 to carbon 12 in plant tissues is often a useful means of distinguishing the *photosynthetic pathway* being used. Most plants photosynthesize by attaching CO_2 obtained from the atmosphere onto an organic compound in a single carbon fixation step that is a part of the Calvin cycle. This reaction is catalyzed by an enzyme known as ribulose bisphosphate carboxylase (Rubisco), and the first stable organic product is a three-carbon molecule. Some of this three-carbon compound enters a biochemical pathway leading to sugar formation, and the remainder is used to maintain the Calvin cycle. Such plants are referred to as *C_3 plants*.

Some plants, such as corn and sugarcane, have two carbon fixation steps. Atmospheric CO_2 is fixed initially by the enzyme phosphoenolpyruvate carboxylase (PEP carboxylase), and the first product is a four-carbon organic acid; these plants are known as *C_4 plants*. This product is moved to the interior of the leaf and broken down, releasing CO_2 into specialized cells known as Kranz-type bundle sheath cells. Within these cells the CO_2 is fixed a second time by the same process used in C_3 plants.

A third group of plants, known as *CAM plants* (for crassulacean acid metabolism), open their stomatal pores (located on the leaf surfaces) primarily at night. CO_2 enters and is fixed with the enzyme PEP carboxylase. The organic acid produced is stored in the cell overnight. During the day, the stomata are closed, and the acid is broken down. The CO_2 released is then fixed by the same method as in C_3 plants.

Discrimination Against Carbon 13

In terrestrial plants, carbon isotope ratios of photosynthetic tissues vary from $^{-}8$ per mil to $^{-}15$ per mil in C_4 plants and from $^{-}20$ per mil to $^{-}35$ per mil in C_3 plants. CAM plants may range from C_4-like to C_3-like in their carbon isotope ratios. For atmospheric carbon dioxide, the ratio of carbon 13 to carbon 12 is about $^{-}8$ per mil, and thus C_4 plant tissues have slightly less carbon 13 than the air. C_3 plants have much less carbon 13 than the air. In other words, during photosynthesis plants tend to discriminate against $^{13}CO_2$ molecules and more readily fix $^{12}CO_2$. This discrimination against carbon 13 is even more pronounced in C_3 plants.

Discrimination against carbon 13 is attributable to the greater mass of this isotope. One consequence is that $^{13}CO_2$ does not diffuse as readily to the site of photosynthesis as does $^{12}CO_2$, which accounts for a small component of discrimination against carbon 13 in all plants. The major difference in carbon isotope ratio between C_3 and C_4 plants, however, results from a difference in discrimination among the initial carbon-fixing enzymes. In C_3 plants, the carbon-fixing enzyme Rubisco results in a $^{-}27$ per mil discrimination against carbon 13. In C_3 plants, this enzyme is present in the cells adjacent to the stomatal pores and thus obtains CO_2 more or less directly from the atmosphere. Because carbon 13 is discriminated against, $^{13}CO_2$ will tend to accumulate, but it readily diffuses out of the leaf when stomatal pores are open.

In C_4 plants, on the other hand, the initial carbon-fixing enzyme, PEP carboxylase, discriminates very little against carbon 13. In C_4 photosynthesis, the secondary carbon-fixing enzyme, Rubisco, is sequestered in the interior of the leaf in the bundle sheath cells, and the CO_2 it fixes is derived from the breakdown of the C_4 fixation product. As Rubisco discriminates against $^{13}CO_2$, this heavier CO_2 accumulates within the bundle sheath cells and diffuses out very slowly. As $^{13}CO_2$ accumulates in the bundle sheath cells, the higher concentration of $^{13}CO_2$ will overcome the discrimination by the enzyme; in effect, the enzyme will be forced to fix $^{13}CO_2$, and thus discrimination is minimal. C_4 plant tissues consequently have less negative $^{13}CO_2/^{12}CO_2$ ratios.

In typical CAM photosynthesis, the atmospheric CO_2 is fixed at night by the enzyme PEP carboxylase, and, as in C_4 plants, this enzyme discriminates very little against $^{13}CO_2$. During the day, the C_4 fixation product is broken down, and the CO_2 that is released is fixed by Rubisco. This enzyme will discriminate against carbon 13, but because the stomata are closed during the day, $^{13}CO_2$ will accumulate within the leaf and eventually be fixed. Consequently, little discrimination occurs. Such CAM plants have ratios similar to those of C_4 plants. Some CAM plants, however, will open their stomatal pores for varying lengths of time during the day or switch to strictly C_3 photosynthesis during certain times of the year. In these plants, the $^{13}CO_2/^{12}CO_2$ ratio will be more similar to that observed for C_3 plants.

In aquatic plants, the $^{13}CO_2/^{12}CO_2$ ratio does not indicate the photosynthetic pathway used. C_3 aquatic plants frequently will have carbon isotope ratios very similar to that of the source carbon from the water: Because the enzyme Rubisco discriminates against carbon 13, $^{13}CO_2$ tends to accumulate in the layer of water around the leaf. Because the diffusion of gases in water is very slow, the plant will eventually be forced to fix the $^{13}CO_2$. Other aspects of the aquatic environment also influence the carbon isotope ratio of aquatic plant tissues.

Jon E. Keeley, updated by Bryan Ness

See also: C_4 and CAM photosynthesis; Calvin cycle; Photosynthesis.

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CARIBBEAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

Agriculture in the Caribbean islands, from the Bahamas to Trinidad, is concentrated in sugarcane, bananas, coffee, tobacco, and some citrus and cacao.

The Caribbean Sea is an extension of the western Atlantic Ocean that is bounded by Central and South America to the west and south and the islands of the Antilles chain on the north and east. At the end of the twentieth century, agriculture was basic to the economies of nearly every island. Two fundamentally different types of agriculture dominate: large-scale commercial, or plantation, agriculture and small-scale semisubsistence, or peasant, farming. Plantation farming provides the most exports, by value, whereas peasant farming involves far more human labor.

Caribbean agriculture operates under various natural and cultural restraints. Most of the islands have rugged terrain, restricting productive agriculture to river valleys and coastal plains. Typically, less than one-third of an island's land area is suitable for crops. The windward portions of islands are commonly very wet, whereas their leeward areas suffer drought, necessitating irrigation. Various hazards also impact agriculture, including the damaging winds of hurricanes, flooding, accelerated erosion, and landslides. In addition, some crops (notably bananas) have suffered from diseases. On the human side, most peasant farms are restricted to steep, unproductive slopes, while plantations control most of the productive lowland soils. Population pressures have led to the loss of some of the best lands and have caused fragmentation of farmland. Farm labor shortages, climbing wages, and foreign competition have added to the burden.


PhotoDisc

Among the Caribbean islands, coffee is raised for export mainly in Haiti, Jamaica, and the Dominican Republic. Its production is largely for European, Japanese, and U.S. markets.

Commercial Agriculture

Modern plantations own large tracts of land and specialize in one crop, commonly sugarcane, bananas, coconuts, coffee, rice, or tobacco. They are more mechanized and better managed than colonial plantations, although they are still largely British-, French-, or American-owned. The largest plantations are found on the largest islands, especially Hispaniola, Jamaica, and Puerto Rico. Cuba also has large-scale farming, but the operations are government-owned. Plantations always have been smaller in the Lesser Antilles, where relatively little land is available.

Sugar dominates the export economies of Cuba, the Dominican Republic, Guadeloupe, and Saint Kitts. Among traditional sugar producers in the Caribbean, notably Jamaica, Puerto Rico, Trinidad, and Barbados, sugar exports are exceeded by those of other commodities. Haiti, a leading sugar producer as a French colony, now produces little. Overall, sugar production in the Caribbean has been on the decline since the 1960's as a result of the variety of problems noted above.

Other commercial export crops grown in the Caribbean region include bananas, coffee, tobacco, and ganja. Bananas, introduced in the sixteenth century by Spanish missionaries, became an important export in the late nineteenth century as markets developed in Europe and the United States. Sweet bananas are significant exports of Guadeloupe, Martinique, the Dominican Republic, Jamaica, Granada, St. Lucia, and St. Vincent. Overall production is not significant on the world scale. Coffee is raised for export mainly in Haiti, Jamaica, and the Dominican Republic. Jamaica's famous Blue Mountain coffee, grown in the Blue Mountains northeast of Kingston, is among the most prized and expensive coffees of the world. Its production and export is largely for European, Japanese, and U.S. markets.

Tobacco was important before the sugar era and has seen a recent resurgence in the Greater Antilles, especially in Cuba, Puerto Rico, Jamaica, and the Dominican Republic, mostly for cigar production. Ganja, marijuana prepared especially for smoking, is illegal throughout the Caribbean region. The product is nevertheless of considerable commercial importance. Its chief producer is Jamaica, and its main destination is the United States. Other significant export crops include cacao (for chocolate) and citrus.

Peasant Farming

Peasant farming in the Caribbean began after emancipation in the nineteenth century, when freed slaves sought out the only land available, in the hills and mountains. Unfortunately, this land is unsuitable for crop agriculture, having thin and erodible soils. Individual peasant farms average less than 5 acres (2 hectares) in area, often in disconnected plots. A variety of crops are raised, including fruits such as mangoes, plantains, akee, and breadfruit; vegetables such as yams, potatoes, and okra; sugarcane; and coffee.

P. Gary White

See also: African agriculture; Asian agriculture; Australian agriculture; North American agriculture; South American agriculture.

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CARIBBEAN FLORA

Category: World regions

The Caribbean region is noted for its diverse and varied vegetation. Flowers thrive in the moist, tropical environment found on many islands. Hibiscus, bougainvillea, and orchids are just a few of the varieties found there. The heavily touristed region faces challenges in balancing development with preserving its flora.

The Caribbean region comprises the islands from the Bahamas to Trinidad and is noted for its tropical vegetation and flowers. This region has been significantly affected by human activities. Deforestation began with the development of sugarcane culture in the seventeenth century. When forests are cut for farmland, soil erosion and depletion often occur. Jamaica, Haiti, and many of the smaller islands have suffered acute ecological degradation. Thorn scrub and grasses have replaced native forests that were cleared for farming. This new vegetation does not protect the ground from the sun and provides little protection against moisture loss during drought. Livestock overgrazing also has contributed to ecological degradation.

However, these complex and fragile island ecosystems are finally being appreciated and protected. Most islands' governments recognize that they must balance development with protection of the natural environment. Many have established active conservation societies and national wildlife trusts for this purpose.

Rain Forest

The only rain forest left in the Caribbean Islands is a small area in Guadeloupe. However, many of the islands still have large stands of good secondary forest that are being harvested selectively by commercial lumber companies. Gommier, balata, and blue mahoe are some of the valuable species of trees cut commercially. Such tropical woods as cedar, mahogany, and palms grow on many islands. Martinique has some of the largest tracts of forest (rain forest, cloud forest, and dry woodland) left in the Caribbean.

While the Caribbean rain forest is not as diverse as those of Central and South America, it supports numerous plant species. Several of these plants are endemic to the region. For example, Jamaica has more than three thousand species with eight hundred endemics. Orchids and bromeliads are stunning examples of climbing and hanging vegetation in the rain forests of the Caribbean. Huge tree ferns, giant elephant ear plants, figs, and balsam trees are also found in these tropical island rain forests.

Plantations of commercial timber (blue mahoe, Caribbean pine, teak, and mahogany) have been established in many locations. These plantations reduce pressure on natural forest, help protect watersheds and soil, and provide valuable wildlife

Image Not Available

habitat. Much of the original forests of the Caribbean have been cut down to make room for sugar plantations and for use as fuel. Haiti, once covered with forests, is now on the verge of total deforestation. Soil erosion and desertification have severely impacted the country.

Saint Kitts, on the other hand, is one of the few places in the world where the forest is actually expanding. It provides abundant habitat for exotic vines, wild orchids, and candlewoods.

Closer to the coasts, dry scrub woodland predominates. Some trees lose their leaves during the dry season. The turpentine tree is common to the dry scrub forests. It is sometimes called the tourist tree because of its red, peeling bark. The trees' bark and leaves are often sold in marketplaces and used for herbal remedies and bush medicine.

Along the marshy coastal waters of many of the islands are dense mangrove swamps. Mangroves grow thick roots that stand above the waterline. These wetlands provide habitat for the endangered manatee, the American crocodile, and for huge numbers of migratory birds and resident birds, such as the egret and heron.

Dominica, one of the windward islands, is known as the "nature island" of the Caribbean. Most of the southern part of the island (17,000 acres, or approximately 7,000 hectares) has been designated the Morne Trois Pitons National Park, which became a World Heritage Site in 1998. Elfin forests of dense vegetation and low-growing plants cover the highest volcanic peaks and receive an abundance of rain. The trees, stunted by the wind, have leaves adapted with drip tips to cope with the excess moisture. Lower down, the slopes are covered with rain forest. Measures are being taken to protect this forest from cutting for farmland or economic gain because it is a valuable water source and a unique laboratory for scientific research.

Carol Ann Gillespie

See also: African flora; Antarctic flora; Asian flora; Australian flora; North American flora; Rain-forest biomes; South American flora; Wetlands.

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CARNIVOROUS PLANTS

Categories: Angiosperms; *Plantae*; poisonous, toxic, and invasive plants

Carnivorous plants have the ability to capture and digest insects and other small animals.

Carnivorous plants are a diverse group. All live in nutrient-poor, often boggy or aquatic environments where minerals from digested prey are essential for survival, or at least for good health. None use captured prey as an energy source, as animals do; rather, carnivorous plants are photosynthetic, like other plants. The mechanisms for capturing prey are varied, and carnivory is found in at least nine distinct plant families, having evolved a number of times independently.

Pitchers

One widespread carnivorous mechanism is the formation of *pitchers*, specialized leaves or portions of leaves that have developed into hollow tubular or pitcherlike structures that contain fluid. The fluid is mostly water but may contain digestive enzymes and mild narcotics. The mouth, or entrance, to the pitcher is generally marked with bright colors and may produce droplets of nectar to attract insects. The throat of the pitcher is usually lined with wax or downward-pointing hairs so that insects will slowly slide downward toward the pool of water but will have great difficulty climbing back out.

Pitchers are found in a number of genera, in several unrelated families. *Sarracenia* is the genus of North American pitcher plants found in bogs, seeps, and marshy areas, primarily in the southeastern United States. The pitchers arise directly from an underground rhizome. A related species, *Darlingtonia californica*, is found in cold-water bogs in northern California and southern Oregon. The genus *Heliamphora* includes many species in South America. The Asian pitcher plants are in the unrelated genus *Nepenthes*. These pitchers hang from the ends of leaves on plants that are generally *epiphytic* (growing on tree branches) or grow on rocky surfaces. The genus *Cephalotus* is not related to any of the foregoing but produces pitchers similar to those of *Nepenthes*. The single species of *Cephalotus* is found in seeps and bogs in southwestern Australia. Finally, in South America there are species in two genera of *bromeliads* (pineapple family), *Catopsis* and *Brocchinia*, that form crude pitchers that have been found to be carnivorous.


Digital Stock

Specialized leaves or portions of leaves of the pitcher plant form hollow, tubular structures which contain fluid, mostly water, that traps insects.

Leaf Traps

The most famous of all carnivorous plants is Venus's flytrap, *Dionaea muscipula*, which is native to bogs in the coastal plain of North and South Carolina. In this species, the two sides of the leaf snap together quickly when trigger hairs on its surface are brushed twice within a short span of time. The closing mechanism involves a wave of rapid cell elongation on the outer surface of the leaf trap that pushes the two sides of the leaf together. The edges of the trap leaves are lined with long spikes which serve as bars to prevent quick-responding insects from escaping during closing. A reddish coloration and drops of nectar lure insects to the trap. Digestive enzymes are secreted from the inner surface of the trap. After the meal is digested, slower growth of cells on the inner surface reopens the trap.

Related to the fly traps are the *sundews*, in the genus *Drosera*, and similar plants in the genera *Drosophyllum*, *Byblis*, and *Tripohylophylum*. Leaves of these plants are covered with tiny glandular hairs, each producing a drop of sticky, nectarlike fluid that attracts the insects and then traps them. Once an animal is tangled in the gluey exudate, digestive enzymes are secreted, and in some, the leaf slowly folds around the prey.

There are many species of sundew, nearly two hundred in Australia alone, with many species in South America, southern Africa, North America, and Europe. The species vary in the size and shape of their leaves and also in their flowers, which come in a variety of colors, sizes, and shapes. They in-

Carnivorous Plants

Common Name	*Genus*	*Species*	*Location*
Australian pitcher plant	*Cephalotus*	1	Southwest Australia
Bladderworts	*Utricularia*	220	Worldwide
Butterworts	*Pinguicula*	80	Asia, Europa, North America
Cobra lily	*Darlingtonia*	1	California, Pacific Northwest
Corkscrew or forked trap	*Genlisea*	20	South America
North American pitchers	*Sarracenia*	10	United States, Southeast
Portuguese sundew	*Drosophyllum*	1	Portugal, western Spain
Rainbow plants	*Byblis*	5	Northwest Australia
Sun pitchers	*Heliamphora*	6	South America
Sundews	*Drosera*	150	Worldwide
Tropical pitcher vines	*Nepenthes*	90	Australia, Indonesia, Madagascar
Venus's flytrap	*Dionaea*	1	North Carolina, South Carolina
Waterwheel plant	*Aldrovanda*	1	Eurasia

habit seeps and bogs or are found in sandy soil that is damp for only a short time. Most of them are tiny rosettes of paddle-shaped to linear leaves, but some are erect, herbaceous tufts 1-2 feet high, or even vines.

One genus of the unrelated family *Lentibulariaceae* also employs leaf traps. This is *Pinguicula*, found in North America in moist, nutrient-poor habitats. Its leaves are flat, somewhat curled at the edges, and moderately sticky, without conspicuous glandular hairs. They do not close around prey. The many species of *Pinguicula* have variously colored, snapdragon-like flowers on long stalks.

Underwater and Underground Traps

The final category of carnivorous plants produces traps under water, or sometimes in damp soil, where they capture tiny crustaceans and other invertebrate animals. *Aldrovanda* is a submerged plant related to Venus's flytrap but is native to Australia. Its miniature underwater traps snap shut when animals swim or bump into them. Another genus with tiny underwater traps is *Utricularia*, related to *Pinguicula*. These traps operate by suddenly expanding to suck water and small animals inside when triggered. The traps are borne on specialized leaves that grow downward into the water or damp soil. Often one only sees the brightly colored, snapdragon-like flowers above the surface. There are hundreds of species of *Utricularia*, found all over the world, particularly in Australia and North America. A third carnivorous genus in the *Lentibulariaceae* is *Genlisea*, which grows in Africa and South America, and which has traps similar to those of *Utricularia*.

Frederick B. Essig

See also: Animal-plant interactions; Coevolution; Leaf anatomy; Metabolites: primary vs. secondary; Nastic movements; Nutrient cycling.

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CELL CYCLE

Categories: Cellular biology; physiology

In plants, as in all eukaryotic life-forms, the cell cycle comprises the processes of cell division, constituted by three preparatory phases (G_1, G_2, and S), followed by mitosis (nuclear division) and cytokinesis (cytoplasm division).

One of the fundamental characteristics of living organisms is their ability to grow and reproduce. At the cellular level, growth is accomplished by a gain of mass, followed by division into two daughter cells. In unicellular species, such as bacteria and green algae, this division results in the production of new organisms. In multicellular organisms, such as plants, cells must divide many times to produce new individuals, and additional processes of differentiation into mature cell types must occur.

Eukaryotic Cell Division

Plant cells are eukaryotic, meaning that they contain a *nucleus* and membrane-bound cellular compartments called *organelles*, such as chloroplasts, the sites of photosynthesis, and the central *vacuole* used for storage. In order for eukaryotic cell division to occur, cells must accomplish several steps. First, a cell must reach a sufficient size to ensure that the daughter cells will be large enough to survive. The cell achieves this status by making needed molecules, using synthetic biochemical reactions, and monitoring the outside environment to ensure continued favorable conditions for reproduction. Next, a cell must replicate all required macromolecules, including the deoxyribonucleic acid (DNA), as well as the organelles. Finally, the cell must be able to distribute appropriately the cellular contents, including the genetic material, to the daughter cells. The cyclical repetition of these steps comprises the eukaryotic cell division cycle or, more simply, the cell cycle.

Cell Cycle Phases

The general arrangement of the cell cycle was first determined through microscopic observations of living cells undergoing cell division. Originally, four stages were identified: G_1 phase, S phase, G_2 phase, and M phase. G_1 and G_2 phases were named as gap phases, because it was presumed that the cell did not appear to accomplish any specific events during these phases. G_1 phase occurs after the previous cell division and is the phase where the cell grows, metabolizes, and prepares to undergo another round of cell division. During G_1 phase, the cell also transcribes and translates the genes required for DNA synthesis. In S phase, the DNA synthetic phase, the cell concentrates its efforts on accurately replicating its genetic material, the DNA genome. In G_2 phase, the cell coordinates both transcription and translation to synthesize proteins that are required specifically for asexual cell division, or mitosis. During M phase, the DNA chromosomes condense and are divided into the two daughter cells. G_1, S, and G_2 phases together are referred to as *interphase*.

Mitosis itself is composed of four phases: (1) *prophase*, in which chromosomes are condensed, homologous chromosomes are paired together, and the spindle apparatus made of microtubules forms; (2) *metaphase*, in which the paired chromosomes are lined up across the center of the cell on the metaphase plate; (3) *anaphase*, in which the homologous chromosomes are pulled to separate poles in the dividing cell by the attached spindle apparatus; and (4) *telophase*, in which the daughter cell chromosomes are collected together at the poles. Mitosis is followed by cytokinesis, or the process by which the two daughter cells are physically separated. Because plant cells have cell walls, the division of one cell into two daughter cells requires the formation of a cell plate to complete cytokinesis. This cell plate grows outward between the two new nuclei. Once the cell plate reaches the walls of the dividing cell, it forms the cell wall that separates the two new cells.

Checkpoints

The cell will die if it goes through any cell cycle phase out of order. Therefore, the cell has evolved sophisticated *checkpoints* to ensure that critical events, such as DNA replication and cell division, occur in the correct order and that each required step is completed prior to movement to the next phase. Additionally, external conditions, such as a change in nutrient availability, can cause a cellular checkpoint response. There are two main points in the cell cycle which are regulated by checkpoints, the G_1-to-S transition and the G_2-to-M transition. The G_1-to-S transition is important because once the cell commits to divide and starts to copy its DNA, it must complete cell division or die. After DNA replication is complete, the G_2-to-M transition is important for the cell to make sure that all of the DNA has been copied correctly, or the daughter cells will not have the full complement of genetic material.

CDKs and Cyclins

Enzymes are proteins that catalyze chemical reactions in the cell. Without enzymes, chemical reactions would occur too slowly to sustain life. Kinases are enzymes that place a chemical group, called a phosphate group, onto other proteins in the cell. Because of the nature of the phosphate chemical group, the addition of these groups causes conformational changes in the three-dimensional structure of the proteins that accept them. The cell cycle is controlled by the actions of kinases called cyclin-dependent kinases, or CDKs. Each CDK has a partner called a cyclin, which is required for the kinase activity to place phosphate groups on target proteins. The CDK/cyclin pairs perform kinase reactions, which activate proteins leading to completion of cell cycle phases. Opposing the action of the CDK and cyclin pairs are cyclin-dependent kinase inhibitors, or CKIs, which act as brakes to prevent CDK/cyclin activity until the cell is ready to go on to the next step in the cell cycle.

Many of the cell cycle control mechanisms have been conserved throughout all eukaryotic cells, including the plant cell. *Arabidopsis* is a genus that has been widely characterized and used as an experimental model for plant growth and differentiation in scientific laboratories worldwide. In plants such as *Arabidopsis*, two major groups of CDKs have been studied, the A-type and B-type CDKs. The A-type CDKs show kinase activity during the S, G_2, and M phases of the cell cycle and regulate the transitions from G_1-to-S and G_2-to-M phases. The B-type CDKs are active during mitosis and regulate only the G_2-to-M transition in plants.

Jennifer Leigh Myka

See also: Angiosperm cells and tissues; Cell theory; Chromosomes; DNA replication; Eukaryotic cells; Mitosis and meiosis; Nucleic acids; Reproduction in plants.

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CELL THEORY

Categories: Cellular biology; history of plant science; physiology

The notion that the cell is the smallest division of life and its attendant principles have been developed over the past three centuries and are collectively known as the cell theory.

Before the invention of the microscope, people studying living organisms saw whole and complete organisms and did not imagine that life was subdivided into smaller compartments. It is now known that the cell is the fundamental unit of life and that all living organisms are composed of cells. Because cells are microscopic, their existence was not discovered until the seventeenth century.

Discovery of the Cell

The discovery of the cell did not come about until the last half of the seventeenth century, after the Dutch inventor Antoni van Leeuwenhoek built the first light microscope. When looking at pond water using his light microscope in 1674, Leeuwenhoek saw many tiny creatures which were invisible to the naked eye. Leeuwenhoek assumed that these tiny "animalcules" were alive because he could see them moving.

However, the first description of the cell is attributed to the English scientist Robert Hooke. In 1665 Hooke first published *Micrographia*, a work devoted to observations made with his compound light microscope. Hooke examined the structure of cork, a dead plant tissue, by cutting cork into very thin slices and observing the slices under his light microscope. Hooke saw the dead cells of the cork outlined by the thickened cell walls of that tissue and determined that cork was composed of a pattern of spaces which resembled small rooms, or "cells." Interestingly, Hooke did not recognize the significance of the cells that he described and thought that the cork cells were merely channels for fluid conduction in the plant.

Cells as Globules

Partly because of problems with chromatic aberrations in early microscopes, scientists thought that living organisms were made of "globules." As early as 1682, plant tissues were described as bladders clustered together. In 1771 William Hewson performed one of the first cell biology experiments by confirming Leeuwenhoek's earlier observation of blood and brain globules and by showing that the blood globules swelled and shriveled in different solutions. By 1812 Johann Jacob Paul Moldenhawer had shown that plant tissue was composed of independent cells, and in 1826 Henri Milne-Edwards determined that all animal tissues were formed from globules. Finally, in 1824 Henri Dutrochet proposed that animals and plants had a similar cellular structure. Ironically, Thomas Hodgkin and Joseph Jackson Lister showed in 1827 that many of the previously observed globules were likely to have been optical artifacts that disappeared when the new achromatic microscope was used. However, the idea that life was made of tiny cells remained.

Cells Compose All Organisms

Matthias Schleiden, a German botanist, suggested in 1838 that all of the structural elements found in plant tissues were composed of cells or cellular products. In 1839 Theodor Schwann, a zoologist, reported that animal tissues were also composed of cells and suggested that all living organisms were actually composed of cells. Based on their contributions, Schleiden and Schwann are considered to have established the official "cell theory." Schwann also contributed to the description of the cell by defining a cell as having three essential components: a cell wall, a nucleus, and a fluid content. The Scottish botanist Robert Brown first described the nucleus of the cell as an essential component of living cells in 1831.

The work of both Schleiden and Schwann contested the notion of *vitalism*, the belief that no single part of an organism was alive but that somehow the substances composing the whole organism together shared the characteristics of life. The idea of vitalism made sense prior to the invention of the microscope (because cells cannot be seen with the naked eye) but did not hold up when cells were observed in all plant and animal tissues. Therefore, the idea that living organisms were made of cells was becoming widespread at this time. An 1830 plant anatomy textbook by Franz Julius Ferdinand Meyen contained a chapter on cell structure and discussed the idea that cells unite to form cellular tissues.

Cell Origins in Organisms

Interestingly, while Schleiden and Schwann realized that all living organisms were made of cells, they did not realize that all cells came from preexisting cells. Indeed, Schwann mistakenly thought that cells had an extracellular origin and could arise de novo. Schwann originally observed plant cells in the endosperm of seeds, where the nuclei multiply before the cell walls form, and he generalized from this unusual system. This idea persisted for a time, even though Hugo von Mohl first described cell division in green algae in 1837. Essentially, von Mohl investigated his hypothesis that all cells must start out very small and gradually grow to full size by observing a filamentous green alga. By studying the alga, Mohl discovered cell division as the algal cells divided and formed partitions between the newly formed daughter cells.

By 1858 the pathologist Rudolf Virchow had expressed the idea that all cells arise from preexisting cells. This idea was important because until that time, the idea of *spontaneous generation* was also popular. Spontaneous generation was the mistaken idea that living organisms could arise spontaneously from nonliving material and was thought to explain such phenomena as the fact that frogs are found in ponds and maggots in rotten meat. In contrast, Virchow wrote: "Where a cell exists, there must have been a preexisting cell, just as the animal arises only from an animal and the plant only from a plant."

Modern Cell Theory

The modern cell theory consists of several principles. As stated by Schleiden and Schwann, all living organisms are composed of one or more cells. Because cells are the smallest units of life, cells must be the site of the chemical reactions that sustain living organisms. Finally, it is clear that all cells arise from preexisting cells, as first stated by Virchow. In order for cells to perform this replication, it is now apparent that all cells contain hereditary information and pass this information from parent cell to daughter cell. Additionally, this hereditary information is contained in the deoxyribonucleic acid (DNA) found in the nuclei of all cells, with this DNA being copied for each daughter cell to use.

Jennifer Leigh Myka

See also: Angiosperm cells and tissues; Cell cycle; Chromosomes; DNA replication; Eukaryotic cells; History of plant science; Mitosis and meiosis; Nucleic acids; Reproduction in plants.

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CELL-TO-CELL COMMUNICATION

Category: Cellular biology

Cell-to-cell communication involves the various stimuli to which plants respond, whether biotic, such as hormones and disease, or abiotic, such as water status, heat, cold, and light.

Throughout their lives, plants and plant cells continually respond to both external and internal signals, which they use to alter their physiology, morphology, and development. The manner in which plants respond to a stimulus is determined by developmental age, previous environmental experience, and internal biological clocks that specify the time of year and time of day.

Chemical Messengers

In complex multicellular eukaryotes, the coordination of responses to environmental and developmental stimuli requires an array of signaling mechanisms. Animals have evolved two systems, the nervous system and the endocrine (hormone) system, for responding to stimuli. While plants lack a nervous system, they did evolve *hormones* and other chemicals, such as phytochrome, as chemical messengers.

The major groups of plant hormones include the auxins, gibberellins, cytokinins, ethylene, and abscisic acid. These hormones serve as signals for a wide range of physiological, biochemical, and developmental responses. These signals may impact different cells at different times, or they may impact the same cells at different sites. A variety of pathways are available for information flow from any one signal. Information from the same signal may travel to different areas of the cell under different environmental conditions. Alternatively, information might travel to the same site after traveling by different pathways. Most signals appear to induce changes in gene expression, and this altered gene expression is responsible for the observed response.

There are two classes of chemical messengers, based on their ability to cross cellular membranes. *Lipophilic messengers* readily diffuse across membranes and combine with intracellular receptor proteins. When activated by the messenger, these proteins function as transcription factors, thereby inducing the transcription of new proteins. In other words, the messenger-receptor complex signals the activation of genes which encode the proteins that produce the response to the stimulus. While animals have numerous lipophilic messengers, such as the steroid hormones in animals, only one, brassosteroid, has been demonstrated in plants.

Most plant messengers are *hydrophilic*, or water-soluble (rather than lipophilic) and are unable to enter the target cell because they cannot diffuse across the hydrophobic ("water-hating") interior of the membrane. These messengers must first bind with a membrane receptor molecule. This messenger-receptor complex then communicates with other molecules inside the cell to initiate a cascade of events referred to as a *signal transduction pathway*. Most signal transduction pathways cause the activation of other chemicals, referred to as second messengers.

Second Messengers

Signal transduction pathways using a variety of second messengers have been well documented in animal systems. Some of the most common second messengers are 3′,5′-cyclic AMP (cAMP), G-proteins, 1,2 diacylglycerol (DAG), inositol 1,4,5-triphosphate (IP_3), and Ca^{2+}, and many of these have been shown to be active in plants. When a chemical messenger such as a hormone binds to a membrane receptor, one or more of these second messengers are elevated. The elevated level of the second messengers results in the activation of regulatory proteins such as protein kinases or phosphatases. Activated protein kinases will *phosphorylate* transcription factors (that is, add a phosphate group), and activated phosphatases will dephosphorylate (remove a phosphate group from) transcription factors.

A typical signal transduction cascade is presented in the following scenario. An environmental stress causes an elevation in the level of the hormone abscisic acid (ABA), which is responsible for leaf fall. ABA binds to receptors in the membranes of the target cells. The ABA-receptor complex activates a G-protein, which then activates the enzyme phospholipase C. This enzyme catalyzes the conversion of a substrate to DAG and IP_3. The IP_3 stimulates the opening of Ca^{2+} channels in the endoplasmic reticulum or tonoplasts (the membranes surrounding vacuoles). The release of Ca^{2+} from these organelles activates protein kinases, which then activate transcription factors by phosphorylation. The activated transcription factors induce transcription of genes, which encode the proteins necessary for the plant to respond to the environmental stress.

Transport of Messengers

As discussed above, cells communicate primarily via chemical messengers. In most instances, particularly in the case of plant hormones, the messengers are produced in one cell and transported to other cells. Plant cells are usually in contact with others around them, and cell communication (transport of messengers) can occur by transport through either the *apoplast* or the *symplast*. The apoplast refers to the free space between cells and cell wall materials. Water moves freely through the apoplast, and certain chemicals can be found moving with the water. Some important developmental molecules, such as the auxins, have been shown to move through the apoplast. The symplast is composed of the living cytoplasm of the cells, and many substances are transported symplastically.

Rapid transport through the symplast is possible because most living plant cells are connected to neighboring cells by *plasmodesmata* that pass through the adjoining cell walls and provide some degree of cytosolic continuity between them. Plasmodesmata are tubelike cytoplasmic extensions that are divided into eight to ten micro-channels. Although the exact pathway of communication has not been determined, some molecules can pass from cell to cell through plasmodesmata, probably by flowing through the micro-channels. Plasmodesmata appear to be gated, which means that they allow the passage of some molecules and restrict the passage of others.

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See also: Active transport; Circadian rhythms; Gene regulation; Growth and growth control; Hormones; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Oxidative phosphorylation; Photoperiodism; Tropisms; Vesicle-mediated transport; Water and solute movement in plants.

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CELL WALL

Categories: Anatomy; cellular biology; physiology

The cell wall is the outer, rigid wall of a cell, dividing the protoplast (the interior, including the cytoplasm and nucleus) from the cell's external environment. The plant cell wall is both unique to and a major feature of plants, perhaps second only to the plant's photosynthetic ability.

The primary functions of the cell wall in plant cells include are to provide protection for the enclosed *cytoplasm* and give mechanical support to the entire plant structure. Plant cell walls are part of the *extracellular matrix*, a complex mixture of extracellular materials found between cells. These materials are synthesized by the intracellular contents and transported through the plasma membrane. All plant cell types consist of at least a *primary cell wall*, and many also produce a *secondary cell wall*. In addition, certain cells also secrete specialized substances into the extracellular matrix.

Primary Cell Wall

The primary cell wall is first synthesized by young, actively growing cells. It is thin and is composed of *cellulose* embedded within a *noncellulose matrix*. Cellulose is a polysaccharide polymer composed entirely of glucose molecules joined together end on end to form long, unbranched chains. These chains may consist of up to several thousand glucose molecules. The chemical bond joining the glucose molecules in cellulose is slightly different from that found in starch, another polysaccharide composed entirely of glucose. It is this difference in bonds that makes cellulose a structural polysaccharide.

Microfibrils are groupings of about 50 to 60 cellulose chains that are parallel to one another and held together by hydrogen bonds. The tensile strength of microfibrils is comparable to steel wire of the same thickness. The cellulose microfibrils make up approximately 25 percent of the primary cell wall and are arranged somewhat randomly (more parallel in fast growing cells) within the noncellulose matrix.

Noncellulose Matrix

The noncellulose matrix of the primary cell well accounts for about 60 percent to 80 percent of the primary cell wall and is composed of *hemicelluloses*, *pectins*, and *extensins*. Hemicelluloses are highly branched polysaccharide structures composed of heterogeneous mixtures of sugars, some of which are chemically modified. Pectins are also heterogeneous mixtures of sugars but are particularly rich in galacturonic acid. Pectic substances are also a major component of the outermost *middle lamella*, which can be thought of as the cement that holds adjacent cells together. Pectins, extracted from unripe fruits, have been used commercially as thickening agents for jellies and jams. The softness of ripe fruits is due to the enzymatic breakdown of pectins within the middle lamella. The hemicelluloses and various pectins are thought to coat and reinforce the cellulose microfibrils. Extensins are protein components of the matrix. They are glycoproteins that contain a high amount of a modified amino acid called hydroxyproline. Extensins make up about 10 percent of the matrix material, add strength to the cell wall, and are involved in cell growth.

Secondary Cell Wall

Cell types that are directly involved in support of the plant body, such as *sclerechyma* and particularly the *tracheids* and *vessels* of the xylem, undergo secondary wall formation. This wall is typically much thicker and is synthesized by the intracellular contents to the inside of the primary cell wall. Secondary cell wall formation occurs as the cell reaches its mature size. In some cell types there may even be two or more distinct layers of secondary cell wall deposition. Its composition is somewhat similar to the primary cell wall but also differs significantly.

Cellulose microfibrils can make up to 45 percent of this wall, while hemicelluloses and pectins can make up to about 20 percent.

However, what most distinguishes the secondary cell wall is the deposition of *lignin*. Lignin is an extremely tough and durable complex compound characterized by interlocking phenolic groups. Lignin is stronger than cellulose microfibrils, and together they are responsible for the superior strength of many types of wood. In cells that undergo secondary cell wall formation, lignin may also be deposited in the preexisting middle lamella and primary cell wall areas.

Specialized Cell Wall Substances

Certain cell types, especially the epidermis, which is exposed directly to the outer environment, secrete a variety of highly waterproof and protective substances, such as *cutin*, *suberin*, and a variety of *waxes*. These substances are deposited on the outside of the primary cell wall. Cutin and suberin are polymers composed of long-chain fatty acids that are linked or esterified at the acid ends. Suberin differs in that it contains dicarboxylic fatty acids and various phenolic compounds. For the most part, cutin is associated with and is the main constituent of the *cuticle* of the aboveground epidermis, while suberin is mostly associated with the belowground epidermis.

Suberin is also the major component of the *Casparian strip* found in the *endodermis* of the root. This important root tissue forces water and dissolved minerals to move intracellularly into the vascular tissue. Additionally, suberin constitutes scar tissue that is formed when cells are injured or otherwise wounded. Waxes are a family of extremely waterproof substances characterized by long-chain alcohols linked with long-chain fatty acids or hydrocarbons. They are typically secreted as droplets on the exterior of the cuticle and crystallize in a variety of geometric patterns.

Plasmodesmata

Plant cells contain cytoplasmic channels called *plasmodesmata* that connect adjacent cells. As cells divide and the *cell plate* is formed, there are areas where new cell wall material is not deposited because of the extension of the endoplasmic reticulum (ER) from the mother cell to the daughter cell. This ER channel is referred to as the *desmotubule*. Thus, each plasmodesma contains an inner desmotubule. Some cells contain areas called *primary pit fields*, in which numerous plasmodesmata are found.

The purpose of plasmodesmata involves cell-to-cell communication via transport of small molecules. Movement is not thought to occur inside the desmotubule, as it is too narrow, but rather through the cytoplasmic channel between the desmotubule and the plasmodesma itself. The presence of plasmodesmata allows for a continuous cytoplasmic connection within plant tissues called the *symplast*.

In cells which form thick secondary cell walls, particularly the xylem vessels and tracheids, which contain no living protoplast at maturity, numerous pit pairs among adjacent cells are found that allow multiple pathways for the flow of water.

Thomas J. Montagno

See also: Angiosperm cells and tissues; Carbohydrates; Cell-to-cell communication; Cytoplasm; Endomembrane system and Golgi complex; Endoplasmic reticulum; Plant fibers; Plant tissues; Plasma membranes; Vesicle-mediated transport; Water and solute movement in plants; Wood.

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CELLS AND DIFFUSION

Categories: Cellular biology; transport mechanisms

Plant cells, like all other living cells, are surrounded by a semipermeable membrane, and any particle moving into or out of the cell must cross this membrane. There are three basic processes by which particles move across plant cell membranes: diffusion, facilitated diffusion, and active transport.

The process of *active transport* requires the direct input of energy to move particles across the cell membrane. Diffusion and *facilitated diffusion* can occur without the direct expenditure of cellular energy.

Diffusion

If one were to drop a sugar cube into glass of water and immediately use a straw to sip a little water from the top of the glass, the water would not have a sweet taste. However, after a few hours, a sip of water from the top would taste sweet. The reason for the change in the taste of the water is diffusion, the net movement of particles down a *concentration gradient* (that is, from an area of higher concentration to an area of lower concentration). Concentration is the number of particles or amount of substance per unit volume, and a gradient occurs when some factor such as concentration changes from one volume of space to another. Hence, the sugar molecules move more frequently from around the cube where they were highly concentrated to other parts of the glass where they were less concentrated. There is always some movement in both directions, but the net movement is down the concentration gradient.

Diffusion is possible because molecules in a liquid or gaseous phase are not static; they are in constant motion as a result of kinetic energy, which exists at temperatures above absolute zero ($^{-}$273.16 degrees Celsius, or $^{-}$459.69 degrees Fahrenheit). As the concentration of a substance increases, its free energy also increases. When molecules move, they collide with one another and exchange kinetic energy, and there is a random but progressive movement from regions of high free energy (high concentration) to regions of low free energy (low concentration). Diffusion can occur quite rapidly over short distances but can be extremely slow over long distances. For example, a molecule of glucose can diffuse across a typical 50-micrometer diameter cell in 2.5 seconds, but it takes thirty-two years for it to diffuse a distance of 1 meter.

Role in Plants

Diffusion is an important process in the lives of plants. Water is an important component of all cells, and water moves into plant cells by the process of *osmosis*. Osmosis is the diffusion of water across a semipermeable membrane. Many plant nutrients reach the root surface via diffusion through the soil solution. Some nutrient molecules diffuse across root cell membranes into the *cytosol* (cell sap or cytoplasm) or from the cytosol of the endodermal cells into the xylem tissue. Carbon dioxide diffuses from the atmosphere through the stomata and into the air spaces of leaves. Water vapor evaporates from the surface of a leaf by diffusion through the open stomata.

Diffusion also plays a role in the movement of photosynthetic products such as sugars into the phloem for transport throughout the plant. Because cellular membranes are composed of a lipid bilayer, lipid-soluble materials use simple diffusion to cross the membrane surface. Substances with low lipid solubility can move across membranes via facilitated diffusion. In this process, the substance binds to a transporter molecule, generally called an ionophore, which transports the substance across the membrane and down its concentration gradient.

Bulk Flow

As previously mentioned, diffusion occurs rapidly over short distances. In order to move substances such as water over long distances—for example from the roots to the leaves, plants use a process referred to as *bulk flow*. Bulk flow is the concerted *en masse* movement of groups of molecules, usually in response to a pressure gradient. A moving stream, water flowing through a garden hose, and wind currents are examples of bulk flow. Pressure-driven bulk flow is the major mechanism behind the movement of water over long distances through the xylem. This process is different from diffusion because it is independent of solute concentration.

Active Transport

Whereas diffusion and facilitated diffusion do not require the direct input of cellular energy because they involve transport down a concentration gradient, moving substances against their concentration gradient requires the expenditure of energy. This "uphill" movement across membranes is called active transport.

The most common source of energy for active transport comes from adenosine triphosphate (ATP). When this high-energy phosphate is hydrolyzed, the stored energy is released to drive cellular reactions such as active transport. More specifically, the substance is moved across the membrane by a carrier protein embedded in the membrane. The carrier protein uses energy from the hydrolysis of ATP (that is, the removal of one phosphate group). Although active transport is primarily for movement against a concentration gradient, it can also be used to move substance down their concentration gradient.

There are two important modifications of the active transport process: *cotransport* and *countertransport*, both of which involve the movement of one substance down its concentration gradient while simultaneously transporting another substance against its specialized membrane proteins. Although these proteins do not require an energy source to operate, ATP is still indirectly consumed. The substance being moved down its concentration gradient would eventually be at equal concentrations on each side of the membrane. To counteract this, active transport, with hydrolysis of ATP as the energy source, is used to pump the substance across the membrane to maintain the gradient.

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See also: Active transport; Gas exchange in plants; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Plasma membranes; Root uptake systems; Vesicle-mediated transport; Water and solute movement in plants.

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CELLULAR SLIME MOLDS

Categories: Microorganisms; molds; *Protista*; taxonomic groups; water-related life

Cellular slime molds, or dictyostelids, were originally considered to be fungi. These microscopic, multicellular organisms are easily mistaken for some of the microfungi that commonly occur as contaminants in laboratory cultures. However, cellular slime molds are more closely related to the protozoans than to fungi.

Although once thought to be fungi, the protists of the phylum *Dictyosteliomycota* actually have more in common with the *paramecium* or *amoeba* that can be observed in a drop of pond water when viewed under the microscope than they do with mushrooms and toadstools. Cellular slime molds are essentially microscopic throughout their entire life cycle, and only rarely can they be observed directly in nature, as is the case for the plasmodial slime molds. Cellular slime molds must therefore be grown under controlled laboratory conditions in order to be studied.

Life Cycle

Since their discovery in the late nineteenth century, cellular slime molds have intrigued biologists. Their life cycle exhibits a curious alternative to the way in which most other creatures on earth grow, develop, and become multicellular, with different specialized tissues produced as a result of the process. Most plants and animals begin life as a single cell (called a zygote) that is the product of the fusion of an egg cell and sperm cell. Shortly after the two cells fuse (through a process termed fertilization), the zygote divides into two cells that stick together. These cells soon divide again to produce a cluster of four cells that in turn divide, and so on. Within hours or days (depending upon the particular plant or animal), clusters of dozens to thousands of cells form an embryo. Specialized cells begin to take form, and the basic shape of the body of the organism begins to become apparent.

Cellular slime molds approach reproduction differently. Like fungi and plasmodial slime molds, they produce *spores* as reproductive structures. When a spore germinates (no fusion of cells is required), it releases a single *amoeboid cell* that begins to engulf and digest bacteria in soil and decaying plant debris, the usual habitats for cellular slime molds. When the amoeboid cell divides, the two cells produced separate and become completely independent of each other, with each continuing to feed and undergo additional divisions for a number of hours or days. Only after the growing population of amoeboid cells depletes the local supply of bacteria is there any indication that a multicellular structure will be produced.

In response to the production of chemical attractants, thousands of amoeboid cells that have been operating as individual single-celled organisms begin to move, either singly or in streaming masses, to form multicellular clumps, or *aggregations*. Shortly thereafter, one or more cigar-shaped structures called *pseudoplasmodia* emerge from each aggregation. A pseudoplasmodium is a unified collection of thousands of what had once been separate, independent amoeboid cells. The cells remain distinct in the pseudoplasmodium but no longer act independently. Instead, they cooperate as parts of a multicellular entity. Remarkably, when amoeboid cells of two or more different species of cellular slime molds are grown together, the amoeboid cells of the different species can recognize each other, so that the cells that form any one aggregation are all of a single species rather than a mixture.

Immediately, or perhaps after the entire structure has migrated a short distance toward a light source, cells of the pseudoplasmodium begin to display different patterns of specialization. Cells that happen to have been positioned near the anterior end of the moving "cigar" begin to secrete a wall consisting of *cellulose*. These cells bind together to form a slender stalk that grows upward from the surface of the substrate upon which the pseudoplasmodium occurs. Other cells, those that happened to have been nearer the posterior end of the pseudoplasmodium, are lifted off the surface on the end of the extending stalk. These cells begin to become encapsulated and specialized as spores. Only the latter live on and produce another generation of amoeboid cells to feed on soil bacteria. The cells that produced the stalk in order to elevate the spore cluster above the substrate eventually die, dry up, and decay.

Reproduction

It appears that cellular slime molds reproduce asexually most of the time, at least under laboratory conditions. All of the cells that originate from the same spore are basically genetically identical to one another and collectively represent a genetic clone. As is the case for asexual reproduction in other life-forms, finding a "mate" is not necessary to perpetuate the species. If amoeboid cells are equipped with the genetic characteristics necessary to survive long enough to produce spores, the same gene combinations will be passed faithfully to all offspring, thus providing the same qualities for survival.

However, a method of sexual reproduction, with its potential of introducing genetic variability, also seems to exist in cellular slime molds. Occasionally in laboratory cultures, a number of large, thick-walled cells are found that are quite different from spores or encysted amoeboid cells. These giant cells are called *macrocysts*. Macrocysts appear to form when several amoeboid cells (sometimes described as being of compatible "mating types") fuse together and rearrange their genetic libraries and those of other amoeboid cells that may be engulfed. When macrocysts germinate, the amoeboid cells that emerge seem to have different combinations of genetic information than the cells that initially formed the macrocysts. This mixing up of genetic information, along with the genetic changes resulting from mutations, provides cellular slime molds with an ability to cope with changing environments.

Distribution and Ecology

Most of what is known about cellular slime molds has been acquired from studying these organisms in laboratory culture. What about the biology of "wild" slime molds in nature? In natural ecosystems, it is quite likely that cellular slime molds play a significant role in controlling the size of bacterial populations in soil and decaying litter. Nutrients that are taken up from decaying plants and animals by bacteria are transferred to cellular slime cells when the latter feed upon these bacteria. The cellular slime molds, in turn, become food for soil protozoans, nematode worms, microscopic arthropods such as mites, and other small invertebrate animals. Because of this, cellular slime molds play an essential role in patterns of energy flow and nutrient cycles within terrestrial ecosystems.

There are about seventy-five described species of cellular slime molds. These have been assigned to one of three genera: *Dictyostelium*, *Polysphondylium*, and *Acytostelium*. Some species of cellular slime molds have been found in almost all parts of the world. Two good examples are *Dictyostelium mucoroides* and *Polysphondylium pallidum*. Numbers of species of cellular slime molds appear to be highest in the American tropics, which suggests that this region represents a center of evolutionary diversification of the group. More than thirty-five different species have been found in the small area around the Mayan ruins at Tikal in Guatemala. In general, numbers of species of cellular slime molds decrease with increasing elevation and with increasing latitude.

Some species have restricted habitat associations. One species (*Dictyostelium caveatum*) has been found only in a single cave system in Arkansas. Another species (*Dictyostelium rosarium*), known from a number of localities worldwide but rarely aboveground, also seems to have an affinity for the type of conditions found in caves. Of the thirty-five species that occur at Tikal, many appear to be restricted to tropical or subtropical locations. *Dictyostelium discoideum* is the most intensively studied cellular slime mold and the one most widely used in research on developmental biology and genetics. Any search for information about cellular slime molds would probably turn up numerous references to this particular form.

Dispersal of Spores

Unlike most spore-producing organisms (including plasmodial slime molds), cellular slime molds produce spores that do not seem to be carried appreciable distances by wind. Instead, dispersal of cellular slime mold spores seems to depend more upon their accidental transport on the body surface or within the digestive tract of some animal. Viable spores of cellular slime molds have been recovered from the droppings of a number of animals, including rodents, amphibians, bats, and even migratory birds that travel great distances between winter and summer homes. In tropical forests, many living plants and considerable amounts of organic material are found high above the ground in the forest canopy. Cellular slime molds have been isolated from the mass of organic material (literally a "canopy soil") found at the bases of epiphytic plants growing on the trunks and branches of trees in these forests. It seems likely that they are introduced to such habitats by being carried up from the ground by birds, insects, or other animals that move between the forest floor and the canopy above it.

John C. Landolt and Steven L. Stephenson

See also: Bacteria; Plasmodial slime molds; *Protista*.

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CENTRAL AMERICAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

Agriculture is generally understood to be concerned with the production of food; however, in Central America, ornamental plants and flowers, forest products, and fibers are also important agricultural commodities.

The nations of Central America are generally considered to be Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama. At the end of the twentieth century, the agricultural sector employed about 46 percent of the available labor force in Central America, most of which was engaged in subsistence agriculture. This percentage is higher than that of the neighboring developing countries of Mexico (28 percent) and Colombia (30 percent). The Central American percentage is higher than those in more developed countries, such as the United States and Canada, each of which is below 4 percent. The percentage of suitable land in Central America is about equal to that in Mexico (12 percent) but significantly more than in Colombia (4 percent). Arable land in the United States is about 19 percent.

Early Agriculture

Considerable archaeological evidence supports the existence of sedentary agriculture in the region for more than two thousand years. The early Maya farmed raised fields in lowland swamp areas and constructed irrigation systems in areas with a dry season. In highland areas, steep slopes were terraced. The most prominent terrace agriculture in the Americas was in the Andean cultures, but Central Americans also used this practice. Agriculture was based mainly on corn, but other crops were widely grown, including squash, beans, and chile peppers. Nonfood crops such as cotton and tobacco were grown for both domestic use and trade. These two crops continue to be important.

Exactly what group of Central Americans established the various agricultural practices, or when, is debatable. However, it is known that agriculture supported large communities of people early in the first millennium. The cities of Tikal, Copán, Caracol, and others had populations of thirty-five thousand or more.

Raised field agriculture had several benefits. Sediment dredged from channel bottoms was added to the fields, raising the surface above the surrounding swamp, creating dry land. This mate-

rial was rich in nutrients from decaying plant matter and wastes from aquatic creatures. Channels of water dividing the dry land provided habitat for fish and turtles, which were a protein-rich food source for people.

Slash-and-burn agriculture was practiced. The process involved stripping forests and burning the debris in place. Trees too large to be cut with primitive stone implements were *girded*; that is, a circle of bark was removed from around the tree, and the tree died afterward. Burned debris added nutrients to the topsoil. Because the soil was generally poor, the fields, usually known as *milpas*, or cornfields, but sometimes referred to as *swidden*, were abandoned after two or three years of production and left *fallow* for up to twenty years. This process is still practiced.

Intercropping, or *polyculture*, was a practice that helped ensure a harvest. The planting of several crops and different varieties provided a harvest even if one crop failed. This practice is also in use today.

Traditional Crops

Since the nineteenth century, certain crops have been raised in Central America as export crops and others principally for domestic consumption. Many of the traditional crops grown are not native to the region. Many of the most widely grown crops are termed *exotics*, that is, plants not native to the region that were introduced by European settlers. Bananas, coffee, and sugarcane are three principal exotic crops, with corn being a fourth. Most of the production of introduced plants is grown for export, although native corn is for local use.

Bananas are grown extensively in the Caribbean and Pacific lowlands but most prominently in the Sula Valley of Honduras, a leading world exporter of this crop. The banana industry flourished under the control of North American growers, especially the United Fruit Company. In the later part of the nineteenth century, the banana export business grew and enjoyed large markets in the United States and Europe. The United Fruit Company also exerted strong influence over governmental policies in the region.

Coffee is grown extensively in the highland areas of all seven Central American countries. A slow-ripening crop, coffee requires as much as two months to harvest. Small-scale growers who sell their product through cooperatives produce much of the area's coffee. The best-quality coffee is shade-grown, and so banana trees often are planted throughout the small fields.

Sugarcane, first introduced by Christopher Columbus to the island of Cuba, is another plant grown throughout a wide area. Sugarcane is labor-intensive during harvest but requires little attention at other times. The harvest of sugarcane begins with the burning of the fields. This practice reduces the volume of foliage and leaves only the stalks, or canes, which are the source of sugar. After the burning—which has the side benefit of chasing out the snakes that inhabit the cane fields—teams of workers with machetes march through the fields cutting the cane.

Corn (maize) is not grown for export. Along with regionally grown rice, it is for domestic consumption. Corn meal is used in the preparation of tortillas, which are eaten at nearly every meal. Rice is commonly served with red or black beans.

Leading Agricultural Crops of Central American Countries

Country	*Products*
Belize	Bananas, cacao, citrus, sugarcane, lumber
Costa Rica	Coffee, bananas, sugar, corn, rice, beans, potatoes, timber
El Salvador	Coffee, sugarcane, corn, rice, beans, oilseed, cotton, sorghum
Guatemala	Sugarcane, corn, bananas, coffee, beans, cardamom
Honduras	Bananas, coffee, citrus, timber
Nicaragua	Coffee, bananas, sugarcane, cotton, rice, corn, cassava, citrus, beans
Panama	Bananas, corn, sugarcane, rice, coffee, vegetables

Source: Data are from *The Time Almanac 2000*. Boston: Infoplease, 1999.

Image Not Available

Export crops have varied in their economic value to the region. A banana disease nearly ruined the industry in the 1930's. The Great Depression in those same years sharply reduced exports to North America. Import quotas imposed by the United States on sugar and the U.S. trade embargo on all Cuban products imposed in the early 1960's provided both a low and a high for Central American sugar producers. Overproduction of coffee by South American producers has led to depressed prices several times. During the late 1990's, the European Union's agricultural import practice of favoring former colonies reduced the value of bananas to growers. In Central America, only Belize (formerly British Honduras) benefits from European tariff regulations.

Nontraditional Crops

Vegetables, high-value crops, and ornamental plants and flowers are being grown at an increased rate. The leading crops are broccoli, cauliflower, snow peas, melons, strawberries, and pineapples.

Palm oil from a nonnative tree is another high-value farm product. Nontraditional crops are labor-intensive and affect the environment because of the heavy requirements for chemical pesticides. Workers face health risks due to these chemical applications, but employment is high. In Costa Rica, the government encourages investment in reforestation using teak from Southeast Asia.

Donald Andrew Wiley

See also: Agriculture: traditional; Central American flora.

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CENTRAL AMERICAN FLORA

Category: World regions

Central America—comprising the nations Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama—is a land bridge that connects North America and South America, and many of its plants are similar to plants found on both those continents.

Lowlands

Tropical *rain forests* lie on the eastern half of Central America and typically have many tall, broad-leaved evergreen trees 130 feet (40 meters) or more in height, and 4-5 feet (1.2-1.5 meters) in diameter that form a dense canopy. Shade-seeking plants, such as palms, figs, ferns, vines, philodendrons, and orchids, form the forest undergrowth beneath the trees.

Epiphytes, such as orchids, ferns, bromeliads, and mosses, cling to the branches of the trees in a dense mat of vegetation—these plants have no roots but grow by clinging to the trunks of trees and drawing moisture and nourishment from the air. Rain-forest trees that are harvested for their commercial value include mahogany, kapok, cedarwood, tagua, ebony, and rosewood for making furniture; breadfruit, palm, and cashew; sapodilla, used to make latex; and the rubber tree. Many brilliantly colored flowers also grow in Central America. The most common of these are orchids (with close to a thousand species), heliconias, hibiscus, and bromeliads.

In the Caribbean lowlands, where the soil is porous and dry, extensive savanna *grasslands* with sparse forests of pines, palmettos, guanacastes, cedars, and oaks are found. Along the Caribbean coast (called the Mosquito Coast), mangroves and coconut palms flourish in swamps and lagoons.

Highlands

The central mountains and highlands of Central America are cooler than the coastal lowlands, and

Cacao: The Chocolate Bean

Cacao (cocoa) beans (*Theobroma cacao*), from which chocolate is made, have been cultivated in Central America for centuries. Although now a major African crop as well, cacao originated in the Americas. Once considered the drink of the gods, chocolate was reserved for royalty. Today, millions around the world enjoy chocolate, especially mixed with sugar and milk.

The beans are actually the berries of the small cacao tree, which grows in shade and is rarely more than 20 feet (6 meters) tall. The tree's football-shaped pods are 6-8 inches (15-20 centimeters) in length. When ripe, the pods can be red, yellow, or orange, depending on the variety. The tree's flowers are tiny, inconspicuous white blossoms that emerge singularly from the lower branches or trunk, not from stem ends. The cacao seeds, or beans, are surrounded by a whitish, gelatinous mass. Cacao beans must be fermented, dried, and cleaned before the chocolate aroma and taste develop.

the vegetation there is mainly deciduous hardwood trees such as walnut, pine, and oak. The eastern slopes of the mountains have abundant rainfall. "Cloud forests" that are 5,000 feet (1,525 meters) above sea level are thick with evergreen oak, sweet gum, pine, and laurel, which grow to a height of about 65 feet (20 meters) and are festooned with ferns, bromeliads, mosses, and orchids.

On the western side of the mountains, facing away from the moist Caribbean winds and receiving rain only seasonally, vegetation is sparse and semiarid, and soils are poor and unproductive. Deciduous tropical forests dominate there, and vegetation is characterized by evergreen herbs and shrubs, plumeria (frangipani), eupatorium pines, myrtles, and sphagnum mosses.

Helen Salmon

See also: African flora; Antarctic flora; Asian flora; Australian flora; Caribbean flora; North American flora; South American flora.

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CHAROPHYCEAE

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

It is almost impossible not to see Spirogyra *floating on the surface of a pond on a hot summer day, but most people dismiss it as pond scum. Few realize that what they are looking at is a member of the* Charophyceae, *a class in the phylum Chlorophyta, or green algae, and a cousin of the ancestor of the* Embryophyta, *or bryophytes and vascular plants.*

Most *Charophyceae*, like *Spirogyra*, live in freshwater habitats, but some also occur in moist soil in terrestrial habitats. *Charophyceae* can live as single cells, colonies, or branched and unbranched filaments and come in a variety of shapes. The characteristics that unite members of the class—and which link them with the embryophytes—include flagellated cells (similar to sperm cells in vascular plants), a nuclear envelope that breaks down during mitosis, mitotic spindles that persist as phragmoplasts (a type of cytoskeletal scaffolding) through cell division either by furrowing or by forming a cell plate, the presence of chlorophylls *a* and *b* and phytochrome, and the storage of starch inside plastids.

Charophytes possess decay-resistant cell walls made of phenolic compounds as well as lignins or ligninlike compounds. Cell walls made of similar compounds are found in bryophytes and vascular plants as well. Likewise, all three groups of plants also contain sporopollenin, the substance in the walls of spores and pollen grains that makes them virtually indestructible. Communication channels between cells are similar, too. Plasmodesmata similar to that seen in embryophyte cells allow between-cell communications in charophytes and embryophytes.

Life Cycle

Charophytes have a two-stage life cycle involving a dominant haploid stage, upon which develops the sex organs; antheridia, which produce sperm cells; and oogonia, which produce egg cells. Typically, individual charophytes produce both antheridia and oogonia, but in some species an individual will produce only one or the other. Fertilization—which in one group, the *Zygnematales*, takes place via conjugation—produces a diploid zygote, which quickly undergoes meiosis. If the environment is unfavorable, the zygote will go dormant and remain so for a long period of time. Dormancy ends when the environment improves.

Classification

Genetic analysis supports the recognition of six orders within the *Charophyceae*: the *Mesostigmatales*, *Chlorokybales*, *Klebsormidiales*, *Zygnematales*, *Coleochaetales*, and *Charales*.

Of these, the most abundant group is the *Zygnematales*, a large order which consists of more than three thousand species, including *Spirogyra* and the desmids, a group of mostly single-celled organisms with a constriction across the middle which nearly divides the cells in two. *Zygnematales* live primarily in freshwater habitats as phytoplankton, as benthic dwellers, or attached to other aquatic plants. Some species live on snow and ice.

The *Charales*, commonly called stoneworts or brittleworts, are a large group of filamentous charophytes that feature complex branching patterns. Some can reach lengths of more than a meter. The branching pattern—branches reach out from nodes along the filament—is similar to that of higher plants. *Charales* reside primarily in freshwater habitats, but some can be found in brackish water as well as on land. The stems of stoneworts and brittleworts can be encrusted with calcium and magnesium carbonates. As a result, their hard bodies are well known from the fossil record. The lineage extends back to more than 400 million years ago. Two current genera, *Chara* and *Nitella*, date back about 200 million years.

The *Coleochaetales* are a small group of complex, microscopic filamentous algae that can be found only in freshwater habitats. *Klebsormidiales* are a small group of unbranched, filamentous charophytes that occur in both freshwater and terrestrial environments. *Mesostigmatales* and *Chlorokybales* are two groups of rare algae. The *Coleochaetales* and *Charales* are more closely related to bryophytes and vascular plants than the other groups.

Evolutionary Significance

For decades, structural similarities led plant biologists to suspect that the *Embryophyta* evolved from charophytes. Recently, cladistic analyses of chemical, structural, and genetic characteristics have opened up research on the topic. In cladistics, characteristics among a number of organisms are analyzed statistically in the hopes of developing a classification system for the group which will reveal evolutionary relationships. Cladistic analyses support the notion that embryophytes are monophyletic; in other words, bryophytes and vascular plants descend from a common ancestor.

Furthermore, several recent analyses support the notion that a member of the *Charophyceae* gave rise to embryophytes. Cladistic analyses were somewhat unclear, however, about the relationships of the charophyte orders with one another and with other green algae (*Chlorophyta*), bryophytes, and land plants.

One of the latest analyses of mitochondrial, chloroplast, and nuclear genes helps resolve some of the confusion. The research indicates that the *Mesostigmatales* were probably the most ancient group of charophytes, followed by the *Chlorokybales*, *Klebsormidiales*, *Zygnematales*, *Coleochaetales*, and *Charales*.

The work also supports earlier suggestions that the *Charales* are the closest living relatives to extant embryophytes and that the charophytes descended from other green algae.

David M. Lawrence

See also: Algae; Aquatic plants; Bryophytes; *Chlorophyceae*; Cladistics; Eukaryotic cells; Evolution of plants; Green algae; Phytoplankton; *Ulvophyceae*.

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CHEMOTAXIS

Categories: Cellular biology; microorganisms; movement; physiology

Chemotaxis is the ability of a cell to detect certain chemicals and to respond by movement, such as microbial movement toward nutrients in the environment.

Many microorganisms possess the ability to move toward a chemical environment favorable for growth. They will move toward a region that is rich in nutrients and other growth factors and away from chemical irritants that might damage them. Among the organisms that display this *chemotactic behavior*, none is simpler than bacteria. Bacteria are single-celled *prokaryotic* microorganisms, which means that their deoxyribonucleic acid (DNA) is not contained within a well-defined nucleus surrounded by a nuclear membrane, as in *eukaryotic* (plant and animal) cells. *Prokaryotes* lack many of the cellular structures associated with more complex eukaryotic cells; nevertheless, many species of bacteria are capable of sensing chemicals in their environment and responding by movement.

Bacterial Flagella

Bacteria capable of movement are called *motile bacteria*. Not all bacteria are motile, but most species possess some form of motility. Although there are three different ways in which bacteria can move, the most common means is by long, whiplike structures called *flagella*.

Bacterial flagella are attached to cell surfaces and rotate like propellers to push the cells forward. A bacterial cell must overcome much resistance from the water through which it swims. In spite of this, some bacteria can move at a velocity of almost 90 micrometers per second, equivalent to more than one hundred bacterial cell lengths per second.

A flagellum is composed of three major structural components: the *filament*, the *hook*, and the *basal body*. The filament is a hollow cylinder composed of a protein called *flagellin*. A single filament contains several thousand spherically shaped flagellin molecules bound in a spiral pattern, forming a long, thin cylinder. A typical filament is between 15 and 20 micrometers long but only 0.02 micrometer thick. The filament is attached to the cell by means of the hook and basal body. The hook is an L-shaped structure composed of protein and slightly wider than the filament. One end of the hook is connected to the filament, and the other end is attached to the basal body. The basal body, also known as the *rotor*, consists of a set of protein rings embedded in the cell wall and plasma membrane. Inside these rings is a central rod attached to the hook. The central rod of the basal body rotates inside the rings, much like the shaft of a motor. As it rotates, it causes the hook and the filament to turn.

Bacteria in Motion

While they are moving, bacteria change direction by reversing the rotation of their flagella. As a bacterium swims forward in a straight line, its flagella spin in a counterclockwise direction. Because of their structure, the flagella twist together when they rotate counterclockwise and act cooperatively to push the cell forward. The forward movement is referred to as a *run*. Every few seconds, a chemical change in the basal body of each flagellum causes it to reverse its spin from counterclockwise to clockwise. When the flagella spin clockwise, they fly apart and can no longer work together to move the cell forward. The cell stops and tumbles randomly until the flagella reverse again, returning to counterclockwise spin and a forward run. This type of movement, in which the cell swims forward for a short distance and then randomly changes its direction, is called *run and tumble* movement.

Certain eukaryotic microorganisms, such as *Euglena* and some other protozoa, are also motile by means of flagella. The structure and activity of eukaryotic flagella are, however, completely different from those of bacteria. Eukaryotic flagella are composed of protein fibers called *microtubules*, which move back and forth in a wavelike fashion to achieve movement. The rotation of bacterial flagella and the run and tumble movement they produce are unique to bacteria.

Attractants and Repellants

Bacteria respond by chemotaxis to two broad classes of substances, *attractants* and *repellants*. They move toward high concentrations of attractants (*positive chemotaxis*) and away from high concentrations of repellants (*negative chemotaxis*). Attractants are most often nutrients and growth factors, such as monosaccharides (simple sugars), amino acids (the building blocks of protein), and certain vitamins required for bacterial metabolism. Repellants include waste products given off by the bacteria as well as other toxic substances found in the environment.

Bacteria respond to attractants and repellants by altering the time between tumbles in their run and tumble movement. When a bacterial cell detects an attractant, the time between tumbles and the time of the runs increase. As long as the cell is moving toward a higher concentration of attractant, its runs will be longer. The opposite effect occurs when a cell encounters a repellant. A repellant causes the time between tumbles to decrease, resulting in shorter runs as the cell changes direction more frequently while trying to avoid the repellant. The net result is that the cell tends to move toward a lower concentration of the repellant.

Chemotactic Receptors

Bacteria recognize attractants and repellants through specialized proteins called *chemotactic receptors*, also called *methyl-accepting chemotactic proteins* (MCPs), which are embedded in their plasma membranes just inside the cell wall. Biologists have identified roughly twenty different receptors for attractants and some ten for repellants. Each receptor protein is believed to respond to only a single type of attractant or repellant.

When an attractant molecule binds to its chemotactic receptor, two separate events occur. First, there is a rapid activation of the receptor. The attractant molecule binds to a special site on the receptor protein to form an activated receptor. This binding is not permanent, however, so a cell must remain in an area with attractant molecules for its receptors to remain activated. The activated receptor sends a chemical signal to the basal bodies of flagella, which causes them to spin in a counterclockwise direction, producing continuous swimming in one direction.

At the same time, there is adaptation of the activated receptors to the attractant. Adaptation is important because it keeps the cell from swimming too long in one direction. It is accomplished by *methylation* of the receptors, a process in which methyl groups are attached to the protein by an enzyme in the cell. (A methyl group consists of an atom of carbon attached to three atoms of hydrogen.) Methylated receptors do not stimulate the basal bodies for counterclockwise rotation as effectively as nonmethylated receptors. After a cell has been in the presence of an attractant for a short while, its receptors adapt to the attractant, and it returns to the original pattern of run and tumble movement. Adaptation is reversed by *demethylation*, the removal of methyl groups from the receptor by a separate enzyme. Together, the balance between methylation and demethylation makes the receptors very sensitive to small changes in attractant concentration, so that cells remain in the region with the greatest concentration of attractant.

The action of repellants appears to be similar to that of attractants. Repellant molecules bind to sites on their chemotactic receptors, activating the receptors. The activated receptors signal the flagella to spin clockwise instead of counterclockwise, causing the cell to tumble and to change direction. Repellant receptors also adapt through methylation and demethylation, much like attractant receptors.

It is not entirely understood how an activated chemotactic receptor can signal flagella to rotate. Four different proteins inside the bacterial cell have been identified as a possible link between the chemotactic receptors and the basal bodies of flagella. These proteins are believed to regulate flagellar rotation using a process called *phosphorylation*. Phosphorylation, the attachment of phosphate molecules to a protein, is used in all types of cells as a kind of "on and off" switch to regulate protein activity.

Jerald D. Hendrix

See also: Bacteria; Flagella and cilia; Prokaryotes.

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CHLOROPHYCEAE

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

Chlorophyceae *(from the Greek word* chloros, *meaning "green") make up an extremely large and important class of green algae. Members may be unicellular, colonial, or filamentous. Cells of unicellular and colonial chlorophyceans may have two or more flagella.*

There are about 2,650 living species of chlorophyceans. The main features of the class (and most plants) are the use of starch as the principal food reserve and the green chloroplasts with chlorophylls *a* and *b*. In spite of plant characteristics, this algal group is not directly related to early land plants. Chlorophyceans are almost entirely restricted to freshwater and terrestrial habitats. Some members of this class have adapted to life on snow as *snow algae*. Snow algae cause snow to appear red-burgundy or orange in color because of high levels of unusual carotenoid pigments within the algal cells.

There are a variety of asexual and sexual reproduction modes among members of this class. Sexual reproduction is characterized by the formation of a zygote produced by gametic fusion. Chlorophyceans show differences during cell division compared to other green algal groups. For example, they produce a set of microtubules, the *phycoplast*, that is parallel to the plane of cell division.

Diversity

The *Chlorophyceae* include some familiar green algae. Perhaps the most famous chlorophyceans are *Chlamydomonas* (from the Greek word *chlamys*, meaning "cloth") and *Volvox* (from the Latin *volvo*, meaning "to roll"). Both are important research models in laboratories. Chlorophyceans fall into several orders, including *Volvocales*, *Chlorococcales*, *Chaetophorales*, and *Oedogoniales*.

Volvocales

Members of the order *Volvocales* include both unicellular organisms, such as those in the genus *Chlamydomonas* with their two equal flagella, and colonial forms. The *Chlamydomonas* are a large genus of chlorophyceans. More than six hundred species have been described worldwide. The *Chlamydomonas* probably represent the most primitive structure among chlorophyceans. Nevertheless, their basic cell features may be found among other representatives of this order.

A cell wall made of glycoproteins, rather than cellulose, surrounds each *Chlamydomonas* cell. Inside the cell, there is a single large chloroplast and a pyrenoid, which forms starch.

Other cytoplasmic structures include the contractile vacuole rather than a central vacuole. The contractile vacuole is responsible for the removal of water from the cell. Cells of *Chlamydomonas* are capable of phototaxis: They swim toward moderate light but away from high-intensity light. Rhodopsin-like pigment is their primary light-sensing photoreceptor. Under dry conditions, *Chlamydomonas* form a palmelloid stage, in which nonflagellate cells are held together by common mucilage.

Chlamydomonas reproduce asexually via cell division. Also, cells of this alga can become gametes. In most species of *Chlamydomonas*, the male and female gametes appear the same; they are designated (+) and (–). Colonial flagellates of the order *Volvocales* range from simple colonies of *Gonium* to visible-without-magnification spheres of *Volvox* with up to several thousands of cells and some sort of cellular specialization.

Volvox are one of the most structurally advanced colonial forms of green algae. Only specialized cells participate in reproduction. During asexual reproduction, some cells of *Volvox* divide and bulge inward, forming new daughter colonies, which are held for some time within the parent colony. *Volvox* are also capable of sexual reproduction.

They produce gametes that differentiate into sperm and eggs.

Chlorococcales

Members of the order *Chlorococcales* include nonmotile unicellular and colonial algae. Typical representatives of the unicellular nonmotile form are found in *Chlorococcum*. They occur as spherical single cells or cell aggregates and produce flagellated zoospores. Examples of colonial representatives of *Chlorococcales* are *Hydrodictyon*, commonly known as the "water net"; *Pediastrum*, famous for their distinctive, starlike shape; and *Scenedesmus*, widespread inhabitants of the freshwater phytoplankton. The order *Chlorococcales* has now been divided on the basis of small subunit ribosomal ribonucleic acid (RNA) sequence data into several groups, including the *Sphaeropleales*, *Tetracystis* clade, and *Dunaliella* clade.

Chaetophorales* and *Oedogoniales

The most complex of the class *Chlorophyceae* are the filamentous members in orders *Chaetophorales* and *Oedogoniales*, some of which exhibit features that are observed primarily in plants. The chaetophoralean green algae have plantlike bodies with a system of primary and secondary branches. The *Draparnaldia* (named for Jacques Phillipe Raymond Draparnaud, a French naturalist) from order *Chaetophorales* have a main filamentous axis with relatively large cells, primary branches with smaller cells, and secondary branches with even smaller cells. One representative of *Oedogoniales*, the green alga *Oedogonium* (from the Greek *oidos*, meaning "swelling"), has been a subject of intense study for its unusual cell division technique. The entire contents of an *Oedogonium* cell may be used in the formation of one large zoospore with multiple flagella. Members of *Bulbochaete* (from the Greek *bolbos*, meaning "bulb") resemble *Oedogonium* in cell division but differ in being branched and having a distinctive hair cell at the end of each branch.

Technological Uses

A few chlorophycean green algae have commercial value. These algae are good candidates for the industrial production of hydrogen gas because they are able to release the gas from water using solar energy. Hydrogen gas is an environmentally desirable fuel because the burning of hydrogen produces water, and it can be converted effectively to electricity.

Another "commercial" organism is *Dunaliella salina*, a saltwater alga that accumulates massive amounts of beta-carotene, a vital antioxidant also used in food coloring and in pharmaceuticals. *Selenastrum capricornutum* are the most widely used algal biomonitors in the detection of water pollution. Chlorophyceans are used in freshwater aquaculture systems as food for fish. One alga with possible potential for salmon feeds is *Haematococcus*. Algae contain large amounts of the pigment astaxanthin, which is responsible for the red coloration typical of salmon flesh. *Chlorella* (formerly classified in the order *Chlorococcales*) are famous both as the experimental systems in the discovery of the photosynthetic Calvin cycle and as health food in Asia.

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See also: Algae; Brown algae; Calvin cycle; *Charophyceae*; Chrysophytes; Cryptomonads; Diatoms; Dinoflagellates; Green algae; Haptophytes; Red algae; *Ulvophyceae*.

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CHLOROPLAST DNA

Categories: Cellular biology; genetics; photosynthesis and respiration; reproduction and life cycles

Plants are unique among higher organisms in that they meet their energy needs through photosynthesis. The specific location for photosynthesis in plant cells is the chloroplast, which also contains a single, circular chromosome composed of DNA. Chloroplast DNA contains many of the genes necessary for proper chloroplast functioning.

A better understanding of the genes in chloroplast deoxyribonucleic acid (cpDNA) has improved the understanding of photosynthesis, and analysis of the deoxyribonucleic acid (DNA) sequence of these genes has been useful in studying the evolutionary history of plants.

Discovery of Chloroplast Genes

The work of nineteenth century Austrian botanist Gregor Mendel showed that the inheritance of genetic traits follows a predictable pattern and that the traits of offspring are determined by the traits of the parents. For example, if the pollen from a tall pea plant is used to pollinate the flowers of a short pea plant, all the offspring are tall. If one of these tall offspring is allowed to self-pollinate, it produces a mixture of tall and short offspring, three-quarters of them tall and one-quarter of them short. Similar patterns are observed for large numbers of traits from pea plants to oak trees. Because of the widespread application of Mendel's work, the study of genetic traits by controlled mating is often referred to as Mendelian genetics.

In 1909 German botanist Karl Erich Correns discovered a trait in the four-o'clock plants (*Mirabilis jalapa*) that appeared to be inconsistent with Mendelian inheritance patterns. He discovered that four-o'clock plants had a mixture of leaf colors on the same plant: Some were all green, many were partly green and partly white (variegated), and some were all white. If he took pollen from a flower on a branch with all-green leaves and used it to pollinate a flower on a branch with all-white leaves, all the resulting seeds developed into plants with white leaves. Likewise, if he took pollen from a flower on a branch with all-white leaves and used it to pollinate a flower on a branch with all-green leaves, all the resulting seeds developed into plants with green leaves. Repeated pollen transfers in any combination always resulted in offspring whose leaves resembled those on the branch containing the flower that received the pollen, that is, the maternal parent. These results could not be explained by Mendelian genetics.

Since Correns's discovery, many other such traits have been discovered. It is now known that the reason these traits do not follow Mendelian inheritance patterns is that their genes are not on the chromosomes in the nucleus of the cell where most genes are located. Instead, the gene for the four-o'clock leaf color trait is located on the single, circular chromosome found in chloroplasts. Because chloroplasts are specialized for photosynthesis, many of the genes on the single chromosome produce proteins or ribonucleic acid (RNA) that either directly or indirectly affect synthesis of chlorophyll, the pigment primarily responsible for trapping energy from light. Because chlorophyll is green and because mutations in many chloroplast genes cause chloroplasts to be unable to make chlorophyll, most mutations result in partially or completely white or yellow leaves.

Identity of Chloroplast Genes

Advances in molecular genetics have allowed scientists to take a much closer look at the chloroplast genome. The size of the genome has been determined for a number of plants and algae and ranges from 85 to 292 kilobase pairs (one kb equals one thousand base pairs), with most being between 120 kb and 160 kb. The complete DNA sequences for several different chloroplast genomes of plants and algae have been determined. Although a simple sequence does not necessarily identify the role of each gene, it has allowed the identity of a number of genes to be determined, and it has allowed scientists to estimate the total number of genes. In terms of genome size, chloroplast genomes are relatively small and contain slightly more than one hundred genes.

Roughly half of the chloroplast genes produce either RNA molecules or polypeptides that are important for protein synthesis. Some of the RNA genes occur twice in the chloroplast genomes of almost all land plants and some groups of algae. The products of these genes represent all the ingredients needed for chloroplasts to carry out transcription and translation of their own genes. Half of the remaining genes produce polypeptides directly required for the biochemical reactions of photosynthesis. What is unusual about these genes is that their products represent only a portion of the polypeptides required for photosynthesis. For example, the very important enzyme ATPase, the enzyme that uses proton gradient energy to produce the important energy molecule adenosine triphosphate (ATP), comprises nine different polypeptides. Six of these polypeptides are products of chloroplast genes, but the other three are products of nuclear genes that must be transported into the chloroplast to join with the other six polypeptides to make active ATPase. Another notable example is the enzyme ribulose biphosphate carboxylase (RuBP carboxylase), which is composed of two polypeptides. The larger polypeptide, called rbcL, is a product of a chloroplast gene, whereas the smaller polypeptide is the product of a nuclear gene.

Image Not Available

The last thirty or so genes remain unidentified. Their presence is inferred because they have DNA sequences that contain all the components found in active genes. These kinds of genes are often called "open reading frames" (ORFs) until the functions of their polypeptide products are identified.

Impact and Applications

The discovery that chloroplasts have their own DNA and the further elucidation of their genes have had some impact on horticulture and agriculture. Several unusual, variegated leaf patterns and certain mysterious genetic diseases of plants are now better understood. The discovery of some of the genes that code for polypeptides required for photosynthesis has helped increase understanding of the biochemistry of photosynthesis. The discovery that certain key chloroplast proteins, such as ATPase and RuBP carboxylase, are composed of a combination of polypeptides coded by chloroplast and nuclear genes also raises some as yet unanswered questions. For example, why would an important plant structure like the chloroplast have only part of the genes it needs to function? Moreover, if chloroplasts, as evolutionary theory suggests, were once free-living bacteria-like cells, which must have had all the genes needed for photosynthesis, why and how did they transfer some of their genes into the nuclei of the cells in which they are now found?

Of greater importance has been the discovery that the DNA sequences of many chloroplast genes are highly conserved; that is, they have changed very little during their evolutionary history. This fact has led to the use of chloroplast gene DNA sequences for reconstructing the evolutionary history of various groups of plants. Traditionally, plant systematists (scientists who study the classification and evolutionary history of plants) have used structural traits of plants, such as leaf shape and flower anatomy, to try to trace the evolutionary history of plants. Unfortunately, there are a limited number of structural traits, and many of them are uninformative or even misleading when used in evolutionary studies. These limitations are overcome when gene DNA sequences are used.

A DNA sequence of a few hundred base pairs in length provides the equivalent of several hundred traits, many more than the limited number of structural traits available (typically much fewer than one hundred). One of the most widely used sequences is the rbcL gene. It is one of the most conserved genes in the chloroplast genome, which in evolutionary terms means that even distantly related plants will have a similar base sequence. Therefore, rbcL can be used to retrace the evolutionary history of groups of plants that are very divergent from one another. The rbcL gene, along with a few other very conservative chloroplast genes, has already been used in attempts to answer some basic plant evolution questions about the origins of some of the major flowering plant groups. Less conservative genes and ORFs show too much evolutionary change to be used at higher classification levels but are extremely useful in answering questions about the origins of closely related species, genera, or even families. As analytical techniques are improved, chloroplast genes show promise of providing even better insights into plant evolution.

Bryan Ness

See also: Chloroplasts and other plastids; DNA in plants; DNA replication; Genetics: Mendelian; Genetics: post-Mendelian; Mitochondrial DNA; Pollination; RNA.

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CHLOROPLASTS AND OTHER PLASTIDS

Categories: Cellular biology; photosynthesis and respiration; physiology

Plastids are highly specialized, double membrane-bound organelles found within the cells of all plants and algae. A type of plastid called the chloroplast is the cellular location of the process of photosynthesis.

Plastids exhibit remarkable diversity with respect to their development, morphology, function, and physiological and genetic regulation. Chloroplasts, a type of plastid, are arguably largely responsible for the maintenance and perpetuation of most of the major life-forms on earth through *photosynthesis*. The process of photosynthesis uses visible light as an energy source to power the conversion of atmospheric carbon dioxide into organic molecules that can be used by living organisms. As a by-product of photosynthesis, oxygen is released into the atmosphere and is used by living organisms in the energy-obtaining process of cellular respiration. Other plastid types are specialized for synthesis and storage of pigments, starch, and other secondary metabolites.

Plastid Structure

The typical plastid from the cell of a flowering plant is surrounded by a double membrane system consisting of an inner and outer membrane, with an intermembrane space between the two. In chloroplasts, the photosynthetic pigments that are responsible for absorbing sunlight are located in the *thylakoid* membrane system. This continuous internal membrane system is found throughout the chloroplast *stroma*, an internal fluid matrix analogous to the cellular cytosol. *Granal thylakoids* are organized into stacks, and the *stromal thylakoids* are unstacked and exposed to the stromal matrix. The internal space within the thylakoid membrane system is called the *lumen*. The pigments and proteins involved in the light reactions of photosynthesis, the processes whereby light energy is converted into chemical energy, are embedded in the thylakoid membrane system. The *dark reactions*, or *Calvin cycle*, which is the carbon fixation pathway that leads to the formation of simple carbohydrates, occurs in the stroma. Small starch granules and oil bodies, termed *plastoglobuli*, are often found in chloroplasts. These serve as energy storage reserves for the plant cell. Plastids other than chloroplasts typically lack thykaloids.

Proplastids

The developmental precursor to all plastid types is the *proplastid*. Proplastids are relatively undifferentiated plastids typically found in young, undifferentiated meristematic cells and tissues. Under the appropriate cellular and environmental conditions, proplastids can undergo development and differentiation to any of three main plastid types: chloroplasts, *chromoplasts*, or *leucoplasts*.

Chloroplasts

Chloroplasts typically contain one or more of the three types of plastid chlorophylls (chlorophyll *a*, *b*, or *c*) and, often, members of the two classes of photosynthetic accessory pigments: *carotenoids* and *phycobilins*. The most obvious and essential physiological process unique to chloroplasts is photosynthesis. In the energy transduction reactions (the light reactions), radiant energy in the form of visible light (mostly of the violet, blue, and red wavelengths) is harnessed primarily by the green pigment chlorophyll. The harnessed energy is then used to phosphorylate adenosine diphosphate (ADP) to produce adenosine triphosphate (ATP) in a process termed *noncyclic photophosphorylation* and reduce the electron carrier nicotinamide adenine dinucleotide phosphate (NADP) to NADPH. Oxygen is liberated through the light-dependent oxidative splitting of water.

In the carbon-fixation reactions (often called the dark reactions, although they can occur in the presence of light) the ATP is used as an energy source for the attachment of atmospheric carbon dioxide to the simple sugar ribulose 1,5-bisphosphate (RuBP). The NADPH is used to facilitate the reduction of RuBP through a series of simple sugars in a biochemical set of reactions known as the Calvin cycle. One of the products of this cycle, glyceraldehydes-3-phosphate (G3P), is used by the chloroplast to make glucose and other carbohydrates. G3P is also needed to perpetuate the Calvin cycle, so only one of every three produced is used for carbohydrate synthesis.

Chloroplasts are also the site of synthesis for the three aromatic amino acids: phenylalanine, tyrosine, and tryptophan. The precursor compound aspartate is imported into chloroplasts from the cell cytosol and is used for the synthesis of the amino acids lysine, threonine, and isoleucine. An intermediate in the synthesis of threonine, called homoserine 4-phosphate, is exported from the chloroplast into the cytosol as a precursor for methionine. Thus, there is a strong integration of function among the chloroplast, cytosol, and nucleus, in that the enzymes involved in these amino acid biosynthetic pathways are nuclear-encoded, their mRNAs are translated using cytosolic ribosomes, and most of the biosynthetic enzymes are imported into the chloroplast.

Fatty acid biosynthesis is another biochemical function that occurs in chloroplasts. Fatty acids, as lipid precursors, might be either incorporated directly into chloroplast lipids via a plastid-localized biochemical pathway or exported into the cytoplasm for conversion into endoplasmic reticulum lipids. Lipids found in the inner plastid membrane are plastid-synthesized, whereas those of the outer plastid membrane are synthesized in the endoplasmic reticulum.

Other Plastids

Other plastid types include *chromoplasts*, which typically contain carotene or xanthophyll pigments and are responsible for the colors of many fruits, flowers, and roots. Under some conditions chromoplasts can differentiate into chloroplasts. Leucoplasts are colorless and lack complex inner membranes. One type of leucoplast, the *amyloplast*, synthesizes and stores starch. Other leucoplasts synthesize a wide range of products, including oils and proteins. Proplastids that are arrested during their normal development into chloroplasts are termed *etioplasts*. These typically are formed when developing plant tissues are deprived of light.

Evolutionary History

Plastids possess a number of features that provide insights into their remarkable evolutionary history. The chloroplasts of eukaryotic cells photosynthesize in a manner similar to the more ancient prokaryotic cyanobacteria by using membrane-bound chlorophyll to capture radiant energy. Some plastids even bear a strong morphological similarity to cyanobacteria, being similar in size and having similar internal structures. Plastids divide by binary fission in a manner similar to bacterial reproduction.

Plastids also have a certain degree of autonomy in terms of their genetic system. Typically, the majority of flowering plant plastids contain multiple copies (50-100) of a circular chromosome, ranging in size from 130 to 180 kilobase pairs (kb) in higher plants. Chromosome size in algae is much more variable, ranging all the way from 57 kb to 1,500 kb. The plastid chromosome contains genes for RNAs, such as rRNA (ribosomal RNA) and tRNA (transfer RNA), and structural genes that code for polypeptides involved in photosynthesis, transcription, protein synthesis, energy transduction, and several other functions. Many of the genes on the chloroplast chromosome are organized into clusters termed *operons* in a manner similar to that found in eubacteria.

The nucleotide sequences of many plastid genes, especially the ribosomal RNA genes, are highly similar to those in eubacteria, and the ribosomes found within plastids have a similar composition and size to eubacterial ribosomes. The plastid-encoded genes are transcribed either by a nuclear-encoded or plastid-encoded RNA polymerase, and the resultant mRNAs are translated by plastid ribosomes found within the stroma. The majority of plastid biochemical processes rely on both nuclear- and plastid-encoded genes. Some proteins, such as RuBP carboxylase/oxygenase (Rubisco), are composed of both nuclear- and plastid-encoded protein subunits, again demonstrating the remarkable coordination of biogenesis and development between organelle and cytosol.

This evidence lends strong support to the *endosymbiotic theory* of the origin of plastids. This theory, in essence, states that plastids were once free-living, *autotrophic* (having the ability to obtain carbon from carbon dioxide), prokaryotic cells that were engulfed through *phagocytosis* by an ancestral *heterotrophic* nucleated cell (a cell having a metabolism where carbon must be obtained from organic molecules) termed a *protoeukaryote*. Typically this engulfment would result in the ingestion and subsequent destruction of the engulfed prokaryotic cell. However, in one—or perhaps several—independent incidents, a symbiotic relationship was gradually established between the engulfed photosynthetic bacterium and the protoeukaryote. The captured bacterium provided an internal source of food production for the heterotrophic eukaryotic cell through photosynthesis. The bacterium, in turn, was provided with protection and a stable external environment in the cytosol of the eukaryotic cell.

To coordinate further the physiological and genetic interactions between the two, massive transfer of genes took place over time from the genome of the photosynthetic bacterium to the nuclear genome of the protoeukaryote, leading to the genetic capture and control of the photosynthetic endosymbiont. Recent investigations have shown that this gene transfer event is an ongoing process, with examples of transfer documented in recent evolutionary time for both plastids and mitochondria in several different evolutionary lineages of flowering plants.

Pat Calie

See also: Algae; Anaerobic photosynthesis; Bacteria; Brown algae; C_4 and CAM photosynthesis; Calvin cycle; Cell theory; Cytoplasm; Diatoms; Eukaryotic cells; Evolution of plants; Extranuclear inheritance; Gas exchange in plants; Green algae; Mitochondria; Photorespiration; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Plant cells: molecular level; Plant tissues; Prokaryotes.

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CHROMATIN

Categories: Cellular biology; genetics; reproduction and life cycles

Chromatin is an inclusive term referring to DNA and the proteins that bind to it, located in the nuclei of eukaryotic cells. The huge quantity of DNA present in each cell must be organized and highly condensed in order to fit into the discrete units of genetic material known as chromosomes. Gene expression can be regulated by the nature and extent of this DNA packaging in the chromosome, and errors in the packaging process can lead to genetic disease.

Scientists have known for many years that the hereditary information within plants and other organisms is encrypted in molecules of *deoxyribonucleic acid* (DNA) that are themselves organized into discrete hereditary units called *genes* and that these genes are organized into larger subcellular structures called *chromosomes*. James Watson and Francis Crick elucidated the basic chemical structure of the DNA molecule in 1952, and much has been learned since that time concerning its replication and expression. At the molecular level, DNA is composed of two parallel chains of building blocks called *nucleotides*, and these chains are coiled around a central axis to form the well-known *double helix*.

Each nucleotide on each chain attracts and pairs with a complementary nucleotide on the opposite chain, so a DNA molecule can be described as consisting of a certain number of these nucleotide base pairs.

The entire human genome consists of more than six billion base pairs of DNA, which, if completely unraveled, would extend for more than 2 meters. It is a remarkable feat of engineering that in each human cell this much DNA is condensed, compacted, and tightly packaged into chromosomes within a nucleus that is less than 10^{-5} meters in diameter. Plants typically have larger genomes than humans; for example, wheat has fifteen billion base pairs of DNA. By contrast, the most widely studied plant among current scientists is *Arabidopsis*. The species *Arabidopsis thaliana* was selected as a model organism in plant research because of its comparatively simple structure: Its 26,000 genes make up "only" 125 million base pairs.

What is even more astounding is the frequency and fidelity with which this DNA must be condensed and relaxed, packaged and unpackaged, for replication and expression in each individual cell at the appropriate time and place during both development and adult life. The essential processes of DNA replication or gene expression (*transcription*) cannot occur unless the DNA is in an open or relaxed configuration.

Chemical analysis of mammalian chromosomes reveals that they consist of DNA and two distinct classes of proteins, known as *histone* and *nonhistone* proteins. This nucleoprotein complex is called chromatin, and each chromosome consists of one linear, unbroken, double-stranded DNA molecule that is surrounded in predictable ways by these histone and nonhistone proteins. The histones are relatively small, basic proteins (having a net positive charge), and their function is to bind directly to the negatively charged DNA molecule in the chromosome. Five major varieties of histone proteins are found in chromosomes, and these are known as H1, H2A, H2B, H3, and H4. Chromatin contains about equal amounts of histones and DNA, and the amount and proportion of histone proteins are constant from cell to cell in all higher organisms, including the higher plants. In fact, the histones as a class are among the most highly conserved of all known proteins. For example, for histone H3, which is a protein consisting of 135 amino acid "building blocks," there is only a single amino acid difference in the protein found in sea urchins as compared with the one found in cattle. This is compelling evidence that histones play the same essential role in chromatin packaging in all higher organisms and that evolution has been quite intolerant of even minor sequence variations between vastly different species.

Nonhistones as a class of proteins are much more heterogeneous than the histones. They are usually acidic (carrying a net negative charge), so they will most readily attract and bind with the positively charged histones rather than the negatively charged DNA. Each cell has many different kinds of nonhistone proteins, some of which play a structural role in chromosome organization and some of which are more directly involved with the regulation of gene expression. Weight for weight, there is often as much nonhistone protein present in chromatin as histone protein and DNA combined.

Nucleosomes and Solenoids

The fundamental structural subunit of chromatin is an association of DNA and histone proteins called a *nucleosome*. First discovered in the 1970's, each nucleosome consists of a core of eight histone proteins: two each of the histones H2A, H2B, H3, and H4. Around this histone octamer is wound 146 base pairs of DNA in one and three-quarters turns (approximately eighty base pairs per turn). The overall shape of each nucleosome is similar to that of a lemon or a football. Each nucleosome is separated from its adjacent neighbor by about fifty-five base pairs of *linker DNA*, so that in its most unraveled state they appear under the electron microscope to look like tiny beads on a string. Portions of each core histone protein protrude outside the wound DNA and interact with the DNA that links adjacent nucleosomes.

The next level of chromatin packaging involves a coiling and stacking of nucleosomes into a ribbonlike arrangement, which is twisted to form a chromatin fiber about 30 nanometers in diameter, commonly called a *solenoid*. Formation of solenoid fibers requires the interaction of histone H1, which binds to the linker DNA between nucleosomes. Each turn of the chromatin fiber contains about twelve hundred base pairs (six nucleosomes), and the DNA has now been compacted by about a factor of fifty. The coiled solenoid fiber is organized into large domains of 40,000 to 100,000 base pairs, and these domains are separated by attached nonhistone proteins that serve both to organize and to control their packaging and unpackaging.

Loops and Scaffolding

Physical studies using the techniques of X-ray crystallography and neutron diffraction have suggested that solenoid fibers may be further organized into giant supercoiled *loops*. The extent of this additional looping, coiling, and stacking of solenoid fibers varies, depending on the cell cycle. The most relaxed and extended chromosomes are found at *interphase*, the period of time between cell divisions. Interphase chromosomes typically have a diameter of about 300 nanometers. Chromosomes that are getting ready to divide (*metaphase* chromosomes) have the most highly condensed chromatin, and these structures may have a diameter of up to 700 nanometers. One major study on the structure of metaphase chromosomes has shown that a skeleton of nonhistone proteins in the shape of the metaphase chromosome remains even after all of the histone proteins and the DNA have been removed by enzymatic digestion. If the DNA is not digested, it remains in long loops (10 to 90 kilobase pairs) anchored to this nonhistone protein scaffolding.

Impact and Applications

Studies on chromatin packaging continue to reveal the details of the precise chromosomal architecture that results from the progressive coiling of the single DNA molecule into increasingly compact structures. Evidence suggests that the regulation of this coiling and packaging within the chromosome has a significant effect on the properties of the genes themselves. In fact, errors in DNA packaging can lead to inappropriate gene expression and developmental abnormalities. In humans, the blood disease thalassemia, several neuromuscular diseases, and even male sex determination can all be explained by the altered assembly of chromosomal structures.

The unifying lesson to be learned from these examples of DNA packaging and disease is that DNA sequencing studies and the construction of genetic maps will not by themselves provide all the answers to questions concerning genetic variation and genetic disease. An understanding of genetics at the molecular level depends not only on the primary DNA sequence but also on the three-dimensional organization of that DNA within the chromosome. Compelling genetic and biochemical evidence has left no doubt that the packaging process is an essential component of regulated gene expression.

Jeffrey A. Knight

See also: Chromosomes; DNA: historical overview; DNA in plants; DNA replication; Genetic code; Mitosis and meiosis; Model organisms; Nucleic acids; RNA.

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CHROMATOGRAPHY

Category: Methods and techniques

Chromatography is a method of separating the components of a mixture over time. Chromatography has allowed for the discovery of many specialized pigments, including at least five forms of chlorophyll.

Chromatography was first described in 1850 by a German chemist, Friedlieb Ferdinand Runge. It was not until the early twentieth century, however, that Mikhail Semenovich Tsvet became the first to explain the phenomenon and methods of this analytical tool.

Chromatography and Photosynthesis

Tsvet's chromatography of plant leaf pigments prompted scientific investigations of photosynthesis—the all-important biochemical reaction that transforms inorganic to organic energy and therefore is at the base of most life. Chromatography has revealed that many different *pigments*, not only green ones, are simultaneously present in leaves. Each pigment absorbs only certain colors of light from sunlight, rather than absorbing all the incident light energy that falls upon it. Each pigment behaves as though it has a tiny "window" that allows the energy of certain wavelengths of light to be harvested. These little bundles of energy are *quantized*, or set, amounts of energy, and they are unique for each different type of pigment. (White sunlight is actually composed of a broad range of wavelengths, with the visible wavelengths appearing as a rainbow of colors when passed through a prism.)

Paper chromatography has allowed for the discovery of many specialized pigments, including at least five forms of *chlorophyll*. Chlorophyll pigments are now known to include chlorophylls *a* through *e*. Also, many different forms of *carotenes* and *xanthophylls* exist. Paper chromatography reveals that red and yellow pigments are always present in the leaves of deciduous trees and shrubs and not just during the fall color change. Because of the high abundance of the green chlorophyll pigments, as compared with the bright reds of carotenes or yellows of xanthophyll, only the dominant green hues are generally seen. In the fall, deciduous trees show a loss of chlorophyll pigments, thereby revealing the brilliant foliage associated with an autumn forest.

Once pigments are separated from one another, they can be chemically characterized and further studied. Carotenes and xanthophylls have been discovered to be of similar chemical composition, with each being made of forty carbon atoms covalently bonded to one another. Different arrangements of these covalent bonds produce the different colors of red and orange.

Chromatography has allowed scientists the opportunity to trace the path that carbon atoms follow through every tiny increment of the photosynthetic process. Paper chromatography, coupled with radioisotopic studies of carbon-labeled (with radioactive carbon 14) compounds, eventually led to the ability to describe the carbon-containing products of each step in the series of reactions of photosynthesis. Today this pathway is called the *Calvin cycle*.

Methodology

A classical demonstration of chromatographic principles utilizes techniques that allow plant pigments to be isolated. Spinach leaves are an excellent tool for the identification of four pigments: chlorophyll *a*, chlorophyll *b*, carotene, and xanthophyll. The stationary phase is a piece of chromatography paper with a dried spot of the plant extract near one end. The mobile phase is an acetone-ligroin mixture, a nonpolar (hydrophobic) solvent mixture. The paper is placed with a small portion of the end with the pigment spot in the solvent, the mobile phase. As the acetone-ligroin mobile phase comes into contact with the paper, *capillary action* allows the liquid to travel upward, against gravity.

The mobile phase has a migrating moisture line, or leading line of wetness, which is called the solvent front. As the solvent travels over the spot, each of the pigments will travel with the mobile phase at different rates from the original spot. Some pigments will adhere to the paper more strongly than others, and thus travel shorter distances along the paper. Yellow-green chlorophyll *b* travels the least distance with the mobile phase. Chlorophyll *b* is a more polar (water-loving) pigment than the other pigments found in spinach extracts and is therefore more strongly attracted to the polar surface of the paper than to the nonpolar solvent.

The remaining pigments travel increasing distances with respect to chlorophyll *b*, beginning with blue-green chlorophyll *a*, followed by yellow-orange xanthophyll and, finally, the orange pigment of carotene. Carotene moves the farthest because it is the most nonpolar of the pigments and it is attracted more strongly to the acetone-ligroin mixture (mobile phase) than to the paper. This stronger, nonbonded interaction with the mobile phase indicates that carotene is the most nonpolar pigment found in spinach chloroplasts.

Once the solvent front is about half an inch from the top of the paper strip, the strip is removed from the chamber. A pencil line must be drawn immediately across the top of the strip to indicate how far up the paper the mobile phase traveled. The paper strip is then referred to as a *chromatogram*.

The *Rf value* is a numerical constant that is unique for each of the four pigments identified in spinach. The ratio of the distance each pigment travels, as compared with the distance traveled by the mobile phase (from the start to finish lines), will be unique to that pigment alone. Thus, chlorophyll *b* will not switch places with carotene on the chromatogram because of the unique interactions it has with the stationary and mobile phases. For this reason, the Rf values determined by the method described above can be generated repeatedly by anyone using this method.

Types of Chromatography

As performed by Runge and Tsvet, chromatography has evolved from the days of paper, chalk, and dyes into a computerized and versatile instrumentation requiring expert training and a significantly larger budget. *Thin-layer chromatography* (TLC) is useful in protein chemistry. The stationary phase of this method consists of thin gel applied to a plastic or glass plate (strip). Various gels can be used to coat the plate. Some coatings may be polar, while others may be nonpolar.

Column chromatography can look for the amounts and types of vitamins in food or diet supplement tablets. Pigments, steroids, alkaloids, and carbohydrates all can be identified and measured using an appropriate column-chromatographic system. Many recent advances in column chromatography now allow for isolation and purification of proteins, DNA, RNA, and many other biological molecules.

High-pressure liquid chromatography (HPLC) can purify biologically important enzymes from living systems without destroying the biological activity of the enzyme. In *gas chromatography* (GC), an inert gas such as helium or nitrogen flows through several feet of a packed and coiled column. The gas acts as the mobile phase by sweeping the sample through the column. The packing is often a solid material, but liquid-coated solid particles are also used. Paper chromatography continues be a popular method for analysis of plant pigments, dyes, inks, and food colorings. It is largely used, however, in academic settings to demonstrate the principles of chromatography.

Mary C. Fields

See also: Calvin cycle; Pigments in plants.

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CHROMOSOMES

Categories: Cellular biology; genetics; reproduction and life cycles

Chromosomes contain the genetic information of cells. Replication of chromosomes assures that genetic information is correctly maintained as cells divide.

The *genome* of an organism is the sum total of all the genetic information of that organism. In eukaryotic cells, this information is contained in the cell's nucleus and organelles, such as mitochondria and plastids. In prokaryotic organisms (bacteria and archaea), which have no nucleus, the genomic information resides in a region of the cell called the *nucleoid*. A chromosome is a discrete unit of the genome that carries many *genes*, or sets of instructions for inherited traits. Genes, the blueprints of cells, are specific sequences of deoxyribonucleic acid (DNA) that code for messenger ribonucleic acids (monas), which in turn direct the synthesis of proteins.

Each eukaryotic chromosome contains a single long DNA molecule that is coiled, folded, and compacted by its interaction with chromosomal proteins called *histone*. This complex of DNA with chromosomal proteins and chromosomal RNAs is *chromatin*. DNA of higher eukaryotes is organized into loops of chromatin by attachment to a *nuclear scaffold*. The loops function in the structural organization of DNA and may increase transcription of certain genes by making the chromatin more accessible.

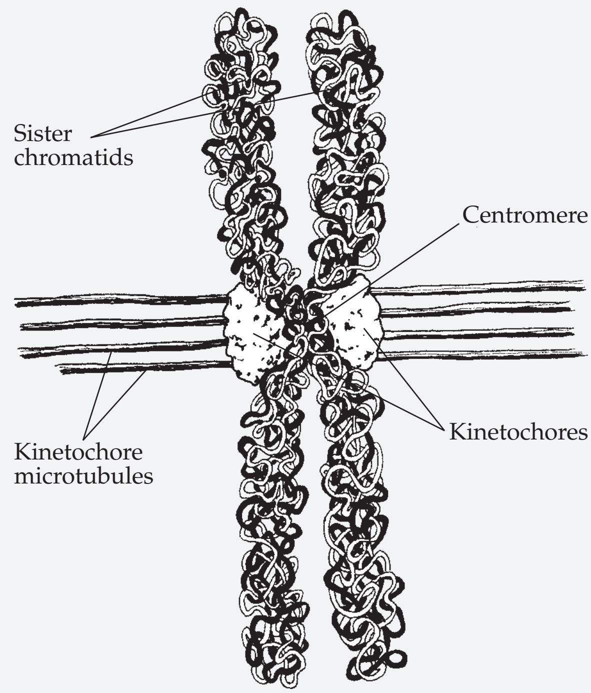
To maintain the genetic information of a cell, it is essential that chromosomes correctly replicate and divide as a cell divides. After DNA replication, chromosomes separate in a process called mitosis. During this process, the nuclear envelope breaks down and chromosomes condense into compact structures. A cellular structure known as the mitotic spindle forms, pulling pairs of replicated chromosomes apart so that the two cells receive identical sets of chromosomes.

Chromosomes are readily visualized when they condense during cell division. All the chromosomes of a cell visualized during mitosis constitute that cell's *karyotype*. Each chromosome has a *centromere*—a constricted area of the condensed chromosome where the mitotic or meiotic spindle attaches to assure correct distribution of chromosomes during cell division—and a *telomere*, the end or tip of a chromosome, which contains tandem repeats of a short DNA sequence.

The number of chromosomes in a gamete (either egg or sperm) is the *haploid* number, n. The haploid number of chromosomes in humans is 23; in corn, 10; in peas, 7; in *Arabidopsis* (the model organism used in much botanical research), 4. Some carp and some ferns have more than 50 chromosomes in the haploid genome. Pollen grains of some plants, such as pear, contain three haploid cells: One directs the growth of the pollen tube down the style to the ovary; the other two are sperm. In flowering plants (angiosperms), there is a unique double fertilization whereby one sperm nucleus fuses with the egg nucleus to form the diploid ($2n$) zygote, and the other sperm nucleus fuses with two polar nuclei to form the triploid nutritive tissue, or *endosperm*, which will nourish the embryo in the seed. The zygote then increases in cell number by *mitosis*, a type of cell division during which chromosomes in a nucleus are replicated and then separated to form two genetically identical daughter nuclei. This is followed by *cytokinesis*, the process of cytoplasmic division, which results in two daughter cells, each having the same number of chromosomes and genetic composition as the parent cell. The mature $2n$ plant forms the haploid (n) gametes by *meiosis*, a type of cell division that reduces the number of chromosomes to the haploid number.

A distinctive feature of plant cell division is the plant cell has three genomes (the nuclear, mitochondrial, and plastid genome) to replicate and divide. The chromosomes of eukaryotes consist of unique genes among a complex pattern of repeated DNA sequences. *Arabidopsis* has only 4 chromosomes containing about 120 million base pairs. There are typically between twenty and one hundred copies of the mitochondrial genome per mitochondrion, ranging in size from two hundred to twenty-four hundred kilobase pairs (or kb; one kilobase pair equals one thousand base pairs). Plant mitochondrial genomes are much larger than the mitochondrial genomes of yeast or animals. Chloroplast genomes range in size from 130 to 150 kb, with 50 to 150 copies of that genome per plastid.

Schematic of a Chromosome



Kimberly L. Dawson Kurnizki

In cell division in plant cells, the two daughter nuclei are partitioned to form two separate cells by a cell plate that grows at the equator of the mother cell. In animal cells, this separation involves the constriction of the cell at a central contractile ring. DNA replication is strictly controlled during the cell cycle. DNA synthesis occurs in the synthesis (S) phase, beginning at origins of replication distributed around the genome, occurring on average every 66 kb in dicotyledonous plants and on average every 47 kb in monocotyledonous plants. *Heterochromatin* is the term for regions of chromosomes that are permanently in a highly condensed state, are not transcribed, and are late-replicating. Heterochromatin contains highly repeated DNA sequences. *Euchromatin* is the rest of the chromosomes that is extended, accessible to RNA polymerase, and at least partially transcribed.

Some plants and animals have extra chromosomes that do not seem to be essential. These are called accessory or *supernumerary chromosomes*. They have been most studied in corn where these extra chromosomes are called *B-chromosomes*. B-chromosomes are usually highly condensed heterochromatin that may or may not be present in an individual of that species.

An increase in the copy number of the genome is common in plants and animals, occurring during the development of individuals. *Polyploids* have three or more complete sets of chromosomes in their nuclei instead of the two sets found in *diploids*. For example, in *Arabidopsis*, tissues of increasing age have an increase in polyploidy, reaching up to sixteen duplications.

Susan J. Karcher

See also: Cell cycle; Chloroplasts and other plastids; Chromatin; Cytoplasm; DNA: historical overview; DNA in plants; DNA replication; Eukaryotic cells; Genetic equilibrium: linkage; Genetics: mutations; Genetics: post-Mendelian; Mitochondria; Mitosis and meiosis; Nucleic acids; Nucleus; Reproduction in plants.

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CHRYSOPHYTES

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

The Chrysophyceae*, classified within the kingdom* Chromista*, are mostly unicellular or colonial organisms found in fresh and salt water throughout the world.*

The *Chrysophyceae* (in some systems corresponding to the phylum *Chrysophyta*) are related to heterokont algae and include more than eight hundred described species that are classified in approximately one hundred genera. They are most closely related to the *Synurophyceae* and other pigmented heterokont algae, including the *Bacillariophyceae* (diatoms), *Eustigmatophyceae*, *Phaeophyceae* (brown algae), and *Xanthophyceae* (yellow-green algae), among others. The classification of chrysophycean species remains in a state of flux. In one system of classification primary importance is placed upon the number of flagella (zero, one, or two) that are present in the motile cell stage. A second classification organizes species based upon the predominant vegetative state of the organism. For example, in this classification amoeboid, coccoid, palmelloid, and flagellate species are assigned to separate orders.

Ecology and Diversity

Chrysophytes are predominantly found in freshwater environments, although some are marine, and a few are reported from soil or snow. Members of the group are widely distributed but are most common in cold-temperate lakes, ponds, bogs, and ditches. Some species are common members of the phytoplankton, whereas others are epibionts or are neustonic (attached to the surface film of quiet water). Other species are only rarely observed.

Most chrysophytes are free-swimming unicellular or colonial flagellates. Others are coccoid (that is, immobile, walled unicells), amoeboid, or palmelloid (with cells enveloped in a gelatinous matrix). A few species are parenchymatous.

Cell Walls

Most chrysophytes lack a cell wall, but others produce species-specific outer coverings of scales or loricae. For example, complex siliceous scales or spines that are produced in silica deposition vesicles cover the cells of *Paraphysomonas*. The scales of *Chrysolepidomonas* are organic and of two types: those that are dendritic (tree-shaped) and those that are canistrate (cylindrical). The cells of other species may be enclosed within an organic vaselike or flasklike lorica composed of cellulose and proteins or chitin (for example, *Dinobryon*, *Pseudokephyrion*, *Poteriochromonas*, *Lagynion*, and *Stenocalyx*). In such species the lorica is typically composed of fine, interwoven fibrils. In *Dinobryon* these fibrils are helically arranged and secreted as the cell rotates about its longitudinal axis. In contrast, the loricae of *Epipyxis* species are composed of imbricate, overlapping scales. The posterior pole of the cell is typically positioned at the base of the lorica and may be attached by a fine cytoplasmic extension; the flagella protrude externally through the lorica opening.

Flagella

Chrysophytes are heterokont, biflagellate organisms that swim with at least one flagellum forwardly directed. The two flagella of motile cells are anteriorly inserted in an apical or subapical position and are unequal in length. The flagella differ morphologically and are heterodynamic. In most species, the basal bodies from which the flagella arise are either oriented at an acute angle to one another or are perpendicular to one another.

In *Hydrurus*, *Chromphyton*, and *Lagynion*, the basal bodies form an obtuse (oblique) angle with respect to one another. The long (immature) flagellum is anteriorly directed and is ornamented with two rows of mastigonemes and finer lateral filaments. Each mastigoneme is composed of a base, a tubular shaft, and one to three terminal filaments; these are known as tripartite tubular hairs. Mastigonemes are produced in the perinuclear space between the two outer membranes of the chloroplast and the two surrounding membranes of the chloroplast endoplasmic reticulum (see below). The long flagellum beats in an undulatory, sine-wave-like motions that are initiated at the base of the flagellum. The relatively stiff short (mature) flagellum is directed laterally or posteriorly, lacks mastigonemes, and rotates helically. A distinct swelling associated with the eyespot is typically present at the proximal base of the smooth flagellum.

In some taxa (such as *Chromulina*, *Chrysococcus*, and *Sphaleromantis*), the short flagellum is highly reduced and may be nonemergent; it is therefore undetectable by light microscopy. In a handful of species the short flagellum is entirely absent, although the mature basal body may persist within the cell. Naked motile cells bearing two visible flagella are often referred to as *Ochromonas*-like (or ochromonadalean), whereas those with one visible flagellum are typically assigned to the genus *Chromulina*.

The transitional region between the basal body and flagellum contains an electron-dense transitional plate, above which lies a coiled, apparently springlike transitional helix. The functions of the transitional plate and helix, which are also found in other flagellates, are uncertain.

In heterotrophic and mixotrophic species, the flagella play a role in prey capture. Particles actively captured by the flagella that are recognized as food are pushed into a feeding basket; those not recognized as food are released. The feeding basket is formed and closed by movements of underlying microtubules (see below). Water currents produced by the undulation of the long flagellum may passively bring food particles in contact with the cells that, in some species, are collected by pseudopodia.

Cell Organization

Cells possess a single pear-shaped nucleus that is positioned at the anterior end of the cell. The narrow end of the nucleus typically lies close to the basal bodies. A prominent Golgi apparatus with distended cisternae lies against the nucleus. Contractile vacuoles (absent in some marine forms) are also found at the anterior end of the cell.

One or more mitochondria with tubular cristae are present in the cell. Because the mitochondria are usually long and coiled, the actual number of mitochondria present is difficult to discern. Fibrous bands, sometimes referred to as connecting fibers, connect the basal bodies to one another. A cross-striated band of fibers known as the rhizoplast extends from the basal apparatus and forms a connection to the nucleus. Typically four microtubular roots (R1, R2, R3, and R4) originate near the basal bodies, take characteristic paths through the cell, and proliferate beneath the plasmalemma. For example, in most species roots R3 and R4 often form a loop beneath the short flagellum. Other microtubules are nucleated from the four major roots that provide the cytoskeletal elements needed to maintain cell shape.

Muciferous bodies or discobolocysts are present in some species. Muciferous bodies are capable of extruding long threads, whereas discobolocysts forcefully eject discoid projectiles. These functions of these organelles have been little studied but may be involved in prey capture or predator avoidance.

Nutrition

The *Chrysophyceae* employ a variety of means to obtain energy. Most chrysophytes are photosynthetic but require an exogenous source of vitamins (such as vitamin B_{12}, biotin, and thiamin) for growth. It is probable that all chrysophytes are opportunistically or facultatively osmotrophic; that is, they are capable of directly absorbing small inorganic or organic molecules (such as sugars and amino acids) from the surrounding medium. Several species, particularly those with leucoplasts, are obligate heterotrophs that are bactivorous or consume small organic particles. Mixotrophic species are also well represented among the chrysophytes. This category includes photosynthetic species that, routinely or under unfavorable conditions, supplement their nutrition via phagotrophy.

Chloroplasts, Photosynthetic Pigments, and Storage Products

The chloroplasts of chrysophytes are typically golden-brown or yellow-green in color, and there are usually one to two chloroplasts per cell. Chloroplasts are peripherally located, and pyrenoids may be present or absent. Four unit membranes surround each chloroplast; the outer two are derived from the endoplasmic reticulum and are typically continuous with the nuclear envelope. Chloroplast lamellae are typically composed of three adpressed thylakoid membranes, and a girdle lamella, which completely encircles the chloroplast, is usually present. The chloroplast deoxyribonucleic acid (DNA) is ring-shaped and lies just beneath the girdle lamella.

The light-harvesting complex of chrysophytes contains chlorophylls *a* and *c*, beta-carotene, and the xanthophylls fucoxanthin, neoxanthin, violaxanthin, and zeaxanthin. Among these, fucoxanthin is dominant and is therefore responsible for the golden-brown color observed in most chrysophytes.

The major product of photosynthesis is a water-soluble o-1,3-linked glucan (known as chrysolaminarin or leucosin) that is stored in cytoplasmic vacuoles in the posterior region of the cell. Lipids may also be produced and are also stored in the cytoplasm.

Eyespots (or stigmata) are present in many, but not all, species. The eyespot takes the form of a single layer of orange or reddish colored, lipidlike droplets that are located just beneath the chloroplast membrane. These droplets lie near a swelling located at the base of the smooth (short) flagellum; together the eyespot and flagellar swelling form a photoreceptor apparatus.

Several chrysophyte genera are known that contain a vestigial chloroplast (leucoplast) that lacks pigments (including *Anthophysa*, *Monas*, *Oikomonas*, *Paraphysomonas*, and *Spumella*).

Reproduction

Asexual reproduction in amoeboid and flagellate species occurs by longitudinal division of the cell; fragmentation is common among colonial, palmelloid, and parenchymatous species. In coccoid species reproduction may proceed via cell division or the formation of autospores that rupture and exit the parent cell wall. Some taxa, such as the parenchymatous genera *Phaeodermatium* and *Hydrurus* or members of the palmelloid family *Chrysocapsaceae*, reproduce by means of flagellated swarmers (zoospores).

Under certain environmental conditions, silicified resting cysts, or statospores, are produced by many species. Statospores are formed endogenously, are roughly spherical or ellipsoidal, and have walls that may be smooth or ornamented. The stomatocyst opening (porus) may be simple, possess a thickened collar, or take the form of a narrow neck. The cyst wall is formed by the deposition of silicate on an internal membrane, and the porus is preformed or produced by resorption of a portion of the cyst wall. Depending on the species, cytoplasm located outside the cyst wall may or may not be absorbed through the porus, which at maturity is occluded by a pectic plug. During excystment the plug is lost, and one or more amoeboid or free-swimming flagellate cells emerge.

Sexual reproduction is known only in a handful of species. In those cases observed, vegetative cells behave as gametes and fuse apically. The resulting quadriflagellate cell (planozygote) will encyst forming sexually derived binucleate hypnozygotes or stomatocysts. It is presumed that karyogamy (nuclear fusion) and meiosis occur within the cyst, but these processes have yet to be studied. Depending upon the species, sexual stomatocysts may give rise to one, two, or four vegetative cells.

J. Craig Bailey

See also: Algae; Brown algae; Cryptomonads; Diatoms; Dinoflagellates; Flagella and cilia; Haptophytes; Heterokonts; Phytoplankton; Photosynthesis; *Protista*.

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CHYTRIDS

Categories: Fungi; taxonomic groups; water-related life

Chytrids are fungi in the phylum Chytridiomycota. *They have motile spores and are primarily aquatic organisms.*

Like all fungi, chytrids live in their food and have an absorptive mode of nutrition in which they secrete digestive enzymes and absorb the breakdown products. Chytrids also have cell walls made of chitin, make the amino acid lysine via the amino adipic acid (AAA) pathway, and possess a ribosomal DNA (deoxyribonucleic acid) sequence that places them more closely with other fungi than with any other group of organisms. The feature that sets them apart from other fungi is the possession of a motile zoospore. All other fungi produce spores without flagella.

Characteristics

A posteriorly oriented, whiplash-type flagellum is the feature that unites all the organisms in the division *Chytridiomycota* within the kingdom *Fungi*. As absorptive heterotrophs, they live either as *saprophytes*, growing on dead organic matter, or as parasites in living plants, other fungi, insects, or algae. The vegetative organism may take the form of a spherical structure, with or without branching rhizoids, on the surface of substrate or host or may send mycelial threads through the material in which it is living. Asexual reproduction occurs by a variety of means described below. Sexual reproduction is known to exist in several types of chytrids and in some species involves the alternation between a gamete-producing phase and a spore-producing phase.

The sporangia that produce the motile zoospores develop in a variety of ways. Two features are used to characterize development: the fate of the nucleus upon encystment of the zoospore and the number of zoosporangia produced from a single zoospore. The three most common types of thallus development are endogenous-monocentric, exogenous-monocentric, and exogenous-polycentric. Endogenous-monocentric development occurs when the zoospore nucleus stays within the encysted zoospore wall, undergoes mitosis, and produces a single zoosporangium. Exogenous-monocentric development occurs when the zoospore nucleus migrates into the germ tube, undergoes mitosis, and produces a single zoosporangium. Exogenous-polycentric development occurs when the zoospore nucleus migrates into the germ tube, undergoes mitosis, and spreads to many locations for zoosporangium production.

The phylum-defining zoospore may be one of four basic morphological types. Though the types are determined by electron microscope, the morphological type can be recognized using light microscopy with experience. The four morphological types are the basis of classification at the ordinal level as described below.

Ecology and Habitats

Because chytrids are absorptive heterotrophs, they grow in their food, digesting complex food molecules and absorbing the simpler breakdown products. When growing in dead material, these fungi are saprophytes and are decomposing organisms in ecosystems. Because the zoospore requires water for dispersal, these fungi are found in aquatic environments. However, they also can be found in soils that are wet with soil water. Chytrids also can live within living organisms as parasites, causing major declines in populations. The gut chytrids, *Neocallimastigales*, live in the rumina (stomachal cavities) of herbivorous mammals.

Taxonomy

There are approximately eight hundred species of chytrids, arranged in five orders. Taxonomy of the different orders is based on the ultrastructure of the zoospore. Ultrastructure features used in taxonomy include the presence or absence of a connection between the nucleus and the kinetosome by microtubules; whether ribosomes are dispersed or collected into a mass surrounded by membranes; the degree of organization of the microbody-lipid complex (MLC); the location and number of lipid globules; and presence or absence of a rumposome—a honeycomblike organelle of unknown function. The main characteristics of the five orders are described below.

Chytridiales. During examination of the main features of the zoospore—lipid globule, microbody, mitochondria, and nucleus—the nucleus seems to occupy whatever space is left over within the zoospore. Rootlet microtubules are located within the plasma membrane connecting the kinetosome to the rumposome. Ribosomes are gathered in the center of the cell, enclosed within membranes. In the MLC, the posteriorly located lipid globules are in close association with the microbody, mitochondrian, and rumposome.

Spizellomycetales. The nucleus of the zoospore is close to the kinetosome or, if separated, is connected to it via microtubules or a rhizoplast. Rootlet morphology is variable, and ribosomes are scattered throughout the cytoplasm. The MLC has a loose association of the microbody and lipid at the anterior end of the zoospore with the mitochondria located toward the rear. There is no rumposome. Ribosomes are dispersed throughout the zoospore.

Neocallimastigales. *Neocallimastix* and other genera of the order are uniflagellate or multiflagellate and live in the rumen of herbivorous mammals. Because they live in this unique environment, rumen chytrids are obligate anaerobes. The zoospores lack any of the MLC organelles and the rumposome. All these anaerobic fungi are cellulolytic and digest plant cell walls of the food upon which sheep and cattle feed.

Monoblepharidales. The zoospores have a centrally located nucleus that is not connected to the kinetosome. Microtubules extend randomly into the cytoplasm from the kinetosome. The MLC has a rumposome in close association with a microbody and anteriorly located lipid globules. The ribosomes are centrally located, surrounding the nucleus. These fungi have a mycelial growth form and reproduce sexually by producing a motile male cell and a nonmotile egg cell.

Blastocladiales. A nuclear cap consisting of ribosomes encased within a membrane located anteriorly to a cone-shaped nucleus and a single large mitochondrian with a side body complex are the two most distinctive features of these fungi. Some of these fungi produce mycelial growth forms, whereas others produce the saclike zoosporangium with rhizoids.

Evolutionary History

Evolutionary history of the chytrids can be traced back to the Pennsylvanian period through fossil evidence. Sequential analysis of the small subunit ribosomal DNA gene from fifty-four chytrids indicates that the *Chytridiomycota* are related to other fungi and that there are natural groups within the division: *Blastocladiales*, *Monoblepharidales*, and *Neocallimastigales*. Despite the diversity of the data, the monophyletic nature of the *Chytridiales* and *Spizellomycetales* is not rejected. The DNA groupings closely resemble groupings based on zoospore ultrastructure.

Representative Organisms

Allomyces is a mycelial member of the *Blastocladiales*, which is interesting because it has an alternation of generations between a gamete-producing thallus (gametothallus) and a spore-producing thallus (sporothallus). In all organisms with alternation of generations, the gametothallus produces gametes by mitosis in gametangia. The gametes are distinguished by size, the male being smaller than the female. The motile male gamete is chemotactically attracted to the hormone sirenin, which is produced by the female gametes and enables fertilization. Upon fertilization, the zygote nucleus undergoes mitosis as the germ tube develops into mycelia without crosswalls. The dichotomously branched mycelia of the sporothallus produce two types of sporangia. The thin-walled sporangia produce diploid spores by mitosis. These diploid zoospores are responsible for increasing numbers of *Allomyces* in its habitat.

The sporothallus also can produce a thick-walled sporangium capable of withstanding harsh environmental conditions. Zoospores in this sporangium are produced by meiosis. When these haploid zoospores geminate, the nucleus divides by mitosis and spreads throughout the dichotomously branched mycelia. The life cycle of the fungus now is completed.

Batrachochytrium is interesting because it parasitizes frogs. Within the last decade, declines in populations of frogs around the world have been described. *Batrachochytrium dendrobatidis* is responsible for this chytridiomycosis in amphibians, including salamanders.

Blastocladiella is a developmental biology tool. The thallus has the exogenous, monocentric developmental pathway resulting in a rhizoidal system with a single thin-walled, colorless sporangium or a single thick-walled, resistant sporangium. The chemical environment of the developing thallus determines which sporangium is produced. High carbon dioxide levels favor the development of the thick-walled sporangium. This shift from a thin-walled sporangium pathway to a thick-walled sporangium pathway has been traced to a disruption of the Krebs cycle. This organism is one of a few nongreen organisms in which light promotes the growth of the organism.

Coelomomyces is a mycelial member of the *Blastocladiales* that parasitizes invertebrate animals. Coelomomyces alternates between a haploid gametothallus and a diploid sporothallus. The unique feature of *Coelomomyces* is that each phase is specific for a different host. The diploid sporothallus parasitizes mosquitoes and grows as wall-less mycelia within the hemocoel of the mosquito larvae. *Coelomomyces* has been studied as a possible mycoinsecticide against mosquitoes. Difficulty in using *Coelomomyces* as a mycoinsecticide occurred until the discovery of the fact that an alternate host was required to achieve completion of the life cycle. The zoospores produced by the thick-walled sporangium within the mosquito are produced by the process of meiosis and are haploid. The haploid zoopore must infect a microcrustacean copopod or ostracod in order for the gametes to be produced. The haploid zoospore develops into the gametothallus, which produces the motile gametes. The resulting zygote will infect mosquito larvae, completing the life cycle.

John C. Clausz

See also: Flagella and cilia; Fungi; Krebs cycle.

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CIRCADIAN RHYTHMS

Categories: Movement; physiology

Circadian rhythms in plants are phases of growth and activity that appear in regular, approximately twenty-four-hour, cycles.

Biological activities that cycle in approximately twenty-four-hour intervals are called circadian rhythms (from the Latin *circa*, meaning "about" and *dies*, meaning "a day"). Circadian rhythms allow plants to anticipate environmental cycles and to coordinate their activities with them. Circadian rhythms are not simply responses to changing external conditions, as they continue even when a plant is placed under constant conditions. This continuation indicates that circadian rhythms are controlled by endogenous (internal) timing mechanisms, collectively referred to as the *biological clock*.

Digital Stock

Many plants, such as these California poppies, open their flowers in the morning and close them at night. These cycles are important for timing pollen availability with the activity of insect, bird, and mammal pollinators. It is essential that flowers of the same species be open at the same time of day or night to promote outcrossing that results in increased genetic variation.

Plant circadian rhythms include cycles in gene regulation, enzyme activity, leaf movements, flower opening, and stomatal opening. Circadian rhythms also interact with photoperiodism in the control of major developmental processes, such as dormancy and the induction of flowering.

History

In 1729 the French astronomer Jean-Jacques Dortous de Mairan discovered the endogenous nature of circadian rhythms when he looked at the sleep movements of leaves of the sensitive plant, *Mimosa*, known as *nyctinastic leaf movements*. Mimosa leaves fold closed at night and open during the day. It had been thought that these leaf movements occurred in response to external cycles of light and darkness. De Mairan examined the plants under constant environmental conditions and discovered that the nyctinastic movements of the leaves continued. This was the first description of a biological activity with an endogenous circadian rhythm. Current models for how plants accomplish circadian rhythms are divided into three parts: entrainment, biological clock, and output pathways.

Entrainment

The synchronization of circadian rhythms to the cycles of the outside world is accomplished via input pathways and is referred to as *entrainment*. In nature, circadian rhythms are entrained primarily by light or temperature cycles to have periods of twenty-four hours. It is essential that circadian rhythms be entrained, because without synchronization of the biological clock with environmental cycles, the advantages of circadian rhythms would be lost.

Biological Clock

The biological clock is also referred to as the central oscillator and the pacemaker. It is endogenous and self-sustaining. Although circadian rhythms are entrained by external stimuli, they continue in the absence of external cycles. Under artificially constant conditions, circadian rhythms do not maintain twenty-four-hour periods but revert to free-running periods that are usually between twenty-one and twenty-seven hours. The molecular mechanisms of the biological clock remain unknown, but they are thought to include autoregulatory feedback mechanisms.

An interesting feature of the biological clock is that the free-running period is generally insensitive to changes in temperature. Most chemical and biological processes are affected by temperature changes; higher temperatures make them go faster, and lower temperatures make them go slower. That the biological clock is able to compensate for temperature changes and maintain timekeeping functions is important to plants experiencing extreme changes in temperature.

Output Pathways

The *output pathways*, or "hands" of the biological clock, are the measurable rhythms exhibited by the plant. Known circadian rhythms range from the subcellular level to the cell and tissue level to the developmental level.

Subcellular Level

Subcellular circadian rhythms include cycles in gene regulation (at the levels of transcription, transcript abundance, translation, and post-translational modification), calcium signaling, and enzyme activity. One well-characterized rhythm is the rate of carbon dioxide assimilation in plants with CAM (crassulacean acid metabolism) photosynthesis. Such plants open their stomata at night to allow for gas exchange, fixing carbon dioxide into an organic acid that is stored in the vacuole. During the day, the plants close their stomata (presumably to conserve water) and continue photosynthesis using carbon dioxide released from the organic acids. The circadian rhythm of carbon dioxide assimilation in CAM plants is controlled by rhythmic changes in the activity of the enzyme (PEP carboxylase) that fixes carbon dioxide into the organic acid.

Cell and Tissue Levels

Cell- and tissue-level circadian rhythms include those controlled by cycles in cell expansion and contraction, such as the obvious rhythms of leaf and petal movements and the opening and closing of stomata. Leaf movements are brought about by a cycling in the expansion and contraction of specialized cells in a region at the base of the leaf that is called the pulvinus. Nyctinastic leaf movements presumably allow a plant to maximize light interception for photosynthesis.

Many plants open their flowers in the morning and close them at night. Other plants open their flowers in the afternoon (such as the four o'clocks, *Mirabilis jalapa*), in the evening (evening primrose, *Oenothera biennis*), or even at night (the bat-pollinated cactus *Cereus*). These cycles are important for timing pollen availability with the activity of insect, bird, and mammal pollinators. It is essential that flowers of the same species be open at the same time of day or night to promote outcrossing that results in increased genetic variation.

Circadian cycles of stomatal opening and closing allow a plant to balance carbon dioxide uptake with water loss. Plants with CAM photosynthesis open their stomata at night, in contrast to plants that carry out C_3 and C_4 photosynthesis, which open their stomata during the day. Other known tissue-level circadian rhythms include hypocotyl elongation, nectar secretion, and hormone synthesis.

Developmental Level

Developmental processes that depend on interactions with circadian rhythms and the biological clock include the photoperiodic control of flowering and dormancy. These photoperiodic responses rely on the ability of a plant to measure relative amounts of light and darkness within each twenty-four-hour period. It remains unknown whether one biological clock controls both photoperiodism and circadian rhythms.

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See also: C_4 and CAM photosynthesis; Dormancy; Flowering regulation; Gas exchange in plants; Heliotropism; Nastic movements; Photoperiodism; Photosynthesis; Tropisms.

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CLADISTICS

Categories: Classification and systematics; disciplines; methods and techniques

Cladistics is a quantitative method of classification of plants that attempts to recover evolutionary relationships, based on observable characters.

Since the dawn of history, humans have classified plants. In primitive cultures classifications were by economic use, such as food, clothing, medicine, and shelter. Later the form (morphology) of a plant became important, for example, trees, shrubs, or herbs. Carolus Linneaus considered the similarity of floral parts to be critical, and this formed the basis of his classification system. Each of these systems is said to be "artificial." That is, the classification was solely for a human purpose and did not attempt to indicate genetic relationships between plants. Since Charles Darwin, the goal of plant systematics has been to develop a "natural," phylogenetic classification, one that represents the natural relationships of each species to all others. Cladistics was developed as a method to construct phylogenetic classifications.

A Brief History

Three systems have evolved to aid systematists (scientists who study the phylogenetic relationships of organisms) in their work. Traditional *phylogenetics* was based on intuition and involved the "art and science" of character weighting. The scientist studied a group of plants and decided which characters he or she thought were important. Evolutionary relationships were then based on these characters. Individual bias led to disagreements that could not be resolved objectively.

Computer-assisted numerical approaches permitted systematists to employ a more objective methodology and analyze large quantities of data, gathered from a variety of sources that range from traditional morphology to the most sophisticated molecular techniques. The earliest attempt, *phenetics*, used computers to determine the degree of total similarity between taxa. Unfortunately, this ignored both parallel and convergent evolution.

The methods of cladistics were first formalized in the 1950's and 1960's by Willi Hennig. This approach requires three assumptions to be met: evolution occurs; evolution is monophyletic (that is, lineages derive from a common ancestor); and characteristics passed from generation to generation are either modified or not. Although phylogenetics is concerned with genealogical relationships, the latter cannot be observed; rather, they must be inferred from observable characters (morphological, biochemical, behavioral, and so on) in much the same way as one infers genotypes when constructing a family pedigree. Cladistics is a quantitative method that attempts to recover evolutionary relationships, based on observable characters, and presents the resulting phylogeny in the form of a treelike diagram called a *cladogram*.

When many different organisms are being classified and when many different characters are being analyzed simultaneously, alternative cladograms may result. The most parsimonious tree (the cladogram requiring the fewest evolutionary changes) is generally preferred, because it is assumed that the simplest pathway is the one most likely to reflect the evolutionary history of the plants being examined.

Constructing a Cladogram

The most important decision to make before beginning construction of a cladogram to represent the relationships among a group of plants is the choice of an appropriate *outgroup*. The outgroup cannot belong to the group of plants being analyzed, but it should be closely related. Much of the work of a phylogenetic study is determining an appropriate outgroup to be used for comparisons.

The next step involves construction of a *character matrix*. A character is any feature of a plant. It may be an observable morphological or biochemical feature or an ecological or physiological attribute. Every useful character will have more than one character state. For instance, the character "root type" may have the character states "taproot," "fibrous root," or "adventitious root."

Characters having a common origin are called homologous. Cladistic analysis recognizes two types of homologies: plesiomorphies and apomorphies. *Plesiomorphies* are considered to be the primitive state of a character; that is, the character is unchanged from the ancestral condition. Plesiomorphies are determined by comparison of the character states in the members of the taxa being investigated with the character state in the outgroup. A character state found in both the outgroup and the taxa being examined is considered to be plesiomorphic. Any modification of the character state is considered to be apomorphic; thus, *apomorphies* are derived from plesiomorphies. Apomorphies shared by two or more taxa are called synapomorphies. Identification of *synapomorphies*, assumed to be derived from increasingly recent common ancestors, provides the basis for constructing cladograms.

Qualitative Approach

The first step toward a qualitative approach to constructing a cladogram is to examine the character matrix and list groupings of taxa according to the apomorphic trait for each character. Next, one character to begin the tree is chosen. Any character will do, but it is simplest to begin with a character in which only the outgroup has the plesiomorphic state and all ingroup taxa share the same apomorphy. For instance, a conifer might be the outgroup for classifying flowering trees. The plesiomorphic reproductive structure would be a cone, and the synapomorphy shared by all ingroup members would be flowers. The tree would have the conifer at the base, with a single line extending to the right to a branch point (node) from which all ingroup members diverge. The character state "flower" would be placed on the line between the conifer and the node, indicating that the shared character state, flowers, evolved prior to the divergence of ingroup taxa from one another.

Next, a second character is added to the existing tree. For instance, the conifer and dicot trees would all share the plesiomorphic character of a taproot, but monocot trees, such as palms, would have fibrous roots. The tree should now be extended to the right to form a second node with the character state "fibrous roots" added to the new stem segment and the monocot trees branching off the second node. The monocot taxa diverged from each other after fibrous roots evolved. The dicots do not have fibrous roots, so they are diagramed at the node to the left of "fibrous roots." The tree is continued by the addition of one character at a time until all have been used.

Quantitative Approach

The qualitative approach becomes increasingly difficult as the number of taxa and number of characters are increased. The advantages of the quantitative approach are that the process can be automated and human bias can be minimized. The following example illustrates "by hand" the way computers can be programmed to produce a cladogram. The first step is to code the character matrix to produce a numerical matrix for analysis. Plesiomorphic characters in the data matrix are coded as 0; different apomorphic character states are coded as successive integers, 1, 2, 3, and so on.

The simplest cladogram consists of a Y-shaped diagram representing three taxa, two from the group being studied and a third being the outgroup. The outgroup is placed at the bottom and serves to "root" the tree. The two ingroup species are located at the top of each arm. The point where the two arms diverge is a node and represents the ancestral taxon derived from the outgroup that gave rise to both ingroup taxa—it represents the common ancestor of the ingroup taxa. A numerical algorithm computes what the character states of this ancestral species must have been.

Additional taxa can now be added to the cladogram, one at a time. A series of new trees are constructed in which the new taxon is added between each existing taxon and each existing node. There are three places a fourth taxon could be added to the simple tree: between the root and the node, between the node and the first ingroup taxon, and between the node and the second ingroup taxon. An algorithm computes which of the three possible trees is the most parsimonious, and this tree is used as the basis for adding the fifth taxon (in one of now five possible positions between the four existing taxa and the two nodes). This process is continued until all taxa have been added to the tree and the cladogram is complete.

Marshall D. Sundberg

See also: Coevolution; Evolution: convergent and divergent; Evolution of plants; Molecular systematics; Systematics and taxonomy; Systematics: overview.

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CLIMATE AND RESOURCES

Category: Environmental issues

Climate is described by the average of weather conditions at a place or in a region, usually recorded as both the mean and the extremes of temperature, precipitation, and other conditions. Resources are the factors and characteristics of the natural environment that people find useful, including climate, land, soil, water, minerals, and wild vegetation. Thus, climate itself is a resource, affecting the character of the plant life and other resources it supports.

The nature and distribution of wild vegetation are to a large degree the products of climate: the temperature, moisture, solar radiation, and other environmental conditions that characterize a region. The major global vegetation types that accompany forest, shrub, grassland, desert, rain forest, tundra, and other biomes reflect climatic controls.

Solar radiation is the basic determinant of climate. The sun's rays are vertical at some time of the year only in the tropics, between the Tropic of Cancer (23.5 degrees north latitude) and the Tropic of Capricorn (23.5 degrees south latitude). These lines determine where the greatest heat supply is found; regions poleward of about 40 degrees north and south latitudes actually have a net loss of reradiation to outer space and depend upon a heat supply from the tropics, which is carried poleward by the general circulation of the atmosphere. The general circulation is the average of wind flow at the surface of the earth and is driven by the surplus of solar radiation in the tropics.

Equatorial Climates

By definition, tropical climates do not experience freezing temperatures, have the least variation in length of day, and consequently experience the least "seasonality" of any latitudes. Seasons in the tropics are characterized more by precipitation contrasts—"dry" and "wet"—than by summer and winter temperatures. The greatest combination of heat and moisture resources on the earth's surface, especially important in creating the conditions under which tropical rain forests flourish, is near the equator.

The depth to which rock and soils are weathered and leached (mineral plant foods dissolved and removed by groundwater flow) is greater near the equator than elsewhere on the earth's surface. Continuous high temperatures work against carbon storage in the soils. Under wild vegetation conditions, where the rain forest canopy protects soils from raindrop impact, erosion rates are not as high as one would expect from the intense rain showers. On sloping land, however, the soils become saturated and flow downslope, often catastrophically in landslides. Where wild vegetation has been removed by human activity, such as farming or development of urban centers, erosion and mass wasting (landslides) are exacerbated during rainy seasons and cause considerable loss of life and property damage.

With increasing distance from the equator, the tropics experience more pronounced seasons, particularly in moisture resources. Precipitation totals decline, and *drought* risk increases. Dry seasons are expected annually because of the shifting of the general circulation of the atmosphere. The timing and extent of this shift determine whether a region experiences drought.

East and South Asia are most affected by shifting atmospheric circulation and the resulting wet and dry seasons. Africa also has pronounced wet and dry seasons. Droughts in this part of the world result in famine: An estimated one million people died in the Sahelian droughts of the late 1960's and 1970's. Thus climate must be defined both in terms of averages and of extremes. Extremes result in hazards that have dire consequences for the inhabitants of the affected region.

The probability of drought increases as precipitation averages decrease. Additionally, most tropical rainfall takes the form of intense thundershowers, which are spatially highly variable. One farm may be drenched by rain while its neighbors con-

The eastern sides of midlatitude landmasses are subject to intense summer storms.

tinue to be tormented by drought. In addition to drought risk on the margins of the tropics, a major climatic hazard is the tropical cyclone, also called a hurricane or typhoon. Cyclones rarely affect the equatorial zone but frequent the tropical transition to the subtropics and midlatitudes. Movement of tropical cyclones is easterly in their early and middle stages, following the general circulation known as the trade winds.

The Subtropics

The climates that exist in the *subtropics*, poleward of the tropics, depend on the side of the continent: West sides are *deserts* or subtropical *drylands*; east sides are the *humid subtropics*, a transition zone with cooler temperatures and more risk of frost with greater distance from the equator. The humid subtropics are subject to occasional easterly flow weather systems, including tropical cyclones. While cyclones represent a serious hazard, claiming both lives and property, these easterly systems also deliver moisture and thus reduce the possibility of drought. The generally warm temperatures and moist conditions make these climates some of the most productive for crop growth, exceeding the potential of the tropics.

In the subtropics, leaching of soils and high erosion rates on cleared fields are nearly as great a problem as in the tropics. The west coast drylands, which include all the world's major deserts—Sahara, Atacoma, Kalahari, Australian, and North American—are a consequence of the general circulation of the atmosphere, which in these locations makes the swing from the prevailing westerlies of the middle latitudes to the easterly trade winds. In the process, high atmospheric pressures prevail, and winds are descending or subsiding, and therefore warming—just the opposite of the conditions required for rainfall. Drylands may extend deep into the continents, as in North America and especially in Africa and Asia. The dryness of the Sahara blankets the Middle East and extends northward into Central Asia. Temperatures along the equatorward flank of these five major dryland zones are tropical, and where irrigation water is available, tropical plants may be grown. Most of the drylands are subtropical or midlatitude, and thus they experience frost as well as drought hazard. Weathering and erosion are appreciably less in the drylands, owing to the absence of moisture. Leaching of the soils is virtually absent. Instead, salts in the soils can build up (*salinization*) to levels that are toxic to most plants—another climate-related hazard.

The Midlatitudes

The *midlatitudes* extend from the subtropics to the polar climates of the Arctic and Antarctic. Temperatures follow a transition from warm on the equatorward flank to too cold for agriculture nearer the poles. This is the realm of the westerlies, with extratropical cyclones delivering most of the weather. It is a zone of contrasting conditions, year by year and day by day, ranging from warmer than average to colder than average, from too humid to too dry on the inland dryland border. The hazards of extreme temperature and precipitation often dominate life, as tropical and polar air masses converge to create the cyclones that march from west to east.

Drought risk is most important on the dryland border and results in the world's great grasslands. Summer heat may be a hazard on occasion. Nearly every winter brings storms with freezing rain, high winds, and heavy snowfalls, particularly on the eastern sides of the continents. The eastern sides are also afflicted with intense summer storms, such as the tornadoes of North America (a winter phenomenon in the adjoining humid subtropics) and the tail ends of hurricanes and typhoons, as these storms become caught up in westerly circulation and curve poleward again. The Arctic fringe of the midlatitudes is too cool for significant agriculture but yields the great subarctic forests of Canada, Scandinavia, and Russia.

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See also: Biomes: definitions and determinants; Biomes: types; Drought; Erosion and erosion control.

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CLINES

Categories: Ecology; ecosystems; genetics

A cline is one form of geographic variation in which characteristics of a species change gradually through the species' geographic range.

Many plant and animal species have populations that differ in terms of their morphological, physiological, and biochemical characteristics. A *species* is generally defined as a group of organisms that have the potential to interbreed and produce fertile offspring. A *population* is defined as a group of organisms which are actively interbreeding. The following example will clarify the relationship between species and populations and simultaneously introduce geographic variation.

Geographic Variation

The ponderosa pine (*Pinus ponderosa*) occupies a broad geographic range in western North America. Leaves (needles) of ponderosa pines in the Rocky Mountains are bundled into groups of two or three, and cones of these trees are more than 9 centimeters long. In contrast, leaves of ponderosa pines in southern Arizona and northern Mexico are bundled in groups of five, and their cones are less than 9 centimeters long. These differences constitute geographic variation which has developed because reproduction between Rocky Mountain ponderosa pines and Arizona-Mexican ponderosa pines was restricted because of geographic separation. Despite their differences, the two groups belong to the same species because they could produce fertile offspring if their geographic separation were overcome. However, they are members of different populations because they are not currently interbreeding. They are different populations of the same species.

Such geographic variation occurs in many species with broad geographic ranges and is often due to differences in the environmental conditions under which the separate populations exist. The different environments select for different genetic adaptations, resulting in hereditary variation. If such geographic variation occurs gradually over the range of the species, it is *clinal variation*.

Clinal Geographic Variation

In the foregoing example, the geographic variation is too abrupt to be considered clinal. However, ponderosa pines in the Sierra Nevada of California do show clinal geographic variation. The pines at the base of the mountains grow appreciably larger than the pines growing at the highest elevation on the mountains. The change in size is gradual; ponderosa pine trees become progressively smaller as elevation increases.

By taking seeds from trees at several elevations and planting them at the same elevation, scientists showed this size variation to be hereditary. Although all the trees were grown under the same conditions, the largest trees grew from the seeds collected at the base of the mountains, and tree size decreased as the elevation of seed origin increased. The advantages to being small in the relatively harsh environment of the high mountains and tall at the mountain base were important enough to code tree size into the trees' genes. The yarrow (*Achillea lanulosa*) and a number of other plant species show similar clinal variation with elevation in mountains.

In clinal variation, populations are not completely separated from one another, and individuals from adjacent populations do interbreed. However, reproduction between populations is not as common as reproduction between members of the same population. As a result, slight differences between adjacent populations are maintained.

Interestingly, in some clines members of the two extreme populations (the populations at the two ends of the cline) may not be able to interbreed and produce fertile offspring. They are still considered to be members of the same species because they exchange genes through the intermediate populations. The seaside goldenrod (*Solidago sempervirens*) illustrates this. It grows along the Atlantic coast of North America and displays a cline in flowering time. Canadian plants flower in August, plants in the middle Atlantic states flower in September and October, and those in Florida do so in November. These are genetically controlled flowering times, so even if grown together, the plants from Florida and Canada could not interbreed.

However, because Canadian plant flowering times overlap those in the northern United States (which overlap those in the central United States, which overlap those to their south, which overlap those in Florida), there is interbreeding between all adjacent populations and, indirectly, between the Canadian plants and the Florida plants. If the cline were to be subdivided into two or more species, where would the separations be drawn without separating interbreeding organisms into different species? The simplest solution is to consider all members of the cline to be members of the same species.

Local Clinal Variation

Great distances are not always required to establish clines. White clover (*Trifolium repens*), a European native which has been introduced all over the world, affords an example. Some white clover plants release cyanide when parts of the plant are eaten by grazers, such as snails and slugs. Others do not. The cyanide protects the plant from further grazing because it is toxic to the grazers. However, the cyanide-releasing form of clover suffers more frost damage than clover plants that do not release cyanide. Plants protect themselves from the cyanide by sequestering it into cellular compartments. Frost damage occurs when cyanide is released into the plant cells after those compartments are ruptured by ice crystals. Cyanide-storing plants also grow more slowly than forms that do not store cyanide, because some energy that could otherwise be used for growth is required to sequester the cyanide.

Latitudinal and elevational temperature gradients generate clines in the production of cyanide, with greater cyanide production at lower elevations and latitudes. More frequent freezing results in more frequent cyanide damage, and low temperatures result in less grazing, because grazers are not as active. Plants that do not go to the expense of storing cyanide are favored under those conditions. This is a classic geographic cline. However, changes in grazing pressure over much smaller distances also generate clines in cyanide storage. Grazing pressure changes over meters when white clover grows in a garden protected by pesticides and in an adjacent, unprotected field. The result is a cline in cyanide storage by white clover very similar to the geographic clines discussed above but on a scale of meters.

Carl W. Hoagstrom

See also: Adaptations; Coevolution; Evolution of plants; Gene flow; Population genetics; Reproductive isolating mechanisms; Selection; Species and speciation.

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CLONING OF PLANTS

Categories: Biotechnology; economic botany and plant uses; genetics

Plant cloning is the production of a cell, cell component, or plant that is genetically identical to the unit or individual from which it was derived.

The term "clone" is derived from the Greek word *klon*, meaning a slip or twig. Hence, it is an appropriate choice. Plants have been "cloned" from stem cuttings or whole-plant divisions for many centuries, perhaps dating back as far as the beginnings of agriculture.

Historical Background

In 1838 German scientists Matthias Schleiden and Theodor Schwann presented their *cell theory*, which states, in part, that all life is composed of cells and that all cells arise from preexisting cells. This theory formed the basis for the concept of *totipotency*, which states that since cells must contain all of the genetic information necessary to create an entire, multicellular organism, all of the cells of a multicellular organism retain the potential to recreate, or regenerate, the entire organism. Thus was the basis for plant cell culture research.

The first attempt at culturing isolated plant tissues was by Austrian botanist Gottlieb Haberlandt at the beginning of the twentieth century, but it was unsuccessful. In 1939 Professor R. J. Gautheret and colleagues demonstrated the first successful culture of isolated plant tissues as a continuously dividing callus tissue. The term *callus* is defined as an unorganized mass of dividing cells, such as in a wound response. It was not until 1954, however, that the first whole plant was regenerated, or cloned, from a single adult plant cell by W. H. Muir et al. Thereafter, an increased understanding of plant physiology, especially the role of plant hormones in plant growth and development, contributed to rapid advances in plant cell and tissue culture technologies in the 1970's and 1980's. Many plant species have been successfully cloned from single cells, thus demonstrating and affirming the concept of totipotency.

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Horticulture

By far, the greatest impact of cloning plants *in vitro* (Latin for "in glass," meaning in the laboratory or outside the plant) has been on the horticultural industry. In the 1980's plant tissue culture technologies propagated and produced many millions of plants. Today, many economically important plants are commonly propagated via tissue culture techniques, including vegetable crops (such as the potato), fruit crops (strawberries and dates), floriculture species (orchids, lilies, roses, Boston ferns), and even woody species (pines and grapes).

The advantages of plant cell, tissue, and organ culture technologies include a more rapid production of plants, taking weeks instead of months or years. Much less space is required (square feet instead of field plots). Plants can be produced year-round, and economic, political, and environmental considerations that hamper the propagation of regional or endangered plant species can be reduced. The disadvantages include the high start-up costs for facilities, the skilled labor required, and the need to maintain sterile conditions.

Two other significant considerations must be considered as a result of plant propagation technologies. As illustrated by the Irish Potato Famine of the 1840's, the cultivation of whole fields of genetically identical plants (*monoculture*) leaves the entire crop vulnerable to pest and disease infestations. The second important consideration when generating entire populations of clones, especially using tissue culture technologies, is the potential for introducing genetic abnormalities, which then are present in the entire population of plants produced, a process termed *somaclonal variation*.

Biotechnology

An absolute requirement for genetic engineering of plants is the ability to regenerate an entire plant from a single, genetically transformed cell, thus emphasizing the second major impact of plant cell culture technologies. In 1994 the U.S. Food and Drug Administration (FDA) approved the first genetically modified whole food crop, Calgene's Flavr Savr tomato. This plant was produced using what is termed anti-sense technology. One of the tomato's genes involved in fruit ripening was reversed, thus inactivating it and allowing tomatoes produced from it to have significantly delayed ripening. Although no longer commercially marketed, the Flavr Savr demonstrated the impact of genetic engineering in moving modern agriculture from the Green Revolution into what has been termed the Gene Revolution.

Other examples of agricultural engineering exist today, such as Roundup Ready Soybeans, engineered to resist the herbicide used on weeds where soybeans are grown, and BT Corn, which contains a bacterial gene conveying increased pest resistance. Since 1987, the U.S. Department of Agriculture (USDA) has required field testing of genetically modified crops to demonstrate that their use will not be disruptive to the natural ecosystem. To date, thousands of field trials have been completed or are in progress for genetically modified versions of several crop species, including potatoes, cotton, alfalfa, canola, and cucumbers.

Henry R. Owen

See also: Biotechnology; Cell theory; Endangered species; Genetically modified foods; Green Revolution; Horticulture; Hybridization; Mitosis and meiosis; Monoculture; Plant biotechnology.

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COAL

Category: Economic botany and plant uses

Coal is one of the world's most important natural resources based on plant life. Fuel in the form of coal can be any of a variety of combustible sedimentary and metamorphic rocks containing a specified amount of fossilized plant remains.

Coal is a general term encompassing a variety of combustible sedimentary and metamorphic rocks containing altered and fossilized terrestrial plant remains in excess of 50 percent by weight, and more than 70 percent by volume. Categories of coal differ in relative amounts of moisture, volatile matter, fixed carbon, and degree of compaction of the original carbonaceous material. Coal is therefore commonly termed a *fossil fuel*. This key resource is the product of the carbon from ancient plants that have undergone sedimentary and metamorphic transformation over millions of years.

Formation

After dead land-plant matter has accumulated and slowly begun to compact, biochemical decomposition, rising temperature, and rising pressure all contribute to the lengthy process of altering the plant debris into coal. The more common coals are of vascular vegetable origin, formed from the compaction and induration of accumulated remains of plants that once grew in extensive swamp and coastal marsh areas. These deposits are classed as *humic* coals consisting of organic matter that has passed through the *peat*, or earliest coal formation, stage. A variety of humic coals are known.

The swamp water environment within which humic coals form must be deficient in dissolved oxygen, the presence of which would ordinarily cause decay of the plant tissue. Under such near-stagnant conditions plant remains are preserved, while the presence of hydrogen sulfide inhibits organisms that feed on dead vegetation. Analog environments under which coal is currently forming are found within the Atchafalaya swamp of coastal Louisiana and the many peat-producing regions of Ireland. A layer of peat in excess of 2 meters in thickness and covering more than 5,000 square kilometers is present in the Great Dismal swamp of coastal North Carolina and Virginia.

The *sapropelic* class of coal, relatively uncommon in distribution and composed of fossil algae and spores, is formed through partial decomposition of organic matter by organisms within oxygen-deficient lakes and ponds. Sapropelic coals are subdivided into boghead (algae origin) and cannel (spore origin) deposits.

The vegetable origin of coal has been accepted since 1825 and is convincingly evidenced by the identification of more than three thousand freshwater plant species in coal beds of Carboniferous (360 million to 286 million years ago) age. The common association of root structures and even upright stumps with layers of coal indicate that the parent plant material grew and accumulated in place.

Detailed geologic studies of rock sequences that lie immediately above and below coal deposits indicate that most coals were formed in coastal regions affected by long-term sea level cycles characterized by transgressing (advancing) and regressing (retreating) shorelines. Such a sequence of rock deposited during a single advance and retreat of the shoreline, termed a cyclothem, typically contains nonmarine strata separated from overlying marine strata by a single layer of coal. In sections of the Interior coal province, a minimum of fifty cyclothems have been recognized, some of which can be traced across thousands of square kilometers. Such repetition in a rock sequence is most advantageous to the economics of a coal region, creating a situation in which a vertical mine shaft could penetrate scores of layers of coal.

The formation of coal is a long-term geologic process. Coal cannot therefore be considered a renewable resource, even though it is formed from plant matter. Studies have suggested that 1 meter of low-rank coal requires approximately ten thousand years of plant growth, accumulation, biologic reduction, and compaction to develop. Using these time lines, the 3-meter-thick Pittsburgh coal bed, underlying 39,000 square kilometers of Pennsylvania, developed over a period of thirty thousand years, while the 26-meter-thick bed of coal found at Adaville, Wyoming, required approximately a quarter of a million years to develop.

Coal formation favors sites where plant growth is abundant and conditions for organic preservation are favorable. Such climates range from subtropical to cold, with the ideal being classed as temperate. Tropical swamps produce an abundance of plant matter but have very high bacterial activity, resulting in low production of peat. Modern peats are developing in temperate to cold climate regions, such as Canada and Ireland, where abundant precipitation ensures fast plant growth, while relatively low temperatures diminish the effectiveness of decay-promoting bacteria.

The first coal provinces began to form with the evolution of cellulose-rich land plants. One of the earliest known coal deposits, of Upper Devonian age (approximately 365 million years ago), is found on Buren Island, Norway. Between the Devonian period and today, every geologic period is represented by at least some coal somewhere in the world. Certain periods of time, however, are significant coal-forming ages.

During the Carboniferous and Permian periods (360 to 245 million years ago) widespread development of fern and scale tree growth set the stage for the formation of the Appalachian coal province and the coal districts of Great Britain, Russia, and Manchuria. Coal volumes formed during these periods of geologic time constitute approximately 65 percent of present world reserves. The remaining reserves, developed mainly over the past 200 million years, formed in swamps consisting of *angiosperms* (flowering plants). The reserves of the Rocky Mountain province and those of central Europe are representative of these younger coals.

Classification of Coal

With the advent of the Industrial Revolution there was a need for a system of classification defining in detail the various types of coals. Up to the beginning of the nineteenth century, coal was divided into three rudimentary classes, determined by appearance: bright coal, black coal, and brown coal. Through the decades other schemes involving various parameters were introduced.

In 1937 a classification of coal rank using fixed carbon and Btu content was adopted by the American Standards Association. Adaptations of this scheme are still in use, listing the steps of progressive increase in coal rank as lignite (brown coal), subbituminous, bituminous (soft coal), subanthracite, and anthracite (hard coal). Some classification schemes also list peat as the lowest rank of coal. Technically speaking, peat is not a coal; rather, it is a fuel and a precursor to coal.

Coalification is the geologic process whereby plant material is altered into differing ranks of coal by geochemical and diagenetic change. With an increase in rank, chemical changes involve an increase in carbon content accompanied by a decrease in hydrogen and oxygen. Correspondingly, *diagenesis* involves an increase in density and calorific value and a progressive decrease in moisture. At all ranks, impurities include sulfur, silt and clay particles, and silica.

Peat, an unconsolidated accumulation of partly decomposed plant material, has an approximate carbon content of 20 percent. In many classification schemes, peat is listed as the initial stage of coal formation. Moisture content is quite high, at least at the 75-percent level. When dry, peat has an oxygen content of about 30 percent, is flammable, and will freely but inefficiently burn slowly and steadily for months at a low heat-content value of 5,400 Btu's per pound. (The British thermal unit, or Btu, is the

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quantity of heat required to raise the temperature of one pound of water one degree Fahrenheit.)

Types of Coal

Lignite, or brown coal, is brownish-black in color, banded and jointed, and subject to spontaneous combustion. Carbon content ranges from 25 to 35 percent. With a moisture content around 40 percent, it will readily disintegrate after drying in the open air. Because lignite has a maximum calorific value of 8,300 Btu's, it is classed as a low heating-value coal.

Deeper burial with even higher temperatures and pressures gradually alters lignite to *bituminous coal*, a dense, dusty, brittle, well-jointed, dark brown to black fuel that burns readily with a smoky yellow flame. It is the most abundant form of coal in the United States. Calorific value ranges from 10,500 to 15,500 Btu's per pound, and carbon content varies from 45 to 86 percent. Moisture content is as low as 5 percent, but heating value is high.

The *subbituminous* class of coal is intermediate between lignite and bituminous and has characteristics of both. Little woody matter is visible. It splits parallel to bedding but generally lacks the jointing of bituminous coal. It burns clean but with a relatively low heating value.

Anthracite is jet-black in color, has a high luster, is very hard and dust-free, and breaks with a conchoidal fracture. Carbon content ranges from 86 to 98 percent. It is slow to ignite, burns with a short blue flame without smoke, and, with a calorific value in excess of 14,000 Btu's per pound, is a high heating fuel. U.S. reserves are found mainly in eleven northeastern counties in Pennsylvania. Subanthracite coal has characteristics intermediate between bituminous and anthracite.

Bedded and compacted coal layers are geologically considered to be rocks. Lignite and bituminous ranks are classed as organic sedimentary rocks. Anthracite, formed when bituminous beds of coal are subjected to the folding and regional deformation affiliated with mountain building processes, is listed as a metamorphic rock. Because peat is not consolidated or compacted, it is classed as an organic sediment. *Graphite*, a naturally occurring crystalline form of almost pure carbon, is occasionally associated with anthracite. While it can occur as the result of high-temperature alteration of anthracite, its chemical purity and common association with crystalline rock causes it to be listed as a mineral.

Worldwide Distribution

While coal has been found all over the world, principal mining activity and approximately 95 percent of world reserves lie in the Northern Hemisphere—in Asia, Europe, and North America.

It is estimated that total world coal resources, defined as coal reserves plus other deposits that are not economically recoverable plus inferred future discoveries, are on the order of 10 trillion tons. Of this amount, estimates of world coal reserves, defined as those deposits that have been measured, evaluated, and can be extracted profitably under existing technology and economic conditions, range up to a high of approximately one trillion tons. World reserves can be divided into two categories, with 73 percent composed of anthracite and bituminous coals and 27 percent composed of lignite. Among nations, the United States possesses the greatest amount (approximately 500 billion tons) of total world reserves.

Modern Use

Historically, coal has been industry's fuel of choice. Countries with large coal reserves have risen commercially, while those less endowed with this resource—or lacking it altogether—have turned to agriculture or stagnated in development. Different ranks of coal are employed for different purposes. In the middle of the twentieth century it was common to see separate listings of coking, gas, steam, fuel, and domestic coals. Each had its specific uses. Coal for home use could not yield excessive smoke, while coal for locomotives had to raise steam quickly and not produce too high an ash content. Immediately after World War II fuel coal use, representing 78 percent of annual production, was divided into steam raising, railway transportation, domestic consumption, electric generation, and bunker coal. The remaining 22 percent was employed in the production of pig iron, steel, and gas.

Fifty years later, more than 80 percent of the approximately 1 billion tons of coal produced annually in the United States was used to generate electricity. Industrial consumption of coal, particularly in the production of coke for the steel and iron manufacturing industry, is the second most important use. Other industrial uses of coal are food processing and the manufacture of paper, glass, cement, and stone. Coal produces more energy than any other known fuel, including natural gas, crude oil, nuclear, and renewable fuels.

While expensive to produce, the conversion of intermediate ranks of coal into liquid (coal oil) and gaseous (coal gas) forms of hydrocarbon fuels will become more economically viable, especially during times of increase in the value of crude oil and natural gas reserves. New uses of coal are constantly being explored and tested. Two promising techniques are the mixing of water with powdered coal to make a slurry which can be burned as a liquid fuel and the underground extraction of coal-bed methane (firedamp). Interest in the latter by-product as an accessible and clean-burning fuel is especially high in Appalachian province localities distant from conventional gas resources.

Coal Mining

Coal has been produced by two common methods: underground (deep mining) and surface (strip mining). Underground mining requires digging extensive systems of tunnels and passages within and along the coal layers. These openings are connected to the surface so the coal can be removed. Prior to the development of the gigantic machinery used in open-pit mining, deep mining was the industry norm. This early period was characterized by labor-intensive pick and shovel work in cramped mine passages. Constant dangers to miners included the collapse of ceilings, methane gas explosions, and pneumoconiosis, known as black lung disease.

Today augers and drilling machinery supplement human labor to a large extent. Mine safety and health regulations have greatly reduced a once-high annual death toll. The common method of underground extraction involves initial removal of about 50 percent of the coal, leaving a series of pillars to support the mine roof. As reserves are exhausted, the mine is gradually abandoned after removal of the pillars. Another modern underground mining technique, with a coal removal rate approaching 100 percent, involves the use of an integrated rotary cutting machine and conveyer belt.

Surface mining of coal, accounting for about 61 percent of U.S. production, is a multiple-step process. First the overburden material is removed, allowing exposure of the coal. Coal is then mined using surface machinery ranging from bulldozers to gigantic power shovels. Finally, after removal of all the coal, the overburden is used to fill in the excavated trench, and the area is restored to its natural topography and vegetation. Economics usually determine whether underground or open-pit techniques are preferable in a given situation. Generally, if the ratio of overburden to coal thickness does not exceed twenty to one, surface mining is more profitable.

With increased concern for the environment, and with federal passage of the Coal Mine Health and Safety Act (1969) and the Clean Air Act (1970), the mining of coal in the United States has undergone both geographic and extraction-technology changes. Because the Rocky Mountain province coals, while lower grade than eastern coals, contain lower percentages of sulfur, the center of U.S. production has gradually shifted westward. The burning of high-sulfur coals releases sulfur dioxide into the atmosphere; it is a significant contributor to acid rain.

Western coals are often contained within layers thicker than those found in the East, are shallow in depth, and can be found under large areas—all conditions amenable to surface mining. As a result, the state of Wyoming, with a 1995 production of 265 million tons of low-sulfur coal, became the leading U.S. coal producer. The 1979 version of the U.S. Department of Energy's annual report on the database of minable coal reserves, titled "Demonstrated Reserve Base of Coal in the United States on January 1, 1979," listed reserves at 475 billion tons. At current levels of production it is estimated that the United States has more than 250 years of future production.

Albert B. Dickas

See also: Fossil plants; Peat.

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COEVOLUTION

Categories: Ecology; ecosystems; evolution

Coevolution is the interactive evolution of two or more species that results in a mutualistic or antagonistic relationship.

When two or more different species evolve in a way that affects one another's evolution, coevolution is taking place. This interactive type of evolution is characterized by the fact that the participant life-forms are acting as a strong selective pressure upon one another over a period of time. The coevolution of plants and animals, whether animals are considered strictly in their plant-eating role or also as pollinators, is abundantly represented in every terrestrial ecosystem throughout the world where flora has established itself. Moreover, the overall history of some of the multitude of present and past plant and animal relationships is displayed (although fragmentally) in the fossil record found in the earth's crust.

Beginnings

The most common coevolutionary relationships between plants and animals surround plants as a food source. Microscopic, unicellular plants were the earth's first *autotrophs* (organisms that can produce their own organic energy through photosynthesis, that is, from basic chemical ingredients derived from the environment). In conjunction with the appearance of autotrophs, microscopic, unicellular *heterotrophs* (organisms, such as animals, that must derive food from other sources, such as autotrophs) evolved to exploit the autotrophs.

Sometime during the later part of the Mesozoic era, angiosperms, the flowering plants, evolved and replaced most of the previously dominant land plants, such as the gymnosperms and the ferns. New species of herbivores evolved to exploit these new food sources. At some point, probably during the Cretaceous period of the late Mesozoic era, animals became unintentional aids in the angiosperm pollination process. As this coevolution proceeded, the first animal pollinators became more and more indispensable as partners to the plants.

Eventually, highly coevolved plants and animals developed relationships of extreme interdependence, exemplified by the honeybees and their coevolved flowers. This angiosperm-insect relationship is thought to have arisen in the Mesozoic era by way of beetle predation, possibly on early, magnolia-like angiosperms. The fossil record gives some support to this theory. Whatever the exact route along which plant-animal pollination partnerships coevolved, the end result was a number of plant and animal species that gained mutual benefit from the new type of relationship.

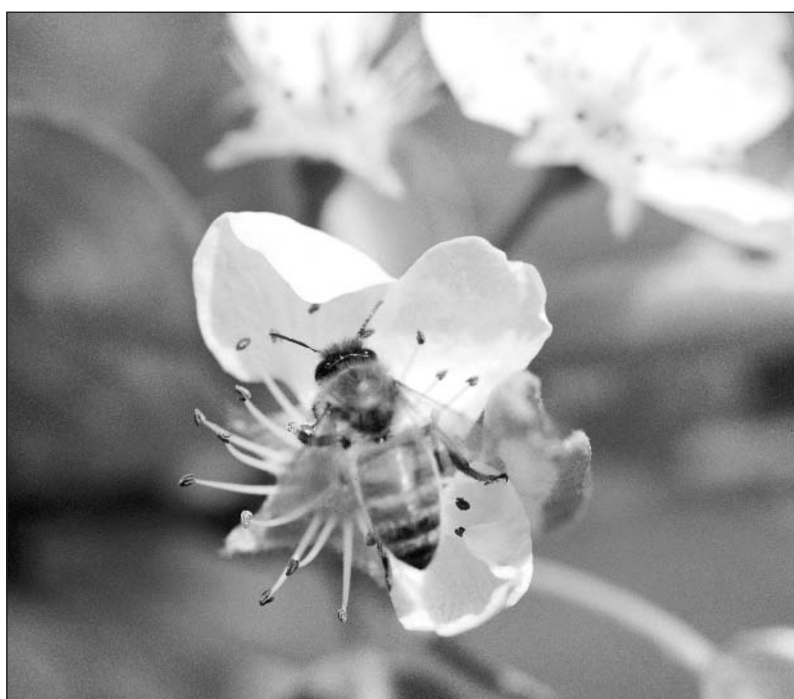
Coevolutionary Relationships

Coevolved relationships include an immense number of relationships between plants and animals, and even between plants and other plants. Among these coevolved situations can be found *commensalisms*, in which different species have coevolved to live intimately with one another without injury to any participant, and *symbioses*, in which species have coevolved to literally "live together."

Such intertwined relationships can take the form of *mutualism*, in which neither partner is harmed and indeed one or both benefit—as in the relationships between fungi and algae in lichens, fungi and roots in mycorrhizae, and ants and acacia trees in a symbiotic mutualism in which the ants protect the acacias from herbivores. In *parasitism*, one partner benefits at the expense of the other; a classic example is the relationship between the mistletoe parasite and the oak tree. Another coevolutionary relationship, *predation*, is restricted primarily to animal-animal relationships (vertebrate carnivores eating other animals, most obviously), although some plants, such as Venus's flytrap, mimic predation in having evolved means of trapping and ingesting insects as a source of food. Some highly evolved fungi, such as the oyster mushroom, have evolved anesthetizing compounds and other means of trapping protozoa, nematodes, and other small animals.

One of the most obvious and complex coevolutionary relationships are the mutualisms that have evolved between plants bearing fleshy fruits and vertebrate animals, which serve to disperse the seeds in these fruits. Over time, plants that produce these fruits have benefited from natural selection because their seeds have enjoyed a high degree of survival and germination: Animals eat the fruits, whose seeds are passed through their digestive system (or regurgitated to feed offspring) unharmed; at times the seeds are even encouraged toward germination as digestion helps break down the seed coat. Furthermore, dispersal through the animals' mobility allows the seeds to enjoy more widely distributed propagation. The coevolutionary process works on the animals as well: Birds and animals that eat the fruits enjoy a higher degree of survival, and so natural selection favors both fleshy-fruit-producing plants and fleshy-fruit-eating animals. Similar selection has favored the coevolution of flowers with colors and smells that attract pollinators such as bees.

Eventually some plant-animal mutualisms became so intertwined that one or both participants reached a point at which they could not exist without the aid of the other. These obligatory mutualisms ultimately involve other types of animal partners besides insects. Vertebrate partners such as birds, reptiles, and mammals became involved in mutualisms with plants. In the southwestern United States, for example, bats and the agave and saguaro cactus have a special coevolutionary relationship: The bats, nectar drinkers and pollen eaters, have evolved specialized feeding structures such as erectile tongues similar to those found among moths and other insects with similar lifestyles. In turn, angiosperms coevolutionarily involved with bats have developed such specializations as bat-attractive scents, flower structures that match the bats' feeding habits and minimize the chance of injuring the animals, and petal openings timed to the nocturnal activity of bats.



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As coevolution proceeded over time, animal pollinators and highly coevolved plants developed relationships of extreme interdependence, exemplified by the honeybees and their coevolved flowers.

Defense Mechanisms

Coevolution is manifested in defense mechanisms as well as attractants: Botanical structures and chemicals (*secondary metabolites*) have evolved to discourage or to prevent the attention of plant eaters. These include the development of spines, barbs, thorns, bristles, and hooks on plant leaves, stems, and trunk surfaces. Cacti, hollies, and rose bushes illustrate this form of plant strategy. Some plants produce chemical compounds that are bitter to the taste or poisonous. Plants that contain organic tannins, such as trees and shrubs, can partially inactivate animals' digestive juices and create cumulative toxic effects that have been correlated with cancer. Grasses with a high silica content act to wear down the teeth of plant eaters. Animals have counteradapted to these defensive innovations by evolving a higher degree of resistance to plant toxins or by developing more efficient and tougher teeth with features such as harder enamel surfaces or the capacity of grinding with batteries of teeth.

Frederick M. Surowiec,
updated by Christina J. Moose

Ants and Acacias

One noted example of mutualism can be found in Mexico and Central America, home to the bull's-horn acacia (*Acacia cornigera*). In its native habitat, colonies of stinging ants (*Pseudomyrmex ferruginea*) live inside the acacia's hollow thorns, found at the base of each leaf. There, the ants enjoy plentiful food, such as the tree's carbohydrate-rich nectar and protein-lipid Beltian bodies, nutritive structures located at the tip of each leaflet. The only known function of the Beltian bodies is to provide food for the symbiotic ants, which make their nests only in this species of tree and are utterly dependent on its food sources.

The acacia benefits from this arrangement as well. When an animal of any size brushes against the tree, worker ants swarm out and sting the animal, thus protecting the plant from herbivory. When epiphytic vines or the branches of another plant touch an inhabited acacia tree, the ants cut away the other plant's bark. By doing so, they destroy the invasive plant branch and allow more sunlight to reach the acacia—a crucial factor for plants in densely growing areas of the tropics. Scientists have found that acacias inhabited by ants grow more rapidly than uninhabited acacias, making ants and acacias mutual beneficiaries.

See also: Animal-plant interactions; Biochemical coevolution in angiosperms; Community-ecosystem interactions; Evolution: convergent and divergent; Lichens; Metabolites: primary vs. secondary; Mycorrhizae.

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COMMUNITY-ECOSYSTEM INTERACTIONS

Categories: Animal-plant interactions; ecology; ecosystems

Ecosystems are complex organizations of living and nonliving components. They are frequently named for their dominant biotic or physical features (such as marine kelp beds or coniferous forests). Communities are groups of species usually classified according to their most prominent members (such as grassland communities or shrub communities). The interactions between species and their ecosystems have lasting impacts on both.

In an ecological sense, a community consists of all populations residing in a particular area. Examples of communities range in scale from all the trees in a given watershed, all soil microbes on an agricultural plot, or all phytoplankton in a particular harbor to all plants, animals, and microbes in vast areas, such as the Amazon basin or the Chesapeake Bay.

An ecosystem consists of the community of species as well as the environment of a given site. A forest ecosystem would include all living things along with climate, soils, disturbance, and other abiotic factors. An estuarine ecosystem, likewise, would include all the living things present, in addition to climate, currents, salinity, nutrients, and more.

Interactions between species in communities and ecosystems range from mutually beneficial to mutually harmful. One such category of interaction is *mutualism*, which usually involves two species. Both species derive benefit from a mutualism. *Commensalism* is used to describe a situation in which one species benefits without harming the other. If the two species are neither helped nor harmed, a *neutralism* is said to occur, and an *amensalism* happens when one species is harmed while the other remains. During *competition*, both species involved are negatively affected. A number of terms are used to describe a relationship in which one species benefits at another's expense, including herbivory, predation, parasitism, and pathogenicity. The choice of term more often than not depends on the relative sizes of the species involved.

Competition

Plants typically compete for resources, such as light, space, nutrients, or water. One way an individual may outcompete its neighbors is to outgrow them, thus capturing more sunlight for itself (and thus producing more sugars and other organic molecules for itself). Another way is to be more fecund than the neighbors, flooding the surroundings with one's progeny and thereby being more likely to occupy favorable sites for reproduction. For example, in closed forests treefall gaps are quickly filled with growth from the canopy, thus shading the ground and making it more difficult for competing seedlings and saplings to survive.

Plants compete in the root zone as well, as plants with a more extensive root network can acquire more of the water and other inorganic nutrients necessary for growth and reproduction than can their competitors. In semiarid areas, for example, trees often have trouble colonizing grasslands because the extensive root systems of grasses are much more effective in capturing available rainwater.

Sometimes plants resort to chemical "warfare," known as *allelopathy*, in order to inhibit the growth of competitors in the surrounding area. The existence of allelopathy remains a controversial topic, and simpler explanations have been offered for many previously alleged instances of the phenomenon. Allelopathy cannot be rejected outright; however, the controversy most likely proves only that many aspects of nature cannot be pigeonholed into narrow explanations.

Competition involves a cost in resources devoted to outgrowing or outreproducing the neighbors. Because of the cost, closely related, competing species will diverge in their ecological requirements. This principle is known as *competitive exclusion*.

Mutualism, Commensalism, and Parasitism

Many flowering plants could not exist without one of the most important mutualisms of all: *pollination*. In concept, pollination is simple: In exchange for carrying out the physical work of exchanging genetic material (in pollen form) between individual plants (thus enabling sexual reproduction), the carrier is rewarded with nutrients in the form of nectar or other materials. Many types of animals are involved in pollination: insects such as bees, flies, and beetles; birds, particularly the hummingbirds; and mammals such as bats.

Another highly important mutualism is that between plant roots and fungal hyphae, or *mycorrhizae*. Mycorrhizae protect plant roots from pathogenic fungi and bacteria; their most important role, however, is to enhance water and nutrient uptake by the plant. In fact, regeneration of some plants is impossible in the absence of appropriate mycorrhizae. Mycorrhizae benefit, in turn, by receiving nutrients and other materials synthesized by the host plant. There are two types of mycorrhizae: *ectomycorrhizae*, whose hyphae may fill the space between plant roots but do not penetrate the roots themselves; and *vesicular-arbuscular mycorrhizae*, whose hyphae penetrate and develop within root cells.

Few people can envision a swamp in the southeastern United States without thinking of bald cypress trees (*Taxodium distichum*) draped in ethereal nets of Spanish moss (*Tillandsia usneoides*), which is actually not a moss but a flowering plant in the monocot family *Bromeliaceae*. *Tillandsia* is an *epiphyte*, a plant that grows on the stems and branches of a tree. Epiphytism is one of the most common examples of a *commensalism*, in which one organism, for instance the epiphyte, benefits without any demonstrable cost to the other, in this case the host tree. Epiphytes are common in tropical rain forests and include orchids, bromeliads, cacti, and ferns. In temperate regions more primitive plants, such as lichens, are more likely to become epiphytes.

Not all epiphytes are commensal, however. In the tropics, strangler figs, such as *Ficus* or *Clusia*, begin life as epiphytes but send down roots that in time completely encircle and kill the host. Mistletoes, such as *Phoradendron* or *Arceuthobium*, may draw off the photosynthetic production of the host, thus severely depleting its resources.

Herbivory and Pathogenicity

Plants, because of their ability to harvest light energy from the sun to produce the organic nutrients and building blocks necessary for life, are the primary *producers* of most of the earth's ecosystems. Thus, they face an onslaught of macroscopic and microscopic *consumers*. If macroscopic, the consumers are generally regarded as *herbivores* (plant-eating animals); if microscopic, they are *pathogens*. Either way, herbivores and pathogens generally devour the tissues of the host.

Plants have evolved a number of defense mechanisms in response to pressure from herbivores and pathogens. Some responses may be mechanical. For example, trees on an African savanna may evolve greater height to escape grazing pressures from large herbivores, but some large herbivores, specifically giraffes, may evolve to grow to greater heights as well. Plants may encase themselves in nearly indestructible outer coatings or arm themselves with spines in order to discourage grazers.

Other responses may be chemical. Cellulose, one of the important chemical components of plant tissues such as wood, is virtually indigestible—unless the herbivore itself hosts a bacterial symbiont in its stomach that can manage the job of breaking down cellulose. Other chemicals, such as phenols and tannins—the class of compounds that gives tea its brown color—are likewise indigestible, thus discouraging feeding by insects. Plants produce a wide range of toxins, such as alkaloids, which poison or kill herbivores. A number of hallucinogenic drugs are made from plant alkaloids.

Phytoalexins are another group of defensive compounds produced by plants in response to bacterial and fungal pathogens. Substances present in the cell walls of bacteria and fungi are released via the action of plant enzymes and spread throughout the plant. The bacterial and fungal substances function as hormones to stimulate, or elicit, phytoalexin production. Hence, these substances are referred to as *elicitors*. The phytoalexins act as antibiotics, killing the infective agents. Tannins, phenols, and other compounds also serve to defend against pathogen attack.

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See also: Allelopathy; Animal-plant interactions; Biomes: definitions and determinants; Biomes: types; Biosphere concept; Community structure and stability; Coevolution; Competition; Ecosystems: overview; Ecosystems: studies; Evolution: convergent and divergent; Metabolites: primary vs. secondary; Mycorrhizae; Nutrient cycling; Pollination; Selection; Succession.

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COMMUNITY STRUCTURE AND STABILITY

Categories: Ecology; ecosystems

An ecological community is the assemblage of species found in a given time and place. The species composition of different ecosystems and the ways in which they maintain equilibrium and react to disturbances are manifestations of the community's stability.

The populations that form a community interact through the processes of *competition*, *predation*, *parasitism*, and *mutualism*. The structures of communities are determined, in part, by the nature and strength of these *biotic* factors. *Abiotic* factors (physical factors such as temperature, rainfall, and soil fertility) are the other set of important influences determining community structure. An ecological community together with its physical environment is called an *ecosystem*. No ecosystem can be properly understood without a careful study of the biotic and abiotic factors that shape it.

Energy Flow

The most common way to characterize a community functionally is by describing the flow of energy through it. Based on the dynamics of *energy flow*, organisms can be classified into three groups: those that obtain energy through *photosynthesis* (called *producers*), those that obtain energy by consuming other organisms (*consumers*), and those that decompose dead organisms (*decomposers*). The pathway through which energy travels from producer through one or more consumers and finally to decomposer is called a *food chain*. Each link in a food chain is called a *trophic level*. Interconnected food chains in a community constitute a *food web*.

Very few communities are so simple that they can be readily described by a food web. Most communities are compartmentalized: A given set of producers tends to be consumed by a limited number of consumers, which in turn are preyed upon by a smaller number of *predators*, and so on. Alternatively, consumers may obtain energy by specializing on one part of their prey (for example, some birds may eat only seeds of plants) but utilize a wide range of prey species. *Compartmentalization* is an important feature of community structure; it influences the formation, organization, and persistence of a community.

Dominant and Keystone Species

Some species, called *dominant species*, can exert powerful control over the abundance of other species because of the dominant species' large size, extended life span, or ability to monopolize energy or other resources. Communities are named according to their dominant species: for example, oak-hickory forest, redwood forest, sagebrush desert, and tall-grass prairie. Some species, called *keystone species*, have a disproportionately large effect on community structure. These interact with other members of the community in such a way that loss of the keystone species can lead to the loss of many other species. Keystone species may also be the dominate species, but they may also appear insignificant to the community until they are gone. For example, cordgrass (*Spartina*) is the dominant plant in many tidal estuaries, and it is also a keystone species because so many members of the community depend on it for food and shelter.

The species that make up a community are seldom distributed uniformly across the landscape; rather, some degree of patchiness is characteristic of virtually all species. There has been conflicting evidence as to the nature of this patchiness. Moving across an environmental gradient (for example, from wet to dry conditions or from low to high elevations), there is a corresponding change in species and community composition. Some studies have suggested that changes in species composition usually occur along relatively sharp boundaries and that these boundaries mark the borders between adjacent communities. Other studies have indicated that species tend to respond individually to environmental gradients and that community boundaries are not sharply defined; rather, most communities broadly intergrade into one another, forming what is often called an *ecotone*.

Degrees of Species Interaction

These conflicting results have fueled a continuing debate as to the underlying nature of communities. Some communities seem to behave in a coordinated manner. For example, if a prairie is consumed by fire, it regenerates in a predictable sequence, ultimately returning to the same structure and composition it had before the fire. This process, called *ecological succession*, is to be expected if the species in a community have evolved together with one another. In this case, the community is behaving like an organism, maintaining its structure and function in the face of environmental disturbances and fluctuations (as long as the disturbances and fluctuations are not too extreme). The existence of relatively sharp boundaries between adjacent communities supports this explanation of the nature of the community.

In other communities, it appears that the response to environmental fluctuation or disturbance is determined by the evolved adaptations of the species available. There is no coordinated community response but rather a coincidental assembly of community structure over time. Some sets of species interact together so strongly that they enter a community together, but there is no evidence of an evolved community tendency to resist or accommodate environmental change. In this case, the community is formed primarily of species that happen to share similar environmental requirements.

Competition and Predation

Disagreement as to the underlying nature of communities usually reflects disagreement about the relative importance of the underlying mechanisms that determine community structure. Interspecific competition has long been invoked as the primary agent structuring communities. Competition is certainly important in some communities, but there is insufficient evidence to indicate how widespread and important it is in determining community structure. Much of the difficulty occurs because ecologists must infer the existence of past competition from present patterns in communities. It appears that competition has been important in many vertebrate communities and in communities dominated by sessile organisms, such as plants. It does not appear to have been important in structuring communities of plant-eating insects. Furthermore, the effects of competition typically affect individuals that use identical resources, so that only a small percentage of species in a community may be experiencing significant competition at any time.

The effects of predation on community structure depend on the nature of the predation. *Keystone predators* usually exert their influence by preying on species that are competitively dominant, thus giving less competitive species a chance. Predators that do not specialize on one or a few species may also have a major effect on community structure, if they attack prey in proportion to their abundance. This frequency-dependent predation prevents any prey species from achieving dominance. If a predator is too efficient, it can drive its prey to extinction, which may cause a selective predator to become extinct as well. Predation appears to be most important in determining community structure in environments that are predictable or unchanging.

Disasters and Catastrophes

Chance events can also influence the structure of a community. No environment is completely uniform. Seasonal or longer-term environmental fluctuations affect community structure by limiting opportunities for colonization, by causing direct mortality, or by hindering or exacerbating the effects of competition and predation. Furthermore, all communities experience at least occasional disturbance: unpredictable, seemingly random environmental changes that may be quite severe.

It is useful in this regard to distinguish between regular disturbances and rarer, less frequent catastrophic events. For example, fire occurs so often in tall-grass prairies that most of the plant species have become fire-adapted—they have become efficient at acquiring nutrients left in the ash and at sprouting or germinating quickly after a fire. In contrast, the 1980 eruption of Mount St. Helens, a volcanic peak in Washington State, was so violent and so unexpected that no members of the nearby community were adequately adapted to such conditions.

Natural disturbances occur at a variety of scales. Small-scale disturbances may simply create small openings in a community. In forests, for example, wind, lightning, and fungi cause single mature trees to die and fall, creating gaps that are typically colonized by species requiring such openings. Large disturbances are qualitatively different from small disturbances in that large portions of a community may be destroyed, including some of the ability to recover from the disturbance. For example, following a large, intense forest fire, some tree species may not return for decades or centuries because their seeds were consumed by the fire, and colonizers must travel a long distance.

Early ecologists almost always saw disturbances as destructive and disruptive for communities. Under this assumption, most mathematical models portrayed communities as generally being in some stable state; if a disturbance occurred, the community inevitably returned to the same (or some alternative) equilibrium. It later became clear, however, that natural disturbance is a part of almost all natural communities. Ecologists now recognize that few communities exhibit an equilibrium; instead, communities are dynamic, always responding to the last disturbance.

Long-Term Community Dynamics

The evidence suggests that three conclusions can be drawn about the long-term dynamics of communities. First, it can no longer be assumed that all communities remain at equilibrium until changed by outside forces. Disturbances are so common, at so many different scales and frequencies, that the community must be viewed as an entity that is constantly changing as its constituent species readjust to disturbance and to one another.

Second, communities respond in different ways to disturbance. A community may exhibit *resistance*, not markedly changing when disturbance occurs, until it reaches a threshold and suddenly and rapidly shifts to a new state. Alternatively, a community may exhibit *resilience* by quickly returning to its former state after a disturbance. Resilience may occur over a wide range of conditions and scales of disturbance in a dynamically robust system. On the other hand, a community that exhibits resilience only within a narrow range of conditions is said to be dynamically fragile.

Finally, there is no simple way to predict the stability of a community. At the end of the 1970's, many ecologists predicted that complex communities would be more stable than simple communities. It appeared that stability was conferred by more intricate food webs, greater structural complexity, and greater species richness. On the basis of numerous field studies and theoretical models, many ecologists now conclude that no such relationship exists. Both very complex communities, such as tropical rain forests, and very simple communities, such as Arctic tundra, may be very fragile.

Alan D. Copsey, updated by Bryan Ness

See also: Community-ecosystem interactions; Competition; Ecosystems: overview; Ecosystems: studies; Species and speciation; Trophic levels and ecological niches.

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COMPETITION

Categories: Ecology; ecosystems; evolution

The struggle for food, space, and pollinators in order to survive can occur between individuals of different species (interspecific competition) or between individuals of the same species (intraspecific competition).

Competition is a major driving force in *evolution*, the process by which living organisms change over time, with better-adapted species surviving and less well-adapted species becoming extinct. Evolution begins with *mutation*, changes in the nucleotide sequence of a gene or genes, resulting in the production of slightly altered genes which encode slightly different proteins. These altered proteins are the expressed traits of an organism and may give the organism an advantage over its competitors. The organism outcompetes its rivals in the environment, and hence the environment favors

Some plant species, including peach trees, release chemicals into the soil that inhibit the growth of other plants that might otherwise compete with them.

the better-adapted, fitter organism, a process called *natural selection*. A mutation may help an organism in one environment but may hurt it in a different environment (for example, an albino squirrel may flourish in snowy regions but may not do as well in warm regions). Mutations are random events whose occurrence can be increased by chemicals called mutagens or by ionizing radiation such as ultraviolet light, X rays, and gamma radiation.

Species Interactions

Natural selection influences the distribution and abundance of organisms from place to place. The possible selection factors include physical factors (temperature and light, for example), chemical factors such as water and salt, and species interactions. According to ecologist Charles Krebs, species interactions include four principal types: *mutualism*, which is the living together of two species that benefit each other (for example, fungi and algae living together as lichens); *commensalism*, which is the living together of two species that results in a distinct benefit (or number of benefits) to one species while the other remains unhurt (for example, plants called *epiphytes* that grow on other plants); *predation*, which is the hunting, killing, and eating of one species by another (examples include insects eating plants or snails eating algae); and *competition*, which is defined as an active struggle for survival among all the species in a given environment.

Competition is related to the acquisition of various resources: food, space, and pollinators. Food is an obvious target of competition. All organisms must have energy in order to conduct the cellular chemical reactions (such as respiration) that keep them alive. Photoautotrophic organisms (plants, algae, cyanobacteria) obtain energy by converting sunlight, carbon dioxide, and water into organic molecules, a process called photosynthesis. Photoautotrophs, also called *primary producers*, compete for light and water. For example, oak and hickory trees in eastern North America grow taller than most pines, thereby shading smaller species and eventually dominating a forest. A few other autotrophs, such as chemoautotrophic bacteria, obtain their energy from inorganic chemical reactions rather than from sunlight.

All other organisms—animals, zooplankton, and fungi—are heterotrophs, also called *consumers*; they must consume other organisms to obtain energy. Heterotrophs include herbivores, carnivores, omnivores, and saprotrophs. Herbivores (plant eaters such as rabbits and cattle) derive their energy from eating plants. Carnivores (meat eaters such as cats and dogs) eat other heterotrophs in order to get their energy needs met. Omnivores (such as humans) eat plants and animals. Saprotrophs (such as fungi and bacteria) decompose dead organisms to meet their energy requirements. Life on earth functions by intricately complex food chains in which organisms consume other organisms in order to obtain energy. Ultimately, almost all energy in organisms comes from the sun.

Types of Competition

Intraspecific competition occurs among individual members of the same population, for example, when sprouts grow from seeds scattered closely together on the ground. Some seedlings will be able to grow faster than others and will inhibit the growth of less vigorous seedlings by overshadowing or overcrowding them.

Interspecific competition involves two or more different species trying to use the same resources. All green plants depend on photosynthesis to derive the energy and carbon they need. Different areas or communities favor different growth characteristics. For plants with high light requirements, a taller-growing plant (or one with more or broader leaves) will have a competitive advantage if its leaves receive more direct sunlight than competitors. If, on the other hand, the species cannot tolerate too much sun, a shorter-growing species that can benefit from sheltering shadows of larger plants nearby will have the competitive advantage over other shade-loving plants.

Competition in nature leads to certain species dominating an environment and evolving to adapt to it, while the outcompeted species move elsewhere or become extinct. Humans are able to utilize the results of competition among species for their own benefit. This principle is useful in agriculture. Certain plant species (such as sunflowers and peach trees) release chemicals into the soil that inhibit the growth of other plants that might otherwise compete with them. Plant competition can be used to fight the growth of weeds and is useful in understanding which plants are compatible.

Competition is also useful in medical microbiological research. Certain fungal species produce and secrete molecules called antibiotics, which kill bacteria. Antibiotics give these fungi an edge in their competition against bacteria. Laboratory production of these antibiotics can treat bacterial diseases in humans.

David Wason Hollar, Jr., updated by Bryan Ness

See also: Allelopathy; Coevolution; Community-ecosystem interactions; Community structure and stability; Ecosystems: overview; Ecosystems: studies; Evolution of plants; Species and speciation.

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COMPLEMENTATION AND ALLELISM: THE CIS-TRANS TEST

Categories: Genetics; methods and techniques

The cis-trans test is a method of determining whether two mutations are in the same or different genes. Genes are normally found in sets of two copies. If one copy is mutated and the other gene makes a normal product that compensates, the mutation is said to be recessive. If both copies of the gene are mutated and no normal product is made, then the phenotype of the organism will be mutant.

The cis-trans test was developed by Seymour Benzer and his coworkers in the 1950's. They worked with a *bacteriophage* (a virus that attacks only bacteria) called T4, studying one T4 viral gene called *rII*. Mutants of *rII* could be easily identified by the size of the *plaques* they made. A plaque is a clear circle in a continuous lawn of bacteria growing on nutrient agar which results when viruses attack and destroy the bacteria in that area.

Complementation (cis-trans) tests between *mutations* in different bacteriophage, or phage, strains which produce mutant plaques can be performed using a procedure called a *spot test*. Phages of one mutant strain are added to bacterial cells, then spread out on a plate containing nutrients and a solidifying agent (usually agar). Later, a drop of fluid containing phages with a different mutant strain is spotted onto the solid surface. In the area of the drop, some bacterial cells will be attacked by phages of both types. If the mutations complement each other, a normal plaque will result in that area. After looking at hundreds of different mutations, all of which had the same *phenotype* (that is, the expression of the gene) of large plaques, scientists at Benzer's laboratory determined that the *rII* gene was actually made up of two functional groups (which they called cistrons) and that every mutant could be assigned to one or the other of these groups.

Genetic Basis

Genes are located on cellular structures called *chromosomes*. For many years, scientists thought that genes were lined up along the chromosomes like beads on a string, each bead representing a different gene, such as for seed shape in plants. If normal or *wild-type* alleles were represented by black beads, it was thought, a red or white or green bead would represent a changed, or *mutant*, allele. This analogy was popular for many years, and genes, like beads, were thought to be indivisible. The work of scientists in the 1940's and 1950's challenged this theory and led to its eventual demise. The cis-trans test was a key part of this work.

The basis of the cis-trans test is the functional role of the gene. It is now known that each gene is made up of a particular sequence of *nucleotides* in *deoxyribonucleic acid* (DNA), defining the nucleotide sequence of a strand of *ribonucleic acid* (RNA). This RNA may, in turn, be used to define the sequence of amino acids in a protein. A mutant allele is a stretch of DNA in which the nucleotide sequence has been altered, resulting in an altered RNA. The result may be an altered protein, or sometimes no protein at all.

In most higher organisms, chromosomes occur in pairs called homologs. Such pairing means every gene (except those on the sex chromosomes) is normally found in two copies. If one copy is mutated and the other gene makes a normal product that compensates, the mutation is said to be *recessive*. If both copies of the gene are mutated and no normal product is made, then the *phenotype* of the organism (that is, the expression of the gene) will be mutant.

Genetic Crosses

In the cis-trans test, genetic crosses are arranged to yield an organism in which two recessive mutant alleles to be tested are on opposite *homologs*. In other words, one chromosome of a pair will have one mutant allele, and the other chromosome will have the other mutant allele. The alleles are then said to be in a *trans configuration*. If the two alleles are mutations of the same gene, the phenotype of the organism will be a mutant one. If the alleles belong to separate genes, the organism will have a normal, or *wild-type*, phenotype. When alleles produce a normal phenotype, they are said to complement each other. If the mutant alleles are arranged in the *cis configuration*, so that both are on the same chromosome, the resulting phenotype will be normal, whether the alleles are in the same or different genes.

For example, harebells (*Campanula*) normally have blue flowers, the wild-type phenotype, but occasionally mutants have white flowers. If a cis-trans test is done with two white-flowered mutants, in some cases the resulting progeny have blue flowers. This shows that the mutations in these two mutants are in different genes and thus display complementation. It is known that the blue pigment is produced by a biochemical pathway with two steps involving two enzymes that modify a colorless molecule. In other cases when a cis-trans test is done, all the progeny are white-flowered. This occurs when both mutants have mutations in the same gene, knocking out the activity of one of the enzymes, and thus complementation does not occur.

Recombination

Before the structure of DNA was understood, the gene was also defined as the basic unit of *recombination*; recombination within a gene was not thought to occur. In the analogy of genes as beads on a string, recombination was thought to involve the breakage and reunion of the string at positions between beads, never within them. It is now known that, in the process of recombination, pieces of chromosomes break off and rejoin in new combinations, although the rules that this process follows are not fully understood.

Recombination is essential to the cis-trans test. Only through recombination can cis configurations be obtained. The frequency of the occurrence of recombination is related to the closeness of two points on a chromosome. If recombination is desired between two regions that are very close, the chance that crossing over will occur is very low. Recombination can even be used to map mutations within a gene (a process called *fine structure analysis*), but it is a very long process, requiring the analysis of an extremely large number of progeny because the distance separating mutations within a gene will be very small.

Using the cis-trans test and recombination together led to the discovery of a small group of mutations called *pseudoalleles*. When two pseudoalleles are examined using the cis-trans test, an organism in trans configuration will have a mutant phenotype, leading to the conclusion that the alleles belong to the same gene. When recombination is used to try to map these mutations, however, it turns out that they are in separate structural genes. Pseudoalleles, then, are found in separate structural genes that interact in some functions.

Several examples of interaction between pseudoalleles can be found in *Drosophila* (fruit flies). In one such example, the two genes postbithorax (*pbx*) and bithorax (*bx*) are both involved in determining the normal formation of the fly's balancing organs (halteres), a pair of winglike structures that help the fly in its flight. These genes are adjacent on the chromosome but are structurally distinct. The fact that the gene products must interact is revealed by the results of the cis-trans test; when mutants for these genes are placed in trans configuration, the phenotype of the fly is mutant.

Lisa A. Lambert, updated by Bryan Ness

See also: Bacteriophages; DNA in plants; DNA replication; Genetics: Mendelian; Genetics: post-Mendelian; Genetics: mutations.

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COMPOSITAE

Categories: Angiosperms; economic botany and plant uses; *Plantae*; taxonomic groups

In number of species, the family Compositae *or* Asteraceae*, commonly known as the sunflower family, is among the largest families of flowering plants.*

The *Compositae* family consists of more than eleven hundred genera worldwide and possibly as many as twenty-three thousand species. Representatives of the family are found on every continent except Antarctica. Species diversity is high in the southwestern United States and Mexico, in southern Brazil and along the South American Andes Mountain range, along the Mediterranean region, in Southwest and Central Asia, in South Africa, and in Australia.

The plants typically are found in open, sunny habitats, although some species are found in lightly forested areas and at the edges of woodlands. Examples of common genera found in North America are goldenrod (*Solidago*), sunflower (*Helianthus*), daisy (*Chrysanthemum*), *Aster*, and ironweed (*Vernonia*). The predominant life-forms within the family are perennial herbs and shrubs, but some species exist as annuals, vines, lianas (woody vines), and trees. Leaf arrangement is most commonly alternate, although some genera do exhibit opposite leaves. Despite this gross morphological diversity, the feature that unites all the members of the family is the unique form of the compound inflorescence, or flowering head.

Inflorescence

At first glance, the flowering head of many *Compositae*, such as that of the sunflower, resembles a single large flower with what appears to be a set of petals surrounding a cluster of anthers and stamens. Upon closer inspection, this compound inflorescence, or capitulum, is really a collection of highly reduced and modified flowers borne on a flowering stalk (peduncle). The expanded and flattened top of the peduncle is the receptacle and is surrounded by a series of leaflike structures termed bracts that collectively comprise the *involucre*.

Two types of reduced flowers can be present within a capitulum, either ray or disc flowers, or both. The ray flower superficially resembles a petal and occupies the outer circumference of the capitulum. It can be either pistillate or sterile. The corolla is fused at the base, gradually expanding in width and eventually tapering to a tip. At maturity the tip of the ray flower corolla is oriented away from the center of the capitulum. The inner disc flowers can be either perfect (all reproductive parts present) or functionally staminate and possessing a corolla tube consisting of fused petals. At maturity the anthers and the stigmas will protrude from the corolla tubes. At the base of the corolla tube is a set of modified sepals termed the *pappus*. The pappus can consist of fine hairs, scales, or bristles, or it may be absent in some species. The seed is an achene and upon maturity is wind-dispersed with the assistance of the pappus.

Digital Stock

Dahlia *is one of numerous genera of* Compositae *that are used as ornamental plants.*

Pollination Biology

A variety of mechanisms account for successful pollination in the *Compositae*, wind pollination being a very common mode. "Hay fever," which in humans is an allergic reaction to plant pollen and other allergens, is greatly exacerbated in the late summer and early fall by the wind-pollinated ragweed (*Ambrosia*). Although often falsely accused, the goldenrods (*Solidago*) are not a major cause of hay fever, as they are pollinated by insects, not wind. By far, the majority of the species in the family are pollinated by insects, which are often attracted to the inflorescences by brightly colored ray flowers. The insect-pollinated flowers are typically generalists, attracting a variety of insects rather than a specific insect species. In some tropical taxa, birds or other animals are largely responsible for pollen exchange.

Economic Uses

Genera that contain species used for human consumption include endive and chicory (*Cichorium*), artichoke (*Cynara*), sunflower seeds and oil (*Helianthus*), lettuce (*Lactuca*), and dandelion greens (*Taraxacum*). Pyrethrum is a naturally occurring pesticide obtained from tansy (*Tanacetum*). Numerous genera are used as ornamental plants, such as marigolds (*Calendula*), *Zinnia*, bandana daisy (*Gaillardia*), and *Dahlia*. A number of plants are used for medicinal purposes. Coneflower (*Echinacea*) and fireweed (*Liatris*) are often used as herbal teas. Extracts from species of the *Compositae* are available from many health food retailers and practitioners of folk medicine. A current focus of pharmacological research is in determining those plant compounds responsible for producing beneficial effects in humans. Some species, however, contain compounds that at sufficient levels are quite toxic to animals, such as humans and livestock.

Evolutionary Success

Current opinion is that the family probably originated in South America or in the Pacific region, perhaps as early as the Tertiary period.

Several reasons have been proposed for the biological success of the family. First, the pappus is a very efficient agent for wind-borne dispersal of mature seeds, serving as a lofting device (similar to a parachute) to carry the small seeds on air currents over great distances. Second, the agents of pollination are diverse, ranging from mechanical (wind) to biological (insect or bird). Third, many members of the family exhibit unique chemical compounds (such as sesquiterpene lactones and polyacetylenes) that may discourage large herbivores and insects from foraging on the leaves, thus allowing plants to mature and engage in reproduction. It is the successful production of viable offspring that constitutes the major measure of evolutionary success in the family.

Pat Calie

See also: Angiosperm evolution; Angiosperm life cycle; Angiosperms; Biochemical coevolution in angiosperms; Eudicots; Flower structure; Flower types; Garden plants: flowering; Heliotropism; Inflorescences; North American flora; Plant domestication and breeding; Pollination; Seeds; South American flora.

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COMPOSTING

Categories: Agriculture; gardening; soil

Compost is a mixture of organic ingredients used for fertilizing or enriching land. Composting is the practice of making and using compost.

Composting is a way for gardeners and farmers to enrich and otherwise improve the soil while reducing the flow of household waste to landfills. Essentially the slow, natural decay of dead plants and animals, composting is a natural form of recycling in which living organisms decompose organic matter.

The decay of dead plants and animals starts when microorganisms in soil feed on dead matter, breaking it down into smaller compounds usable by plants. Collectively, the breakdown product is called humus, a crumbly, dark brown, spongy substance. Adding humus to soil increases its fertility. Compost and composting derive from the Old French *composter*, “to manure” or “to dung.”

History

The origins of human composting activities are buried in prehistory. Early farmers discovered the benefits of compost, probably from animal manure deposited on or mixed with soil. In North America, American Indians and then Europeans used compost in their gardens. Public accounts of the use of stable manure in composting date back to the eighteenth century. Many New England farmers also found it economical to use fish in their compost heaps.

While living in India from 1905 to 1934, British agronomist Sir Albert Howard developed today's home composting methods. Howard found that the best compost pile consists of three parts plant matter to one part manure. He devised the Indore method of composting, alternating layers of plant debris, manure, and soil to create a pile. Later, during the composting process, he turned the pile or mixed in earthworms.

How Composting Works

Composting is a natural form of recycling that takes from six months to two years to complete. Bacteria are the most efficient *decomposers* of organic matter. Fungi and protozoans later join the process, followed by centipedes, millipedes, beetles, or earthworms. By manipulating the composition and environment of a compost pile, gardeners and farmers can reduce composting time to three to four months. Important factors to consider are the makeup of the pile, the surface area, the volume, the moisture, the aeration, and the temperature of the compost pile.

Yard waste, such as fallen leaves, grass clippings, some weeds, and the remains of garden plants, make excellent compost material. Other good additions to a home compost pile include sawdust, wood ash, and kitchen scraps, including vegetable peelings, egg shells, and coffee grounds. Microorganisms digest organic matter faster when they have more surface area on which to work, so gardeners can speed the composting process by chopping kitchen or garden waste with a shovel or running it through a shredding machine or lawn mower.

The volume of the compost pile is important because a large compost pile insulates itself, holding in the heat of microbial activity, which in turn accelerates decomposition. A properly made heap will reach temperatures of about 140 degrees Fahrenheit in four or five days. Then the pile will settle, a sign that the process is working properly. Piles 3 feet cubed (27 cubic feet) or smaller cannot hold enough heat, while piles 5 feet cubed (125 cubic feet) or larger do not allow enough air to reach the microbes in the center of the pile. These portions are important only if the goal is fast compost. Slower composting requires no exact proportions.

Moisture and air are essential for life. Microbes function best when the compost heap has many air passages and is about as moist as a wrung-out sponge. Microorganisms living in the compost pile use the carbon and nitrogen contained in dead matter for food and energy. While breaking down the carbon and nitrogen molecules in dead plants and animals, they also release nutrients that higher organisms, such as plants, can use.

The ratio of carbon to nitrogen found in kitchen and garden waste varies from 15 to 1 in food waste to 700 to 1 in wood. A carbon-to-nitrogen ratio of 30 to 1 is optimal for microbial decomposers. This balance can be achieved by mixing two parts grass clippings (carbon to nitrogen ratio 19:1) and one part fallen leaves (carbon to nitrogen ratio 60:1). This combination is the backbone of most home composting systems.

Uses and Practice

In the twenty-first century, composting remains an invaluable practice. In landfills, yard and kitchen wastes use up valuable space. These materials make up about 20 to 30 percent of all household waste in the United States. Composting household waste reduces the volume of municipal solid waste and provides a nutrient-rich soil additive. Compost or organic matter added to soil improves soil structure, texture, aeration, and water retention. It improves plant growth by loosening heavy clay soils, allowing better root penetration. It improves the water-holding and nutrient-holding capacity of sandy soils and increases the essential nutrients of all soils. Mixing compost with soil also contributes to erosion control and proper soil pH balance, the amount of acidity or alkalinity present.

Some municipalities collect and compost leaves and other garden waste and then make it available to city residents for little or no charge. Some cities also compost sewage sludge, or human waste, which is high in nitrogen and makes a rich fertilizer. Properly composted sewage sludge that reaches an internal temperature of 140 degrees Fahrenheit

Image Not Available

contains no dangerous disease-causing organisms. One possible hazard, however, is that it may contain high levels of toxic heavy metals, including zinc, copper, nickel, or cadmium.

The basic principles of composting used by home gardeners also are used by municipalities composting sewage sludge and garbage, by farmers composting animal and plant waste, and by some industries composting organic waste. Food and fiber industries, for example, compost waste products from canning, meat processing, and dairy and paper processing.

J. Bradshaw-Rouse

See also: Biofertilizers; Organic gardening and farming; Soil; Sustainable agriculture.

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CONIFERS

Categories: Forests and forestry; gymnosperms; *Plantae*

The conifers, which are woody plants consisting mostly of evergreen trees, make up the phylum Coniferophyta, one of four phyla of gymnosperms that have living representatives. The word "conifer" means cone-bearing. Most conifers bear their reproductive structures in cones.

With 50 genera and 550 of the 700 known gymnosperm species, the phylum *Coniferophyta* includes the bulk of the *gymnosperms*. *Coniferophyta* is also the most widespread and, in terms of numbers of individual trees, the most abundant of the gymnosperm phyla. The abundance and economic and ecological importance of the *Coniferophyta* are out of all proportion to the number of species, which does not begin to compare to the 235,000 species of angiosperms (phylum *Anthophyta*).

Conifers grow over almost the entire world. They are especially abundant in northern temperate and boreal regions. They predominate in the taiga, or northern boreal forest, which covers immense stretches of northern North America and northern Eurasia. They dominate that forest by virtue of large numbers of individuals of only about a dozen species, mainly of spruce, fir, and larch. They show greater diversity in midlatitude, mountain forests of the Northern Hemisphere. Conifers also occur in cool mountain areas of the tropics. In temperate regions of the Southern Hemisphere, they are widespread but less dominant than in the north. Junipers and pines are the most wide-ranging conifers, occurring across the northern continents and into the tropics. In the Southern Hemisphere, the most widely distributed conifer genus is *Podocarpus*.

Due to their abundance and wide range, their typically arboreal habit, and their stem structure, conifers are the only gymnosperms that yield timber on a commercial scale. They are the source of all of the world's softwood timber and nearly half of its total annual lumber supply.

A Long Fossil Record

The oldest known conifer fossils date to the late Carboniferous period of the Paleozoic era, some 300 million years ago. The earliest known angiosperms are less than half this old. Conifers diver-

Conifer Leaves

Many conifers are characterized by drought-resistant, needlelike, scalelike, or comblike leaves covered in a waxy outer layer that assists in water retention during cold winters, when water uptake from the frozen soil is limited.

sified greatly during the Paleozoic's relatively dry, cold Permian period (290-245 million years ago), which followed the Carboniferous. The drought-resistant, needlelike leaves characteristic of many modern conifers may have evolved during that dry period.

The modern families of conifers began to differentiate in the Mesozoic era (245 million to 65 million years ago). Conifers were the dominant vegetation during much of that era. They gradually gave way to the angiosperms, which achieved worldwide dominance by about ninety million years ago, during the Cretaceous period of the Mesozoic, and remain dominant today. In the early Tertiary period of the Cenozoic era, which dawned about 66 million years ago, a diverse coniferous flora covered large areas of the Northern Hemisphere.

Classification of Conifers

Class *Pinopsida*
- Order *Pinales*
  - Family *Araucariaceae* (araucarias)
    - Genera: *Agathis*, *Araucaria*, *Wollemia*
  - Family *Cephalotaxaceae* (plum yews)
    - Genus: *Gephalotaxus*
  - Family *Cupressaceae* (cypresses)
    - Genera: *Actinostrobus*, *Austrocedrus*, *Callitris*, *Calocedrus*, *Chamaecyparis*, *Cupressus*, *Diselma*, *Fitzroya*, *Fokienia*, *Juniperus*, *Libocedrus*, *Microbiota*, *Neocallitropsis*, *Pilgerodendron*, *Tetrachnis*, *Thuja*, *Thujopsis*, *Widdringtonia*
  - Family *Pinaceae* (pines)
    - Genera: *Abies*, *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pinus*, *Pseudolarix*, *Pseudotsuga*, *Tsuga*
  - Family *Phyllocladaceae*
    - Genus: *Phyllocladus*
  - Family *Podocarpaceae* (podocarps)
    - Genera: *Acmopyle*, *Afrocarpus*, *Dacrycarpus*, *Falcatifolium*, *Halocarpus*, *Lagarostrobos*, *Lepidothamnus*, *Microcachrys*, *Microstrobos*, *Nageia*, *Parasitaxus*, *Prumnopitys*, *Retrophyllum*, *Saxegothaea*, *Sundacarpus*
  - Family *Taxodiaceae* (redwoods)
    - Genera: *Athrotaxis*, *Cryptomeria*, *Cunninghamia*, *Glyptostrobus*, *Metasequoia*, *Sciadopitys*, *Sequoia*, *Sequoiadendron*, *Taiwania*, *Taxodium*
- Order *Taxales*
  - Family *Taxaceae* (yews)
    - Genera: *Amentotaxus*, *Austrotaxus*, *Pseudotaxus*, *Taxus*, *Torreya*

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA, and Southern Illinois University at Carbondale, College of Science, http://www.sciencie.siu.edu/landplants/Coniferophyta.

Vegetative Features

Conifers have certain notable vegetative characteristics. For example, many, though not all, of them have needlelike leaves, and such leaves occur only in conifers. Some conifers have scalelike leaves, and a few have bladelike ones.

The stems and roots of conifers are also noteworthy, resembling the woody eudicots and magnoliids of *Anthophyta* in producing a dense mass of *secondary xylem*—that is, wood.

Reproductive Characteristics

In conifers, the ovules, which contain the eggs and eventually ripen into seeds, are not enclosed in ovary tissues within flowers as they are in the angiosperms. Instead, like other gymnosperms, conifers have *naked ovules*. These ovules are borne on scales that are arranged spirally along the axes of cones. Due to a complex evolutionary history, the structure of these cones is compound rather than simple.

In addition to ovulate, or female, cones, conifers produce male cones, which are smaller, shorter-lived, and generally less woody. The axis of a male cone bears reduced leaves, each with two *pollen sacs* on the undersurface. The pollen grains formed within the sacs contain the immature sperm. In most conifers, cones of both genders are present on the same tree. Although gymnosperms other than conifers may produce cones, conifers are distinctive in combining simple pollen cones with compound ovulate cones. The yews (genus *Taxus*) bear their ovules singly, at the tips of branchlets, rather than in cones. The seeds that develop from these ovules are enclosed in a fleshy covering called an *aril*.

In the spring, the male cones of conifers release their pollen to the wind. Some of it reaches female cones, which have their cone scales widely separated to receive it. After pollination, the female cones close their scales. Fertilization usually occurs, within the ovule, about three days to three or four weeks after pollination. In the pines, however, it is delayed for about fifteen months.

In most conifers, the mature seeds, with their contained embryos, are dispersed in the autumn of the year in which fertilization occurs. The most common dispersal agent is the wind, aided in many species by wings on the seeds. Conifer seeds that lack wings generally depend on dispersal agents such as birds or mammals. In some pines, the cones need the heat of a forest fire to open the scales and release the seeds.

Pine Family

Of the families of living conifers, the *Pinaceae*, or pine family, is the largest, containing ten to twelve genera, with about two hundred species worldwide. Most of these are resin-bearing trees.

This family is the most widespread and abundant conifer family in the Northern Hemisphere and very important economically. It supplies a great deal of lumber, pulpwood, and paper products. It is also important ecologically, providing essential cover, nesting habitat, and food for many species of wildlife.

The pine family's range is mainly in Eurasia and North America. Genera that occur all across this expanse are *Pinus* (pines), *Picea* (spruces), *Abies* (firs), and *Larix* (larches). Douglas firs (*Pseudotsuga*) and hemlocks (*Tsuga*) are restricted to North America and Asia. The true cedars (*Cedrus*) occur only in warm-temperate regions of Eurasia and northern Africa. Three genera of the pine family are restricted to China.

Pinus, the oldest genus in the pine family, arose at least 130 million years ago, in the early Cretaceous period. It grows predominantly in the Northern Hemisphere. The pines number more than ninety species, nearly half the total species of the *Pinaceae*. One of the world's oldest known plants is the bristlecone pine (*Pinus longaeva*), which grows in Utah, Nevada, and a small area of western California. Some bristlecone pines are about forty-six hundred years old. In contrast to other conifers, pines produce their adult needles in *fascicles*, or bundles. The number of needles per fascicle depends on the species.

Other Conifer Families

According to a commonly used classification system, there are seven families of conifers in addition to the *Pinaceae*. A notable one is the *Taxodiaceae*, which is today represented by widely scattered species that are the remnants of populations that were much more widespread during the Tertiary period. Bald cypress belongs to the *Taxodiaceae*, as do two redwood species renowned for their size and longevity. The coast redwood (*Sequoia sempervirens*) grows along coastal California and Oregon, and the "big tree" (*Sequoiadendron giganteum*) occurs on the western slope of the Sierra Nevada mountains in California. The coast redwood is generally the taller of the two species, reaching up to 117 meters in height. The big tree, however, generally exceeds the coast redwood in total mass and can live to be several thousand years old.

Another notable member of the *Taxodiacae* is the dawn redwood (*Metasequoia glyptostroboides*). This species was first known to science only from fossils discovered in the early 1940's. Not long afterward, the tree was found growing in China. A more recent living-fossil find belongs to the *Araucariaceae*, a conifer family restricted to the Southern Hemisphere. This tree, the Wollemi pine (*Wollemia nobilis*), had been thought to have gone extinct fifty million years ago. Then, in 1994, a stand was found growing in Australia.

The *Cupressaceae*, or cypress family, includes *Chamaecyparis* (false cypress), *Juniperus* (junipers, often called "cedars" in North America), and *Thuja* (arbor-vitae). These plants are distributed throughout the world. Some are important as timber or ornamentals.

The *Taxaceae* family, which includes the yews, is widely distributed in the Northern Hemisphere. The *Podocarpaceae* is largely restricted to the Southern Hemisphere. The *Sciadopityaceae* and *Cephalotaxaceae* are confined to east Asia.

Jane F. Hill

See also: Asian flora; European flora; Evolution of plants; Forest fires; Gymnosperms; North American flora; Pollination; Seeds; Taiga; Wood.

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CORN

Categories: Agriculture; economic botany and plant uses; food

The most important cereal in the Western Hemisphere, corn is used as human food (ranking third in the world), as livestock feed, and for industrial purposes.

Corn (*Zea mays*) is a coarse, annual plant of the grass (*Gramineae*) family. It ranges in height from 3 to 15 feet and has a solid, jointed stalk, and long, narrow leaves. A stalk usually bears one to three cobs, which develop kernels of corn when fertilized. Corn no longer grows in the wild; it requires human help in removing and planting the kernels to ensure reproduction. In the United States and Canada, "corn" is the common name for this cereal, but in Europe, "corn" refers to any of the small-seeded cereals, such as barley, wheat, and rye. "Maize" (or its translation) is the term used for *Zea mays* in Europe and Latin America.

Explorer Christopher Columbus took corn back to Europe with him in 1493, and within one hundred years it had spread through Europe, Asia, and Africa. It is said that a corn crop is being harvested somewhere in the world each month. Corn grows as far north as Canada and Siberia (roughly 58 degrees north latitude) and as far south as Argentina and New Zealand (40 degrees south). Although adaptable to a wide range of conditions, corn does best with at least 20 inches of rainfall (corn is often irrigated in drier regions) and daytime temperatures between 70 and 80 degrees Fahrenheit (about 24 degrees Celsius). Much of the United States meets these criteria, hence its ranking as the top corn-producing country in the world.

Origins and Hybridization

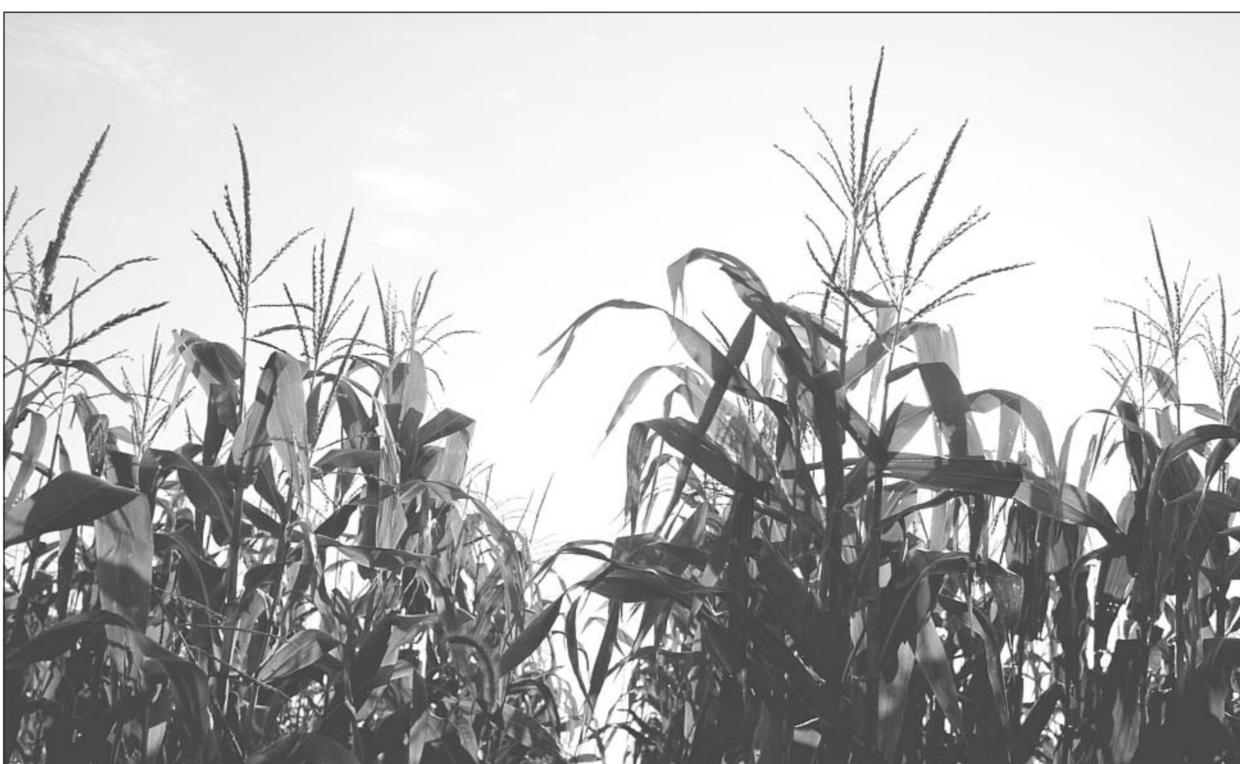
Corn's exact origins remain uncertain, but historical records show the gathering of wild corn, called *teosinte*, in ancient Mexico began around 7000 B.C.E. This corn evolved through unknown means to have tiny, eight-rowed "ears" of corn less than an inch long. Corncobs and plant fragments have been dated to 5200 B.C.E. (and up to a millennium earlier, according to some studies). By 3400 B.C.E., the fossil record shows a marked change in corn, notably increased cob and kernel size, indicating greater domestication. Fully domesticated corn (which could not survive without human help) had replaced the wild and other early types of corn by 700 C.E.

Extensive attempts at *hybridization* began in the late nineteenth century, but the increase in yield was usually a disappointing 10 percent or so. By 1920 researchers had turned to inbreeding hybridization programs. In these, corn is *self-fertilized*, rather than being allowed to *cross-pollinate* naturally. Following a complex sequence of crossing and testing different varieties, the lines with the most desirable traits were put into commercial use, and they often produced 25 to 30 percent gains in yield. Although these early hybrids focused on increasing the yield, researchers later began to look for insect-resistant and disease-resistant qualities as well. One of the hybridizers of the 1920's was Henry A. Wallace, founder of Pioneer Seed Company (the world's largest seed company) and later U.S. vice president under Franklin D. Roosevelt. By the 1950's hybrid corn varieties were in widespread use.

Types and Uses

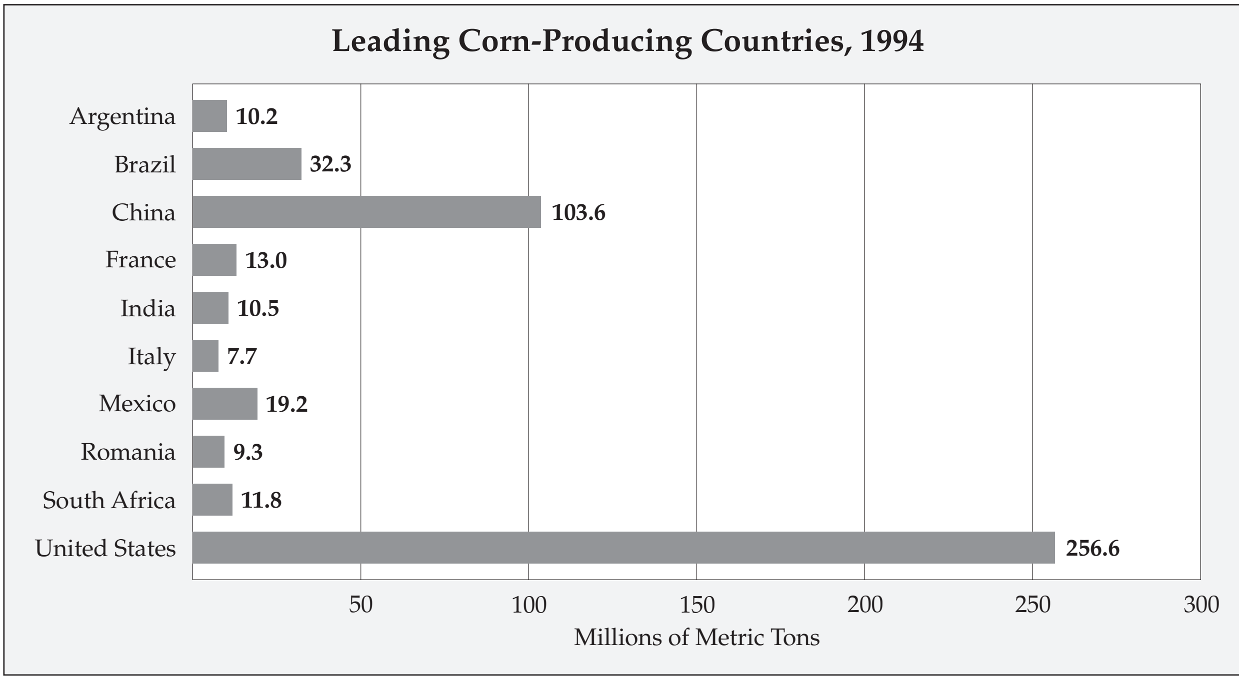
The types of corn still in use are dent, flint, flour, pop, and sweet. Dent corn, characterized by a "dent" in the top of each kernel, is the most important commercial variety. Flint corn tends to be resistant to the rots and blights known to attack other types; it is also more tolerant of low temperatures and therefore appears at the geographical edge of corn's range. Flour corn is known for its soft kernel, making it easier to grind into flour and thus popular for hand-grinding. A mainstay at American movie theaters and as a snack food, popcorn will, with an optimum moisture content of about 13 percent, explode to as much as thirty times its original volume when heated. Also popular in the United States and eaten fresh, sweet corn is so named because, unlike other types, most of the sugars in the kernel are not converted to starch.

Commercially, corn is used mostly for livestock feed and industrial processing. It is high in energy and low in crude fiber but requires supplements to make a truly good feed. Industrial processing creates a great variety of products found in everyday



PhotoDisc

Corn, one of the world's three major staple crops, no longer grows in the wild; it requires that humans remove and plant the kernels (seeds) to ensure reproduction.



Note: World total for 1994 was approximately 570 million metric tons.
Source: U.S. Department of Commerce, *Statistical Abstract of the United States, 1996*, 1996.

life—underscoring the importance of corn to the world's economy.

Processing takes place in one of three ways: wet milling, dry milling, or fermentation. In wet milling, corn is soaked in a weak sulfurous acid solution, ground to break apart the kernel, and then separated. The resulting by-products are found nearly everywhere. The cornstarch supplies corn syrup (it is sweeter than sugar and less expensive, and billions of dollars' worth is produced for soft drink manufacturers each year), starches used in the textile industry, ingredients for cooking and candymaking, and substances used in adhesives, to name a few. Other by-products provide cooking oil; oil used in mayonnaise, margarine, and salad dressing; soap powders; and livestock feed. Dry milling is a simpler process, involving the separation of the *hull* from the *endosperm* (the food storage organ, which is primarily starch in most corn) and the *germ* (the plant embryo) by repeated grinding and sieving. Dry milling produces hominy, grits, meal, and flour, all of which are used for human consumption. Fermentation of corn changes the starch to sugar, which is then converted by yeast to alcohol. The process eventually results in ethyl alcohol, or ethanol (which is blended with gasoline to reduce carbon monoxide emissions), acetone, and other substances.

Brian J. Nichelson

See also: Agricultural revolution; Agriculture: traditional; Agriculture: world food supplies; Central American agriculture; Grains; Grasses and bamboos; Green Revolution; Hybridization; North American agriculture; South American agriculture.

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CRYPTOMONADS

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

The phylum Cryptophyta *describes tiny, motile, unicellular organisms with two slightly unequal flagella bearing lateral hairs. Cryptomonads live mainly in marine and freshwater environments.*

Some cryptomonads are alga-like, with blue-green, red, and olive-brown photosynthetic pigments including chlorophylls *a*, *c2*, alpha-carotene, xanthophylls (alloxanthin, crocoxanthin, zeaxanthin, and monadoxanthin), and phycobiliproteins (phycoerythrin and phycocyanin). Cryptomonads are found in a variety of moist places, such as algal blooms in the ocean or in fresh water, and on beaches. Some members are intestinal parasites in animals.

Classification

Historically, botanists and zoologists alike have adopted cryptomonads. Botanically, cryptomonads would be included in kingdom *Plantae*, phylum *Cryptophyta*, class *Cryptophyceae*, order *Cryptomonadales*, and family *Cryptomonadaceae*. Zoologists would place the cryptomonads in kingdom *Animalia*, phylum *Sarcomastigophora*, class *Phytomastigophora*, order *Cryptomonadida*, and family *Cryptomonadidae*. Also, the cryptomonads are currently included in a separate kingdom, *Protoctista* (also known as *Protista*), with phylum, class, order, and family taxa being the same as that for the botanical taxa above.

Synonyms for *Cryptophyta* are *Cryptomonadales*, *Cryptophyceae*, and *Chromophyta*, and they were once placed with the algae. Genera for the cryptomonads include the following: *Chilomonas*, *Chroomonas*, *Cryptomonas*, *Cyathomonas*, *Falcomonas*, *Geminigera*, *Goniomonas*, *Guillardia*, *Hemiselmis*, *Komma*, *Plagiomonas*, *Pyrenomonas*, *Rhodomonas*, *Storeatula*, and *Teleaulax*. *Guillardia theta*, formerly known as *Cryptomonas phi*, has been studied most extensively, and the complete chloroplast genome is known (Genbank accession number AF041468).

Ecology

The cryptomonads are part of the nanoplankton (typically phytoplankton between 2 to 20 micrometers in diameter) and are a relatively small but ecologically and evolutionarily important taxon. Both freshwater and marine representatives are known. Many photosynthetic species likely retain their capacity to eat prey (mixotrophy). Fluctuations in their numbers are correlated with increases in levels of nitrogen in the water in which they live. Some species of cryptomonads form gelatinous colonies. A few cryptomonads have reached the palmelloid or sessile stage of organization, but most are free-living flagellates common in nutrient-rich water. A weakly filamentous member of the cryptomonads is *Bjornbergiella*. Well-known examples of cryptomonads are *Cryptomonas ovata*, *C. similis*, and *Chilomonas paramecium*.

The cryptomonads can form major blooms in Arctic and Antarctic waters as well as in North America's Chesapeake Bay. They can be very important food sources for smaller heterotrophic or mixotrophic plankton, including ciliates and dinoflagellates. Cryptomonads are found in freshwater lakes, ponds, and ditches—especially in colder waters. They are dominant species in many Antarctic lakes, and they are also found in interstitial water on sandy beaches. Reproduction in the cryptomonads is generally asexual in culture, but sexual reproduction has been documented in the *Cryptophyta*.

Characteristics

Cryptomonads are tiny flagellates, 5 to 30 microns (most around 10 to 20 microns). They are flattened dorsiventrally in shape and are asymmetrical, with a *periplast* (a proteinaceous structure that lies inside the plasmalemma and is attached to it). Cryptomonads are mostly algal forms, with an anterior (ventral) groove or pocket and a gullet, which has refractile *ejectosomes* or *trichocysts*. The unequal flagella are inserted nearly parallel to the pocket, not inside the gullet as in the euglenophytes. Mitochondria have flat cristae, while the plastids are secondary with a highly reduced eukaryotic nucleus, the *nucleomorph*.

Although there are a few colorless forms, such as *Chilomonas*, most cryptomonads have a chloroplast. The chloroplast is not contained directly, however, because there is a reduced eukaryote symbiotic within the cell containing a normal prokaryote chloroplast. Usually, there are two chloroplasts, which are secondary plastids. The chloroplast is bound by four membranes (two being chloroplast endoplasmic reticulum, or CER, continuous with the nuclear envelope and homologous to a food vacuole) with a tiny nucleus (nucleomorph) between the middle two membranes. Much like the dinoflagellates (with which the cryptomonads were formerly grouped), it has chlorophylls *a* and *c*; chlorophyll *b* is never present. Thylakoids are paired, and phycobilin pigments are present in the spaces between the thylakoids but not in phycobilisomes, such as in the cyanobacteria and *Rhodophyta*. Food reserves are starchlike, accumulating in the periplastidal space stored between the starch envelope and the chloroplast reticulum. If there is an eyespot, it is inside a plastid not associated with the flagella.

There is a large nucleus at the posterior end. Mitosis is open, and centrioles are not associated with mitosis. Cell division is by furrowing. No histones are associated with the chromosomes. The unique nucleomorph has deoxyribonucleic acid (DNA), is contained within a double membrane, and also has a nucleolus-like region. Molecular data suggest and strongly support the idea that the nucleomorph is a vestigial nucleus from the original endosymbiont, which became the cryptophyte chloroplast. Three chromosomes are associated with the nucleomorph: 240 kilobase pairs (kb), 225 kb, and 195 kb. The bulk of chromosome II (175 kb) is now sequenced with a preponderance of "housekeeping genes" apparently existing for the service of just a few genes encoding plastid proteins. There are parallels between the nucleomorphs of cryptomonads and chlorarachniophytes. The cryptomonad nucleomorph is depauperate in introns, with ribosomal ribonucleic acid (rRNA) genes at the chromosome ends just within the telomeres.

The longer flagellum has two rows of *mastigonemes* (lateral hairs), while the shorter flagellum has a single row. Mastigonemes are two-parted bristles or hairs made up of a rigid, tubular base and, usually, two terminal hairs. These bristles are formed within the endoplasmic reticulum (or nuclear envelope) and are thus transported to the exterior of the cell. The flagella are covered with scales, too.

Trichocysts or *ejectosomes* are in the oral groove, and they are scattered around the cell surface. There is a tightly spooled protein in the trichocysts, which can undergo a very rapid, irreversible conformational change in which it pops out of the cell, pushing the cell backward as a result. The trichocysts are considered a defense mechanism or are perhaps involved in predation.

Evolution

Evolution and phylogeny of cryptomonads have not been well documented using molecular techniques. An 18S ribosomal RNA phylogeny of cryptomonads has been made, however. The nucleus of the endosymbiont (the nucleomorph) does not seem to have a complete complement of genes for photosynthesis, these being relocated to the host nucleus now. Plastid targeting mechanisms of cryptomonads for light-harvesting complex proteins have been studied, though.

The primary plastid is of unknown origin and remains under scrutiny but is probably from a red algal lineage, as the presence of phycobilins is suggestive of the *Rhodophyta* (red algae). Chlorophyll *c* is unknown among the red algae, however. Molecular phylogenetic studies place the nucleomorph close to red algae, and the chloroplast genome map has characteristics suggesting a reduction series from red algae to cryptomonads to heterokonts. This does not imply any descendant relationship among extant groups but rather retention of ancestral character states from common ancestors.

Lateral gene transfer from an ancestral cryptomonad to a dinoflagellate is postulated from sequence analysis of two nuclear-encoded glyceraldehyde-3-phosphate dehydrogenase (GAPDH) genes isolated from the dinoflagellate *Gonyaulax polyhedra*. The plastid sequence forms a monophyletic group with the plastid isoforms of cryptomonads, distinct from all other plastid GAPDHs. This provides the first example of genetic exchange accompanying symbiotic associations between cryptomonads and dinoflagellates, which are common in present-day cells.

F. Christopher Sowers

See also: Algae; Chloroplasts and other plastids; Dinoflagellates; Heterokonts; Photosynthesis; Phytoplankton; Plant science; *Protista*; Red algae; Systematics and taxonomy; Systematics: overview.

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CULTURALLY SIGNIFICANT PLANTS

Categories: Economic botany and plant uses; food; medicine and health

Plants are often used as a tool for ceremonial purposes, as artistic media to express indigenous traditions, or as herbal remedies or hallucinogenics to fulfill cultural needs and expectations. Culturally significant plants grow on all continents and are used by all ethnicities.

Historically, humans have appropriated plants for numerous cultural applications. Since prehistoric times, plants have served as symbolic organisms to represent aspects of the life cycle and seasonal changes, to worship, and to make offerings to gods. Plants were incorporated into mythology and legends to show their meanings to various cultures.

Ethnobotany

American Indians are an example of a historic ethnic group which selected specific plant species for cultural uses, such as rituals and ceremonies. These plants have significant roles in the lives of modern American Indians involved in preserving botanical cultural activities by recording information about the horticultural habits of their ancestors, such as knowing where plants grow, when and how they are harvested, how they are prepared and for what functions, and their role in sustaining tribal ethnicity.

Ethnobotanists investigate how cultures identify with and use plants. This scientific field addresses how people throughout time have managed plants, including cultivation methods to improve the quantity and quality of yields and to meet specific needs and requirements. Researchers compare societies' interactions with plants to theorize and determine why people at varying times and places selected certain plants for ceremonies or social uses. The U.S. Department of Agriculture's National Plant Data Center (NPDC) issues culturally significant plant guides which update ethnobotany theories and knowledge.

Religious Uses

Plants, especially trees, have been assigned spiritual roles since prehistory. Humans' daily lives have been influenced by how they perceive and integrate plants into their activities. Christians use plants and flowers, such as the Easter Lily, to represent the history of Jesus Christ. At Palm Sunday ceremonies, palms are the primary Christian botanical symbol for immortality and are used to designate martyrs and divine people and places. Ancient legends describe the Tree of the Cross, which provided the wood for Christ's crucifixion.

Because trees can attain sizable heights and girths, humans have considered them remarkable and worthy of veneration. The strength and longevity of most trees reinforced people's ideas that groves have mythical qualities, and tree cults were formed to protect them. The rarity of trees in many regions, particularly in the Middle East and in African deserts, convinced people that trees were divine and that specific trees could be regarded as sacred.

In Siberia, ancient people were silent when in shaman forests to express respect for gods and spirits they believed dwelled there. Celtic tribal names were derived from tree nomenclature. Many cultures' rituals involved ceremonies with oak trees, because ancient people thought the dead resided inside oaks. Pagan peoples used trees to mark heroes' graves.

Image Not Available

Germanic tribes erected trunks as pillars, and in the ninth century the Frankish king Charlemagne had them cut down in his effort to Christianize Europe. Christians destroyed groves where tree cults worshiped and built churches on these sites. The interior decorations of cathedrals often included tree and acorn imagery that reminded worshipers of the groves. Other types of architecture incorporated plants in designs, such as palm fronds and bark on columns and branchlike arches.

Roman legends tell how the Trojan War hero Aeneas and his guide, the Sybil, were permitted entry to the Elysian Fields, a blessed place, by presenting the Golden Bough. Pre-Columbian people living on the American continents gave cacti as sacraments, hoping this would enable them to have communion with the gods. At Zeus's sanctuary in ancient Greece, an oak was believed to be an oracle because its leaves made noises which priestesses interpreted as Zeus's voice.

In Norse mythology, the ash tree Yggdrasil's roots and branches connected the underworld and heaven. One of the most famous culturally significant plants was the Tree of Knowledge of Good and Evil in the biblical Garden of Eden. Medieval miracle plays often featured the Garden of Eden. The Hanging Gardens of Babylon, an ancient wonder of the world, was an artificial, terraced mountain with lush greenery, which archaeologists have been unable to prove existed. Tales about the gardens enticed the imagination in the ancient world.

Trees are significant to many religions' origin. The Bodhdruma, or Bo Tree, is sacred to Buddhists because it is a pipal tree (*Ficus religiosa*, a form of fig tree) under which Siddhartha Gautama sat to receive enlightenment to become Buddha. In modern Thailand, Buddhists sprinkle water on religious statues of Buddha adorned with orchids, and many temples keep orchids in large pottery bowls filled with water to serve this purpose. Tree myths and traditions are also practiced in other parts of Asia. Indians believe that ghosts awaiting reincarnation live in fig trees. Because they are evergreen, pines represent immortality to many cultures.

Ceremony

Many plants are identified with ceremonial activities that commemorate holidays or anniversaries or celebrate a rite of passage in which an individual enters a new phase of life. When celebrating the new year, ancient peoples used plants in symbolic acts, such as drinking cactus juice to appeal to gods to bless them with sufficient rains and large crop yields. Before emancipation, African-American slaves jumped over a broom made from straw as a way to validate publicly their commitment to marriage when such unions were illegal.

In the modern world, vestiges of these ceremonial uses of plants retain some of their symbolic significance. Flowers are often used symbolically in romantic courtship. Plants convey meanings of love, fidelity, and longevity at weddings and are selected in accordance with personal preferences as well as regional and religious customs.

Plants memorialize people. In the United States on Mother's Day, women wear corsages that indicate whether their mother is alive or deceased. Red poppies pay tribute to soldiers' sacrifices on veterans' and memorial holidays. On Decoration (Memorial) Day, many people place flowers on graves as a form of respectful remembrance. Roses are often thrown into oceans near offshore plane crash sites. Flowers form makeshift memorials where people tragically died or at their homes.

At holidays, including Valentine's Day and Christmas, people give symbolic plants with meanings, such as renewal and protection, that have developed from religious and historical customs. Holly was sacred to Romans who feted Saturn, god of agriculture, at Saturnalia festivals during the winter solstice. Early Christians decorated with holly to avoid persecution; later, that plant was incorporated into Christian rituals. People went "wassailing" to pay tribute to apple orchards by anointing their roots with cider to wish for large spring yields.

Uses

Plants are used culturally for nutrition. Ancient peoples from diverse civilizations revered various crop spirits, including the Corn Mother and the Corn Maiden, which appeared in various forms in Europe, the Americas, Asia, and Africa. Often, people believed that spirits of crops resided within specific people in their communities. Human sacrifices and the ceremonial slaying of figures representing agricultural phases were sometimes held in the hope that such offerings would appease gods and assure ample harvests.

Many plants are harvested for medicinal uses. Often, plants are incorporated as drugs in religious rituals. Peyote has been used ceremonially by native peoples since pre-Columbian times for its hallucinogenic properties, which users thought assisted communication with gods and brought on supernatural powers. American Indians are guaranteed legal rights to use otherwise illegal plants for religious purposes.

Plants express cultural values. Plant fibers are used to weave baskets and clothing. Crushed plant parts create dyes which can be used to stain fabric, write, or draw. Plants inspire superstitions: For example, three-leaf clovers are considered lucky because Saint Patrick convinced Druid leaders to convert to Christianity by stating the shamrock was proof of the Trinity. Often, plants have different meanings: Peonies, for example, represent faithfulness to some cultures and shame in others. Literature and works of art—including Aesop's fables, William Shakespeare's plays, the children's story "Jack and the Beanstalk," and Wagnerian operas—have featured plant themes.

Cornfields are shorn into mazes for amusement. In the United States, nostalgia for old-fashioned plants resulted in heirloom seeds becoming popular. Authorities and ethnic groups are attempting to preserve, restore, and reestablish culturally significant plants in natural settings in order to retain traditional use of such plants for ceremonies, food, and craftsmanship and perhaps develop innovative future applications.

Elizabeth D. Schafer

See also: Agricultural revolution; Agriculture: traditional; Corn; Garden plants: flowering; Herbs; Human population growth; Medicinal plants; Plant fibers; Plants with potential; Spices; Textiles and fabrics.

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CYCADS AND PALMS

Categories: Angiosperms; economic botany and plant uses; gymnosperms; paleobotany; *Plantae*

Members of the phylum Cycadophyta, *cycads are descendants of giant, prehistoric seed-bearing, nonflowering plants that thrived when dinosaurs lived. Palms are flowering plants with primitive origins that share characteristics with cycads but are not related to them.*

Cycadophyta is one of the four phyla of *gymnosperms* in the kingdom *Plantae*. At one time, cycads grew on every continent. Fossil cycads have been located in areas where no modern cycads grow, such as Antarctica and Europe, suggesting that those places once had milder temperatures.

Origins and Habitat

The oldest cycad fossils are 245 to 208 million years old, from the Triassic period. The first cycads are believed to have appeared in the Permian period 270 million years ago. Some botanists hypothesize that cycads originated as *progymnosperms* in the Devonian period about 408 million to 360 million years ago. During the Jurassic and Cretaceous periods (65 million to 195 million years ago), cycads flourished on earth, dominating plant life. With the beginning of the Ice Age, cycads gradually diminished in population but did not disappear. Some Paleozoic- and Mesozoic-era cycad genera became extinct.

Modern cycads are classified in 150 to 200 species, 11 genera, and 3 families. The most commonly seen cycad species belong to the genus *Cycas* and exhibit some structural characteristics found in palms, conifers, and ferns. Botanists consider cycads valuable in the study of plant evolution. Modern cycads live primarily in the tropics and other regions with warm temperatures and high humidity and are indigenous to Asia, Africa, Australia, and Latin America. Growing in Florida, *Zamia integrifolia* is the only North American cycad species.

Cycad Structure

Cycads consist of a stem with large, long, narrow leaves similar to palm fronds, gathered at the top in a circular crown. Seeds are located in cones on branch ends. Trunks vary from tall stems as high as 20 meters (66 feet) to short trunks standing about 2 meters (6.5 feet). Some have tuberous stems below the soil surface. A trunk's base and crown are of almost equal thickness. New leaves are tender, hardening as they mature, and their bases form armor on stems. They vary in length from 20 centimeters to 3 meters (8 inches to 10 feet).

Cycads lack growth rings, but their age can be estimated by counting the number of whorls on leaf scars on stems to determine how many annual or biennial leaf productions have occurred. Using this method, botanists have speculated that it is possible, although rare, for some cycads to have life spans of one thousand years.

Seedling cycads have a taproot that is later replaced by secondary roots called *coralloid roots*, and subterranean stems anchor the aboveground stem to the soil. Some roots have bacteria which manufacture helpful amino acids and fix nitrogen. The *Zamia pseudoparasitica* is the only epiphytic cycad species.

Image Not Available

Cycad Reproduction

The reproductive cycle can last as long as fourteen months. Female and male cones grow on separate cycads. Pollen with spermatozoids, which are motile sperm, is produced in male cones and fertilizes female cones. Insects (not wind, as was believed until 1993) deliver pollen. Cone-generated heat creates a minty scent appealing to insects. Each cone can produce as much as 200 cubic centimeters (12.2 cubic inches) of pollen annually.

Seeds are scattered when cones fall apart. Only fertilized seeds germinate. Seedlings often require several years before their trunks emerge from the ground. Cycads aid scientists in developing theories about reproduction of extinct seed plants and provide insight on how insect polli-

Classification of Cycads

Class *Cycadopsida*
Order *Cycadales*
Family *Cycadaceae* (cycads)
Genus:
Cycas
Family *Stangeriaceae*
Genera:
Bowenia (natal grass)
Stangeria
Family *Zamiaceae* (sago palm family)
Genera:
Ceratozamia
Chigua
Dioon
Encephalartos
Lepidozamia
Macrozamia
Microcycas
Zamia

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA, and Christopher J. Earle, http://www.botanik.uni-bonn.de/conifers.

nation evolved. Such pollination occurred prior to the existence of angiosperms, or flowering plants (the phylum *Anthophyta*).

Palms

Although cycads and palms can outwardly resemble each other, palms are members of a different phylum and family, the family *Arecaceae* within the phylum *Anthophyta* (angiosperms). Modern palms are represented by approximately twenty-six hundred species. They are the fourth largest group of monocots. (Monocots are one of two large divisions of the angiosperms.) The earliest known palm fossils are eighty million years old and from the Late Cretaceous period. Fossilized palms with pollen indicate that these plants were some of the earliest flowering plant families.

Palms thrived during the Eocene epoch, and a variety of primitive genera grew in Asia, Europe, and North America. Most modern palms live in forests, deserts, swamps, and mountains of tropical regions in Asia, Africa, the South Pacific, the Mediterranean Basin, and the Americas. Some species are confined to specific islands, such as the *Maxburretia gracilis* on the Langkawi Islands. Some palm stands cover hundreds of square miles and consist of millions of plants.

Structurally, palms are similar; all have slender trunks. Most species lack branches and have a leafy cluster on top. Some palms are as tall as 30 meters (98 feet). Seedlings grow a large tip, and most of the bulk forms underground. Upon maturity, trunks maintain the same diameter. Coconut palms have an average diameter of 45 centimeters (18 inches). A network of roots both above and below the surface secures trunks to the ground. Palms are mostly vertical, although some grow horizontally or like vines. Some climbing rattan palms are 182 meters (597 feet) long.

Palm stems consist of masses of densely compacted fibrous strands. Leaves grow from nodes at the tips of stems, causing sharp scars when leaves are shed. Date palms have leaves 3 meters (10 feet) long, and coconut palm leaves average more than 4 meters (13 feet) long. Leaf production offers hints about the age of palms, which average 50 to 100 years, with some *Lodoicea maldivica* attaining 350 years and an Australian *Livistona eastonii* reaching 720 years. Palms first produce seeds approximately eight years after germination and mature at age thirty.

Palms have masses of small flowers, often numbering in the thousands, which are composed of sepals, petals, and male stamens. The female pistil in flowers either forms a soft, berrylike fruit, containing one or more seeds, or a more rigid fruit (a coconut or date), referred to as a drupe, which has a husk and shell encasing one seed. Insects, bats, and wind pollinate palms. Animals eat the fruit, distributing the seeds in their feces.

Uses of Cycads and Palms

Sago is a starch extracted from the stems of palms and cycads. It is used for cooking after the alkaloid is removed. Some leaves and seeds are also edible, but many seeds are poisonous. An amino acid produced by cycads, B-methylamino-L-alanine (BMAA), causes dementia in people who ingest the chemical. Researchers have attempted to discern why cycads manufacture this neurotoxin and do not react like other plants to its presence. The mapping of genes for susceptibility to BMAA may one day help to treat people with neurodegenerative conditions. Cycasin, the carcinogenic compound methylazoxymethanol, a glucoside found in cycad seeds, is also toxic.

Palms yield vegetable oil, waxes, sugars, fats, and saps which are distilled into liquor. Dates and coconuts are popular foods produced by palms. A date palm produces several hundred dates yearly. People consume stems, leaves, nuts, and roots. Rattan palm fibers are used for making furniture, baskets, bags, and other items. Some palm wood is appropriated for veneers, cups, and canes.

Coconut palms can each grow more than one hundred nuts annually. Palms provide essential nutrients for many world populations. Oily coconut liquid and coconut milk are considered delicacies. Leaves from coconut palms make useful thatching material. Coir, the husk's fiber, is twisted into rope. Coconuts have meat that is eaten or processed into *copra* for candles, oil, and other oil-based products. Palm products are crucial in regional and global trade.

Cycads and palms are used ornamentally for landscaping gardens. Some species are suitable for bonsai in interior displays. Because they are often poached to meet collectors' demands, cycads risk extinction. Smugglers locate and ship cycads (such as sago "palms") to clients throughout the world. A limited number of licenses to gather and trade cycads and other protected plants are issued by the Convention on International Trade in Endangered Species (CITES), a 1975 agreement observed by 156 ratifying countries as of 2001 to establish protective legal guidelines to monitor international trade of approximately twenty-five thousand rare plant species and five thousand rare animal species. CITES forbids collection activities that pose risks to wild plant populations.

In Hot Springs, South Dakota, Fossil Cycad National Monument was designated in 1922. In 1957 the site became the first national park service unit to be closed permanently, after collectors removed all of the 120-million-year-old fossils from a prehistoric cycad forest. Cycad conservation efforts in-


Digital Stock

Palms are angiosperms (flowering plants). Date palms like these can produce several hundred dates yearly.

clude guarding habitats and artificially propagating species. Rare specimens such as the South African *Encephalartos woodii* cycad, of which only thirty-eight, all male, specimens existed in 2001, are implanted with microchips to track their shipment to botanical exhibitions.

Nong Nooch Tropical Gardens near Pattaya, Thailand, has one of the world's largest collections of Asian cycad and palm varieties. Botanists saved an undescribed cycad species that grows on limestone cliffs from being destroyed when limestone was gathered for construction material in Bangkok. The gardens hosted the 1998 International Palm Society Biennial and the 2002 Sixth International Symposium on Cycad Biology. In South Africa, the Modjadji Cycad Nature Reserve has both cycads and palms, including the largest stand of the enormous *Encephalartos transvenous* (Modjadji palm).

Elizabeth D. Schafer

See also: Culturally significant plants; Endangered species; Evolution of plants; Fossil plants; Fruit crops; Paleobotany; Plant fibers; Pollination.

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CYTOPLASM

Categories: Anatomy; cellular biology

The cytoplasm is defined as all of the living matter within the plasma membrane of a cell, except for the nucleus, which is isolated from the cytoplasm by the nuclear envelope.

The cytoplasm, bounded by the plasma membrane, is composed of fluid called the *cytosol* in which floats a large variety of molecules and molecular assemblages, *ribosomes* (responsible for polypeptide synthesis), and a variety of other structures called *organelles* (literally meaning "little organs"). Numerous biochemical processes occur in the cytosol, including protein synthesis (*translation*) and *glycolysis*.

Vacuoles

The *vacuole* is the largest, most noticeable, organelle in plant cells (up to 40 micrometers in length). Vacuoles are membrane-bound sacs that can occupy up to 90 percent of the plant's cell volume. The vacuole serves a wide range of purposes, depending on the cell type. It is filled with water and a variety of salts, sugars, organic acids, pigments, or proteins. The vacuoles of flower petal cells contain blue, red, or pink water-soluble pigments. In other cells, the vacuole is full of toxic compounds that deter insect attack. Vacuoles in seed cells contain storage proteins that are remobilized during seed germination and used for early seedling growth.

Plastids

Plastids are the next largest easily observable organelle (5 to 10 micrometers in diameter). *Plastids* are surrounded by a double membrane and are involved in a variety of biosynthetic reactions in the plant cell. All plastids start as immature *proplastids* in *meristematic* (young and undifferentiated) cells. Then, depending upon which tissue type grows from that meristem, proplastids may develop into one of several different mature plastid types.

The most prominent type of plastid is the *chloroplast*, contained primarily in leaf cells. Chloroplasts are colored by the green pigment *chlorophyll*. They are the site of *photosynthesis* and a number of other biosynthetic reactions. *Chromoplasts* are red, orange, or yellow, as a result of their high levels of *carotenoids*. They are found in the petals of flowers, old leaves, some fruits, and even in some roots, such as the carrot.

Parts of the Plant Cell

Part	*Location in Cell*	*Description/Purpose*
Cell wall	Outer layer	Outer boundary of cell, comprising middle lamella, primary wall, sometimes a secondary wall, and plasmodesmata.
Chloroplasts	Cytoplasm	Two-membrane-bounded organelles where photosynthesis occurs.
Chromatin	Nucleus	Site of the chromosomes (genetic material: DNA, histones).
Chromoplasts	Cytoplasm	Two-membrane-bounded organelles where attractants promoting pollination and seed dispersal are made.
Cytoplasm	Cytoplasm	One of three major parts of the cell, containing plastids and cytosol.
Cytoskeleton	Cytoplasm	Contains microtubules, actin filaments.
Cytosol	Cytoplasm	Viscous fluid in which other parts of the cell (membranes, plastids, and other organelles) are suspended.
Endomembrane system	Cytoplasm	Consists of the endoplasmic reticulum, Golgi complex, and vesicles.
Endoplasmic reticulum	Cytoplasm	Membranes in the cytoplasm that form transport pathways and other compartments. Rough endoplasmic reticulum has ribosomes attached to the cytoplasmic face.
Golgi complex	Cytoplasm	Stacks of membranes located near the nucleus where cell products are modified and prepared for secretion from the cell.
Leucoplasts	Cytoplasm	Two-membrane-bounded organelles that store starch and generate oils.
Microtubules	Cytoskeleton	Hollow cylinders of tubulin protein molecules that form networks in the cytoplasm and the mitotic spindle.

Leucoplasts are a nonspecific group of plastids named for their lack of pigments (the prefix *leuco* means “white”). They include *amyloplasts*, which synthesize and store starch, such as in potatoes, and a variety of other plastids specialized for synthesis of oils, proteins, and other products. Amyloplasts are also found in the cells of the *root cap*, where they are involved in gravity sensing, or *geotropism*, by the root tips. Plastids divide by fission, and there may be ten to one hundred per cell.

Mitochondria

Mitochondria are a medium-sized organelle (1 to 2 micrometers in length) with a double membrane. Mitochondria are the sites of *cellular respiration*, the major chemically derived source of adenosine triphosphate (ATP) in many cells. The outermost of the two membranes controls transport of molecules into and out of the mitochondrion. The inner membrane is the site of the *electron transport chain* and *oxidative phosphorylation*, two components of respiration. The aqueous space bounded by the inner membrane is the site of the *Krebs cycle*. Like chloroplasts, mitochondria divide by fission, and there may be ten to one hundred mitochondria per cell, depending upon cell type.

Microbodies

Small (0.5 to 1.5 micrometers in diameter) organelles called *peroxisomes* are bounded by a single membrane. Some peroxisomes contain the enzymes involved in the recycling and detoxification of the products of *photorespiration*. *Glyoxysomes*, an-

Part	*Location in Cell*	*Description/Purpose*
Middle lamella	Cell wall	Sticky layer between cells, binding them together.
Nuclear envelope	Nucleus	Binds nucleus.
Nucleoli	Nucleus	These substructures are composed of genes that encode RNA.
Nucleoplasm	Nucleus	Fluid-filled matrix contained within the nuclear membrane.
Nucleus	Nucleus	One of three major parts of cell, within cytoplasm.
Oil bodies	Cytoplasm	Organelles that store lipids, primarily triacylglycerols.
Peroxisomes	Cytoplasm	One-membrane-bounded organelle that contains enzymes that produce hydrogen peroxide.
Plasma membrane	Inside cell wall	Outer boundary of cytoplasm.
Plasmodesmata	Cell wall	Strands going through cell walls to move substances between protoplasts of contiguous cells.
Plastids	Cytoplasm	General name for chloroplasts, chromoplasts, leucoplasts: two-membrane-bounded organelles.
Primary wall	Cell wall	Outer wall, site of pit fields, division, metabolism.
Proplastids	Cytoplasm	Precursors to other plastids.
Ribosomes	Cytoplasm, nucleus	Structures composed of RNA, responsible for making proteins.
Secondary wall	Cell wall	Inner wall, rigid, with pits; found only in some cells.
Tonoplast	Cytoplasm	Membrane that surrounds the vacuole in a plant cell; also known as a vacuolar membrane.
Vacuoles	Cytoplasm	Organelle bounded by one membrane (the tonoplast) and filled with fluid; in many plant cells, there is a large central vacuole.

other type of peroxisome, are found in germinating seeds. They contain the enzymes involved in the conversion of fats to sugars during the mobilization of storage lipids.

Endomembrane System

The *endoplasmic reticulum* is a series of connected tubules that traverses the cytosol and is the largest member of the *endomembrane system*. The interior of the tubules is called the *lumen*. *Rough endoplasmic reticulum* (RER) is studded with *ribosomes*, while smooth endoplasmic reticulum (SER) is bare. Proteins synthesized on the ribosomes of the RER are inserted into the lumen during synthesis, where they are delivered to the *Golgi complex* for processing. The SER is typically where lipids are made but is rarely seen in plant cells because plastids perform most of the lipid synthesis in plants.

The Golgi complex is a series of stacked membranes that process and package proteins or polysaccharides for transport within or secretion out of the cell. Individual units are called *Golgi bodies* or *dictyosomes*, while collectively they are referred to as the Golgi complex. The endomembrane system gets its name from the fact that many of its components are connected in various ways.

Ribosomes

Ribosomes are small (25 nanometers in diameter), complex assemblies of proteins and *ribosomal RNA* (rRNA). They have two subunits, one large and one small, each made up of a unique mixture of proteins and rRNA. Ribosomes are the sites of protein synthesis. All proteins are large strings of *amino acids* bonded end-to-end. During protein synthesis, a strand of *messenger RNA* (mRNA) from the nucleus travels to the cytoplasm, and one end binds to a ribosome. The ribosome travels down the mRNA and "reads" the genetic information contained on it. The ribosome then "translates" that genetic information into a protein by stringing amino acids together, one at a time, in accordance with the information on the mRNA. Some ribosomes float freely in the cytosol, and others are bound to the endoplasmic reticulum, which is then called "rough ER" because of its appearance under the electron microscope. Proteins made on free ribosomes are released into the cytosol. Proteins made on ribosomes bound to rough endoplasmic reticulum cross the ER membrane and are released into the lumen of the ER for further processing and transport.

Cytoskeleton

All plant cells are surrounded by a *cell wall*. However, the cytoplasm itself is further structured and organized by components of the *cytoskeleton*. The three major components of the cytoskeleton are *microtubules*, *intermediate filaments*, and *microfilaments*.

Microtubules are hollow tubes 24 nanometers in diameter, made of individual, repeating subunits of the protein *tubulin*. They are involved in positioning and moving the chromosomes during *mitosis* and *meiosis*, in directing the laying down of cellulose strands during cell wall formation, and in determining where a new cell plate will form during cell division (that is, *cytokinesis*). Microtubules do not work alone, and numerous microtubule-associated proteins have been identified.

Intermediate filaments are a broad class of cytoskeletal components, and each type is composed of different proteins. They are all solid rods 8-12 nanometers in diameter. In animal cells (where they have been much more fully studied), intermediate filaments have been shown to provide flexible support to skin, nerve, and muscle cells. Although intermediate filaments have been found in plant cells, their exact roles are not yet fully understood. Much research remains to be done in this area.

Microfilaments are thin filaments (7-8 nanometers in diameter) made up of individual, repeating subunits of the protein *actin*. Microfilaments are involved in moving cellular organelles, such as plastids and mitochondria, around the plant cell and, like microtubules, interact with a variety of other proteins, especially *myosin*. In fact, the actin and myosin interaction is so well documented that many researchers refer to them together by simply calling them actinomyosin.

Robert R. Wise

See also: Angiosperm cells and tissues; Cell cycle; Cell theory; Chloroplasts and other plastids; Cytoskeleton; Cytosol; Endomembrane system and Golgi complex; Endoplasmic reticulum; Eukaryotic cells; Membrane structure; Microbodies; Nucleus; Oil bodies; Peroxisomes; Photosynthesis; Plant cells: molecular level; Plasma membranes; Respiration; Ribosomes.

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CYTOSKELETON

Categories: Anatomy; cellular biology

The cytoskeleton is a complex network of fibers that supports the interior of a cell. Cross-linked by molecular connectors into systems that support cellular membranes, it holds internal structures, such as the nucleus, in place and controls various kinds of cell movement.

Virtually all eukaryotic cells, including plant cells, have a cytoskeleton. Cytoskeletal systems extend internally from the membrane covering the cell surface to the surface of the membrane system surrounding the cell's nucleus. There are indications that a cytoskeletal support system reinforces the interior of the nucleus as well. The fibers of the cytoskeleton also anchor cells to external structures through linkages that extend through the surface membrane. The cytoskeletal material, rather than being fixed and unchanging, varies in makeup and structure as cells develop, move, grow, and divide.

Structural Elements

The cytoskeleton, depending on the cell type, is assembled from one or more of three major structural fibers: microtubules, microfilaments, and intermediate filaments. *Microtubules* are fine, unbranched hollow tubes with walls built from subunits consisting of the protein tubulin. Microtubules are about 25 nanometers in diameter, have walls about 4 to 5 nanometers thick, and range in length from a few to many micrometers. These structural elements, which may be arranged singly or in networks or parallel bundles, probably provide tensile strength and rigidity to cellular regions containing them. A tubular form combines lightness with strength and elasticity.

Microfilaments, also called actin filaments, are linear, unbranched fibers built up from the protein actin. Microfilaments are solid fibers that are much smaller than microtubules—about 5 to 7 nanometers in diameter, not much thicker than the wall of a microtubule. Microfilaments occur singly, in networks, and in parallel bundles in the cytoskeleton. The consistency of the *cytoplasm* (the living matter of a cell, exclusive of the nucleus), which can vary from highly liquid to solid and gel-like, is regulated by the degree to which microfilaments are cross-linked into networks. Microfilaments are also arranged in parallel bundles that give tensile strength and elasticity to cell regions and extensions. Many cell types contain numerous fingerlike extensions that are reinforced internally by internal parallel bundles of microfilaments.

Both microtubules and microfilaments form the basis for almost all cellular movements. In these motile systems, microtubules and microfilaments are acted upon by motile proteins that are able to convert chemical energy into the mechanical energy of movement. The motile proteins cause the microtubules or microfilaments to slide forcefully, or move cell structures and molecules over the surfaces of the two elements.

Microtubules and microfilaments occur as structural supports of the cytoskeleton of all plant, animal, fungal, and protozoan cells. The third structural element, the *intermediate filament*, is more abundant in animal cells than in plant cells. This type of fiber, called "intermediate" because its dimensions fall between those of microtubules and microfilaments, is about 10 nanometers in diameter. Unlike microtubules and microfilaments, which are each highly uniform in structure and made from a single type of protein, intermediate filaments occur in six different types, each made up of a different protein or group of proteins. Although the proteins making up the various intermediate filaments are different, they are related in both their three-dimensional structures and amino acid sequences.

Intermediate filaments occur in networks and bundles in the cytoplasm. They appear to be much more flexible than either microtubules or microfilaments, so it is considered likely that they form elastic ties holding cell structures in place, much like cellular rubber bands. However, the actual roles of these elements in the cytoskeleton remain uncertain in plant cells.

Assembly-Disassembly Reactions

Both microtubules and microfilaments can be readily converted between assembled and disassembled forms. In the conversion, the protein subunits of microtubules and microfilaments are exchanged rapidly between the fully assembled element and large pools of disassembled subunits in solution in the cytoplasm. Cells can control the balance between assembly and disassembly with high precision. As a result, the protein subunits can be recycled, and cytoskeletal structures containing microtubules and microfilaments can be set up or taken apart as the cell changes its function. As cell division occurs, for example, microtubules and microfilaments forming cytoskeletal structures typical of growing cells are rapidly disassembled and then reassembled into structures that take part in cell division. The assembly-disassembly reactions of microtubules and microfilaments proceed so readily that it is relatively easy to carry them out in a test tube. Microtubules and microfilaments, in fact, were among the first cell structures to be taken apart and put back together experimentally.

Cytoplasmic Streaming and Cell Division

Among the cell activities with which microfilaments are associated is *cytoplasmic streaming*, or cyclosis. The primary function of cytoplasmic streaming, which occurs within all live cells, is unknown. However, moving currents of cytoplasm are thought to facilitate the transport of nutrients, enzymes, and other substances between the cell and its surroundings, and within the cell itself.

A typical plant cell consists of a *cell wall* and its contents, called the *protoplast*. The protoplast consists of the cytoplasm and a nucleus. Within the cytoplasm are *organelles*, membranes, and other structures. Suspended in the cytoplasmic fluid is one or more liquid-filled *vacuoles*, and a vacuole is bounded by a membrane called the *tonoplast*.

In cytoplasmic streaming, the organelles and other substances travel within moving currents in between the microfilaments and the tonoplast. The organelles in the streaming cytoplasm are thought to be indirectly attached to the microfilaments, and this attachment creates a pulling or towing motion, responsible for the movement of cytoplasmic particles.

The microfilaments, in their constantly changing arrays, also facilitate specific activities within the cell, including cell cleavage during *mitosis*. Microfilaments mediate the movement of the cell nucleus before and following cell division. The microtubules, which are longer, move the split chromosomes to the newly forming cells in mitosis, and they play a role in cell plate formation in dividing cells.

In organizing other components of the cell, the cytoskeleton is thus intimately involved in the processes of cell division, growth, and differentiation. The cytoskeleton maintains the cell's overall shape and is responsible for the movement of various organelles within it. In single-celled organisms such as the amoeba, the cytoskeleton is responsible for the locomotion of the cell itself.

Stephen L. Wolfe, updated by Bryan Ness

See also: Cell theory; Cell wall; Cytoplasm; Eukaryotic cells; Mitosis and meiosis; Plant cells: molecular level.

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CYTOSOL

Categories: Anatomy; cellular biology

Within each eukaryotic cell are a number of distinct, membrane-bounded structures, generically called organelles, including the nucleus, mitochondria, the endoplasmic reticulum, and chloroplasts (only found in plants, algae and some protists). Each organelle is a specialized structure that performs a specific function for the cell as a whole. The rest of the cell, excluding the organelles, cell wall, and plasma membranes, is called the cytosol: the fluid mass that surrounds and provides a home for the organelles.

The cytosol is organized around a framework of fibrous molecules and protein filaments that constitute the *cytoskeleton*. Although the cytosol consists mostly of water, it contains many chemicals that control cell metabolism, including signal transmission and reception, cellular respiration, and protein transcription factors. The cytosol makes up more than 40 percent of the plant cell volume and contains thousands of different kinds of molecules that are involved in cellular biosynthesis. Because cytosol has so much material dissolved in it, it has a gelatinous consistency.

Function

The cytosol provides locations in the cell where chemical activities and energy transformations responsible for growth, repair, and reproduction can occur. Through *diffusion* and *active transport*, cytosol collects many essential nutrients from its surroundings, including carbon, hydrogen, oxygen, potassium, nitrogen, phosphorus, and a variety of *micronutrients*. The constant motion of the cytosol provides a mechanism for moving and supplying these vital nutrients by ionic transport to the organelles so that they can perform their specific jobs.

Cytosol also assists with the removal of unwanted waste products from the cell. *Glycolysis*, the initial step in cellular respiration, occurs in the cytosol. In cellular energy transactions, the cytosol helps distribute useful energy and dissipate the associated heat.

Cytosol plays a key role in the vital processes of protein production, sorting, and transportation. All plant proteins are synthesized by *ribosomes* in the cytosol. Cytosol provides the medium that assists in the transporting of *messenger ribonucleic acid* (mRNA) to ribosomes, where they synthesize proteins. The first portion of the amino acid sequence of a protein contains a *signal sequence* that is checked by proteins in the cytosol. Signal sequences are like street addresses that tell where the growing protein is to be transported. Some signal sequences direct a ribosome to the *endoplasmic reticulum* (ER), where the protein sequence is completed, is stored in the ER's *lumen* (the space inside the ER), and is eventually transported in a vesicle to another organelle or is exported through the cytosol out of the cell. Proteins lacking a signal sequence are completed by the ribosome and released into the cytosol.

Alvin K. Benson

See also: Active transport; Cell theory; Chloroplasts and other plastids; Cytoplasm; Cytoskeleton; Endoplasmic reticulum; Eukaryotic cells; Mitochondria; Nutrients; Osmosis, simple diffusion, and facilitated diffusion; Plant cells: molecular level; Proteins and amino acids; Ribosomes.

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DEFORESTATION

Categories: Forests and forestry; environmental issues

Deforestation is the loss of forestlands through encroachment by agriculture, industrial development, nonsustainable commercial forestry, or other human as well as natural activity.

Concerns about deforestation, particularly in tropical regions, have risen as the role that tropical forests play in moderating global climate has become better understood. Environmental activists decried the apparent accelerating pace of deforestation in the twentieth century because of the potential loss of wildlife and plant habitat and the negative effects on biodiversity. By the 1990's research by mainstream scientists had confirmed that deforestation was indeed occurring on a global scale and that it posed a serious threat to global ecology.

Deforestation as a result of expansion of agricultural lands or nonsustainable timber harvesting has occurred in many regions of the world at different periods in history. The Bible, for example, refers to the cedars of Lebanon. Lebanon, like many of the countries bordering the Mediterranean Sea, was thickly forested several thousand years ago. A growing human population, *overharvesting*, and the introduction of grazing animals such as sheep and goats decimated the forests, which never recovered.

Countries in Latin America, Asia, and Africa have also lost woodlands. While some of this deforestation is caused by a demand for tropical hardwoods for lumber or pulp, the leading cause of deforestation in the twentieth century, as it was several hundred years ago, was the expansion of agriculture. The growing demand by the industrialized world for agricultural products such as beef has led to millions of acres of forestland being bulldozed or burned to create pastures for cattle. Researchers in Central America have watched with dismay as large beef-raising operations have expanded into fragile *ecosystems* in countries such as Costa Rica, Guatemala, and Mexico.

A tragic irony in this expansion of agriculture into tropical rain forests is that the soil underlying the trees is often unsuited for pastureland or raising other crops. Exposed to sunlight, the soil is quickly depleted of nutrients and often hardens. The once-verdant land becomes an arid desert, prone to *erosion*, that may never return to forest. As the soil becomes less fertile, hardy weeds begin to choke out the desirable forage plants, and the cattle ranchers move on to clear a fresh tract.

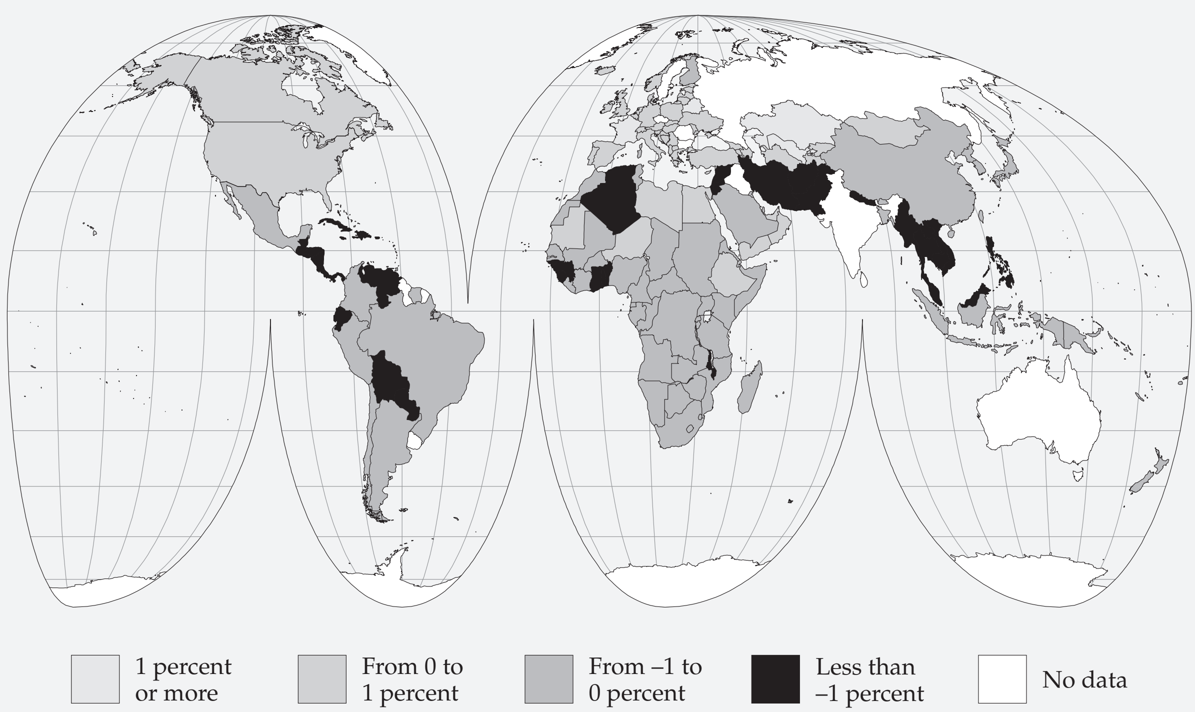
Slash-and-Burn Agriculture

Beef industry representatives often argue that their ranching practices are simply a form of *slash-and-burn agriculture* and do no permanent harm. It is true that many indigenous peoples in tropical regions have practiced slash-and-burn agriculture for millennia, with only a minimal impact on the environment. These farmers burn shrubs and trees to clear small plots of land.

Anthropological studies have shown that the small plots these peasant farmers clear can usually be measured in square feet, not hectares as cattle ranches are, and are used for five to ten years. As fertility declines, the farmer clears a plot next to the depleted one. The farmer's family or village will gradually rotate through the forest, clearing small plots and using them for a few years, and then shifting to new ground, until they eventually come back to where their ancestors began one hundred or more years before.

As long as the size of the plots cleared by farmers remains small in proportion to the forest overall, slash-and-burn agriculture does not contribute significantly to deforestation. If the population of farmers grows, however, more land must be cleared with each succeeding generation. In many tropical countries, traditional slash-and-burn agriculture can then be as ecologically devastating as the more mechanized cattle ranching operations.

Percentage of Annual Deforestation by Country, 1990-1995



Source: United Nations Food and Agriculture Organization.

Logging

Although logging is not the leading cause of deforestation, it is a significant factor. Tropical forests are rarely clear-cut by loggers, as they typically contain hundreds of different species of trees, many of which have no commercial value. Loggers may select trees for harvesting from each stand. Selective harvesting is a standard practice in sustainable forestry. However, just as loggers engaged in the disreputable practice of *high-grading* across North America in the nineteenth century, so are loggers high-grading in the early twenty-first century in Malaysia, Indonesia, and other nations with tropical forests.

High-grading is a practice in which loggers cut over a tract to remove the most valuable timber while ignoring the damage being done to the residual stand. The assumption is that, having logged over the tract once, the timber company will not be coming back. This practice stopped in North America, not because the timber companies voluntarily recognized the ecological damage they were doing but because they ran out of easily accessible, old-growth timber to cut. Fear of a timber famine caused logging companies to begin forest plantations and to practice sustainable forestry.

While global satellite photos indicate significant deforestation has occurred in tropical areas, enough easily harvested old-growth forest remains in some areas that there is no economic incentive for timber companies to switch to sustainable forestry.

Logging may also contribute to deforestation by making it easier for agriculture to encroach on forestlands. The logging company builds roads for use while harvesting trees. Those roads are then used by farmers and ranchers to move into the logged tracts, where they clear whatever trees the loggers have left.

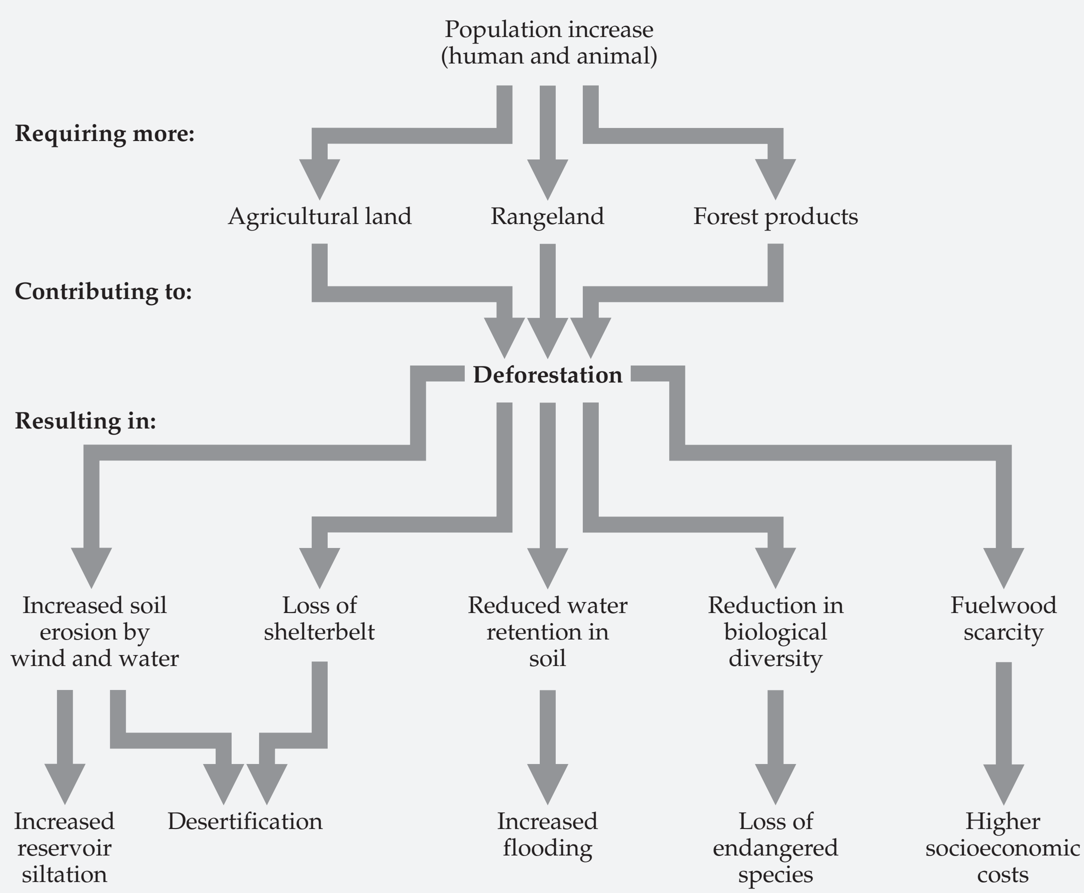
Environmental Impacts

Despite clear evidence that deforestation is accelerating, the extent of the problem remains debatable. The United Nations Food and Agriculture Organization (FAO), which monitors deforestation worldwide, bases its statistics on measurements taken from satellite images. These data indicate that between 1980 and 1990, at least 159 million hectares (392 acres) of land became deforested. The data also reveal that, in contrast to the intense focus on Latin America by both activists and scientists, the most dramatic loss of forestlands occurred in Asia. The deforestation rate in Latin America was 7.45 percent, while in Asia 11.42 percent of the forests vanished. Environmental activists are particularly concerned about forest losses in Indonesia and Malaysia, two countries where timber companies have been accused of abusing or exploiting native peoples in addition to engaging in environmentally damaging harvesting methods.

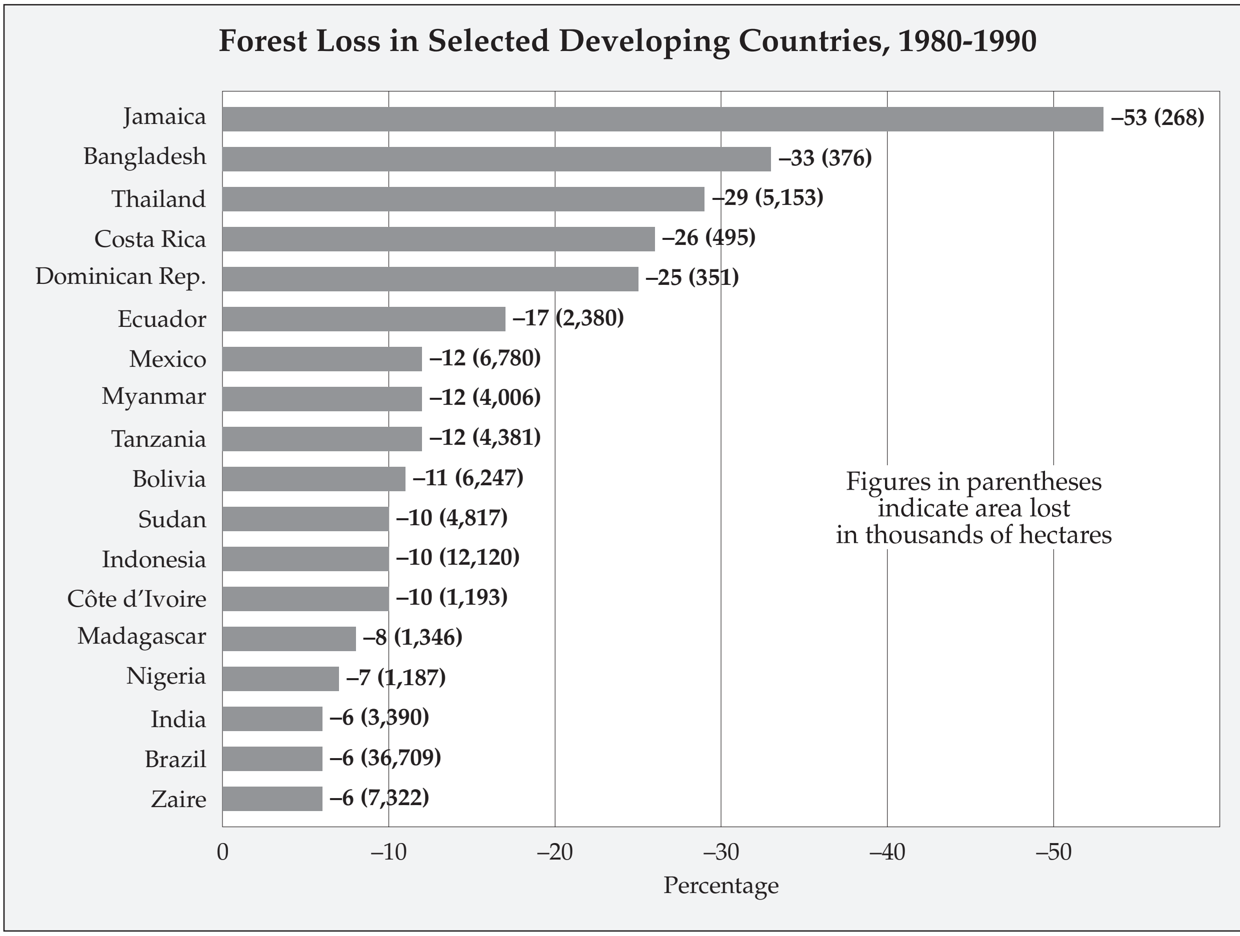
Researchers outside the United Nations have challenged the FAO's data. Some scientists claim the numbers are much too high, while others provide convincing evidence that the FAO numbers are too low. Few researchers, however, have tried to claim that deforestation on a global scale is not happening. In the 1990's the reforestation of the Northern Hemisphere, while providing an encouraging example that it is possible to reverse deforestation, was not enough to offset the depletion of forestland in tropical areas. The debate among forestry experts centers on whether deforestation has slowed, and, if so, by how much.

Deforestation affects the environment in a multitude of ways. The most obvious effect is a loss of *bio-*

Results of Deforestation



Source: Adapted from A. K. Biswas, "Environmental Concerns in Pakistan, with Special Reference to Water and Forests," in *Environmental Conservation*, 1987.



Source: United Nations Food and Agriculture Organization (FAOSTAT Database, 2000).

diversity. When an ecosystem is radically altered through deforestation, the trees are not the only thing to disappear. Wildlife species decrease in number and in variety. As forest habitat shrinks through deforestation, many plants and animals become vulnerable to extinction. Many biologists believe that numerous animals and plants native to tropical forests will become extinct from deforestation before humans have a chance to even catalog their existence.

Other effects of deforestation may be less obvious. Deforestation can lead to increased flooding during rainy seasons. Rainwater that once would have been slowed or absorbed by trees instead runs off denuded hillsides, pushing rivers over their banks and causing devastating floods downstream. The role of forests in regulating water has long been recognized by engineers and foresters. Flood control was, in fact, one of the motivations behind the creation of the federal forest reserves in the United States during the nineteenth century. More recently, disastrous floods in Bangladesh have been blamed on logging tropical hardwoods in the mountains of Nepal and India.

Conversely, trees can also help mitigate against drought. Like all plants, trees release water into the atmosphere through the process of *transpiration*. As the world's forests shrink in total acreage, fewer greenhouse gases such as carbon dioxide will be removed from the atmosphere, less oxygen and water will be released into it, and the world will become a hotter, dryer place. Scientists and policy analysts alike agree that deforestation is a major threat to the environment. The question is whether effective policies can be developed to reverse it or if short-term economic greed will win out over long-term global survival.

Nancy Farm Männikkö

See also: Deserts; Drought; Erosion and erosion control; Forest management; Logging and clear-cutting; Old-growth forests; Rain-forest biomes; Slash-and-burn agriculture; Sustainable forestry.

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DENDROCHRONOLOGY

Categories: Ecology; forests and forestry; gymnosperms; methods and techniques; paleobotany

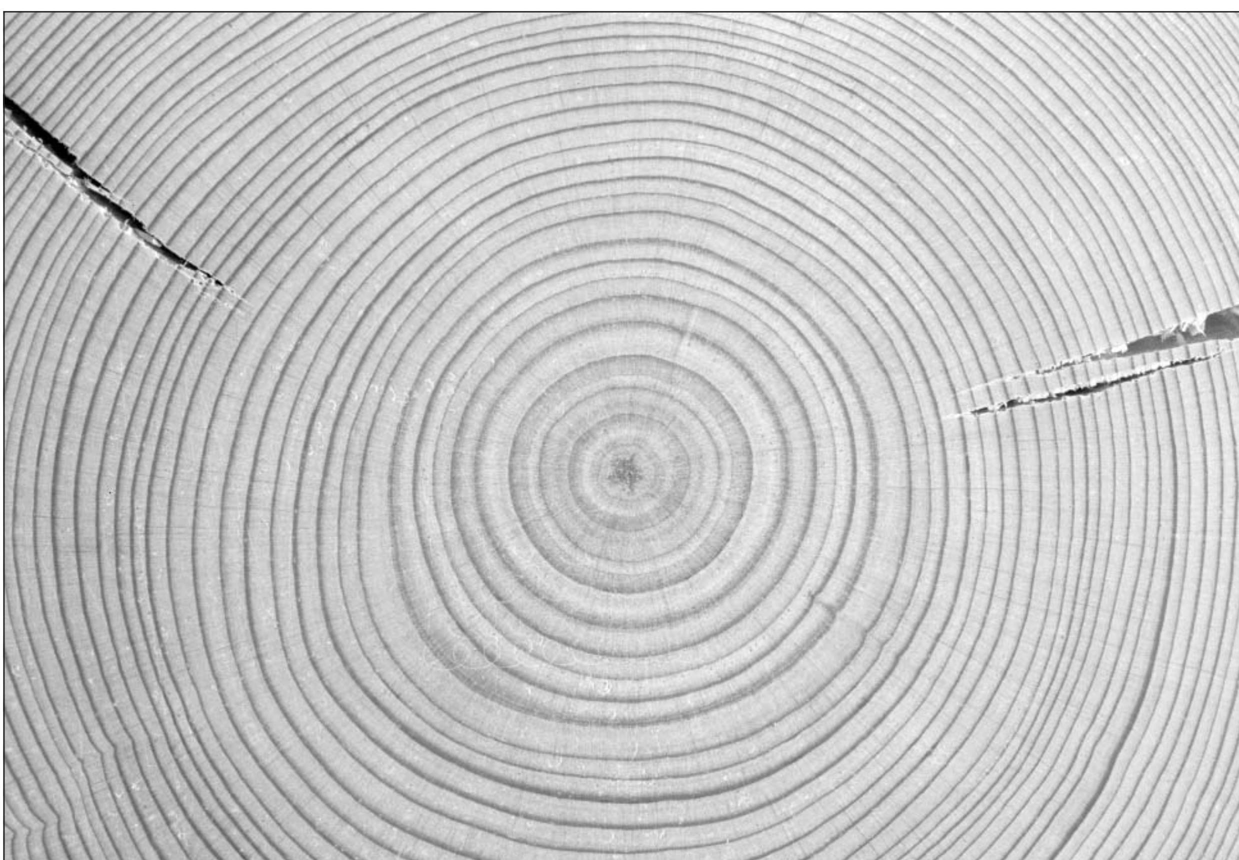
Dendrochronology is the science of examining and comparing growth rings in both living and aged woods to draw inferences about past events and environmental conditions.

In forested regions with seasonal climates, trees produce a growth ring to correspond with each growing season. At the beginning of the growing season, when conditions are optimum, the *vascular cambium* produces many files of large *xylem* cells that form wood. As the conditions become less optimal, the size and number of cells produced decreases until growth stops at the end of the growing season. These seasonal differences in size and number of cells produced are usually visible to the unaided eye. The layers produced during rapid early growth appear relatively light-colored because the volume of the large cells is primarily intracellular space. These layers are frequently called *springwood* because in northern temperate regions spring is the beginning of the growing season. Wood formed later, *summerwood*, is darker because the cells are smaller and more tightly compacted. The juxtaposition of dark summerwood of one year with the light springwood of the following year marks a distinct line between growth increments. The width of the ring between one line and the next measures the growth increment for a single growing season. If there is a single growing season per year, as in much of the temperate world, then a tree will produce a single *annual ring* each year.

Tree Rings and Climate

Leonardo da Vinci is credited with counting tree rings in the early 1500's to determine "the nature of past seasons," but it was not until the early 1900's that dendrochronology was established as a science. Andrew Douglass, an astronomer interested in relating sunspot activity to climate patterns on earth, began to record the sequences of wide and narrow rings in the wood of Douglas firs and ponderosa pines in the American Southwest. Originally, trees were cut down in order to examine the ring patterns, but in the 1920's Douglass began to use a Swedish increment borer to remove core samples from living trees. This instrument works like a hollow drill that is screwed into a tree by hand. When the borer reaches the center of the tree it is unscrewed, and the wood core sample inside is withdrawn with the borer. The small hole quickly fills with sap, and the tree is unharmed. Borers range in size from 20 centimeters to 100 centimeters or more in length, so with care, samples can be taken from very large, very old living trees.

Counting backward in the rings is counting backward in time. By correlating the size of a ring with the known regional climate of the year the ring



PhotoDisc

Dendrochronology, or tree ring counting, can be used to assess the age of a tree because the width of the ring between one line and the next measures the growth increment for a single growing season.

was produced, a researcher can calibrate a core sample to indicate the surrounding climate during any year of the tree's growth. By extending his work to sequoias in California, Douglass was able to map a chronology extending back three thousand years.

Tree Rings and History

In order to extend his chronologies so far back in time, Douglass devised the method of *cross-dating*. By matching distinctive synchronous ring patterns from living and dead trees of the same species in a region, researchers can extend the pattern further into the past than the lifetime of the younger tree. Archaeologists quickly realized that this was a tool that could help to assign the age of prehistoric sites by determining the age of wood artefacts and construction timbers. In this way archaeologists could calculate the age of pre-Columbian southwestern ruins, such as the cliff dwellings at Mesa Verde, Arizona, by cross-dating living trees with dead trees and the latter with timbers from the sites. In 1937 Douglass established the Laboratory of Tree-Ring Research at the University of Arizona, which continues to be a major center of dendrochronological research.

Fine-Tuning

In the mid-1950's Edmund Schulman confirmed the great age of living bristlecone pines in the Inyo National Forest of the White Mountains of California. In 1957 he discovered the Methuselah Tree, which was more than forty-six hundred years old. The section of forest in which he worked is now known as the Ancient Bristlecone Pine Forest. During the next thirty years, Charles Ferguson extended the bristlecone chronology of this area back 8,686 years. This sequence formed the basis for calibrating the technique of *radiocarbon dating*. In the 1960's, radiocarbon analysis began to be used to determine the age of organic (carbon-based) artefacts from ancient sites. It has the advantage of being applicable to any item made of organic material but the disadvantage of having a built-in uncertainty of 2 percent or more. Tree-ring chronologies provide an absolute date against which radiocarbon analyses of wood samples from a site can be compared.

At about the same time, Valmore LaMarche, a young geologist, began to study root growth of the ancient trees to determine how they could be used to predict the erosional history of a site. By cross-referencing growth ring asymmetry to degree of exposure and slope profiles, he was able to estimate rates of soil erosion and rock weathering, which in turn could be cross-referenced to the climatic conditions predicted by growth rings in the stem. LaMarche and his colleagues, particularly Harold Fritts, continued to "fine-tune" the reading of growth rings to be able to take into account factors such as soil characteristics, frost patterns, and daily, weekly, and monthly patterns.

The Oldest Tree

The Methuselah Tree, mentioned above, is the oldest known living tree. Schulman also cored a forty-seven-hundred-year-old living specimen in the White Mountains, but he did not name it or identify its location. While most of the living specimens older than four thousand years are found in the White Mountains, the oldest living tree was discovered in the Wheeler Peak area of what is now Great Basin National Park in eastern Nevada. This tree, variously known as WPN-114 and the Prometheus Tree, was estimated to be between forty-nine hundred and fifty-one hundred years old when it was cut down in 1964 as part of a research project. The controversy that followed has left many interesting but unanswered questions.

Marshall D. Sundberg

See also: Evolution of plants; Growth and growth control; Petrified wood; Plant tissues; Stems; Wood; Wood and timber.

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DESERTIFICATION

Category: Environmental issues

Desertification is the degradation of arid, semiarid, and dry, subhumid lands as a result of human activities or climatic variations, such as prolonged drought.

Desertification is recognized by scientists and policymakers as a major economic, social, and environmental problem in more than one hundred countries. It impacts about one billion people throughout the world. *Deserts* are climatic regions that receive fewer than 25 centimeters (10 inches) of precipitation per year. They constitute the most widespread of all climates of the world, occupying 25 percent of the earth's land area. Most deserts are surrounded by *semiarid* climates referred to as steppes, which occupy 8 percent of the world's lands. Deserts occur in the interior of continents, on the *leeward* side of mountains, and along the west sides of continents in subtropical regions. All of the world's deserts risk further desertification.

Deserts of the World

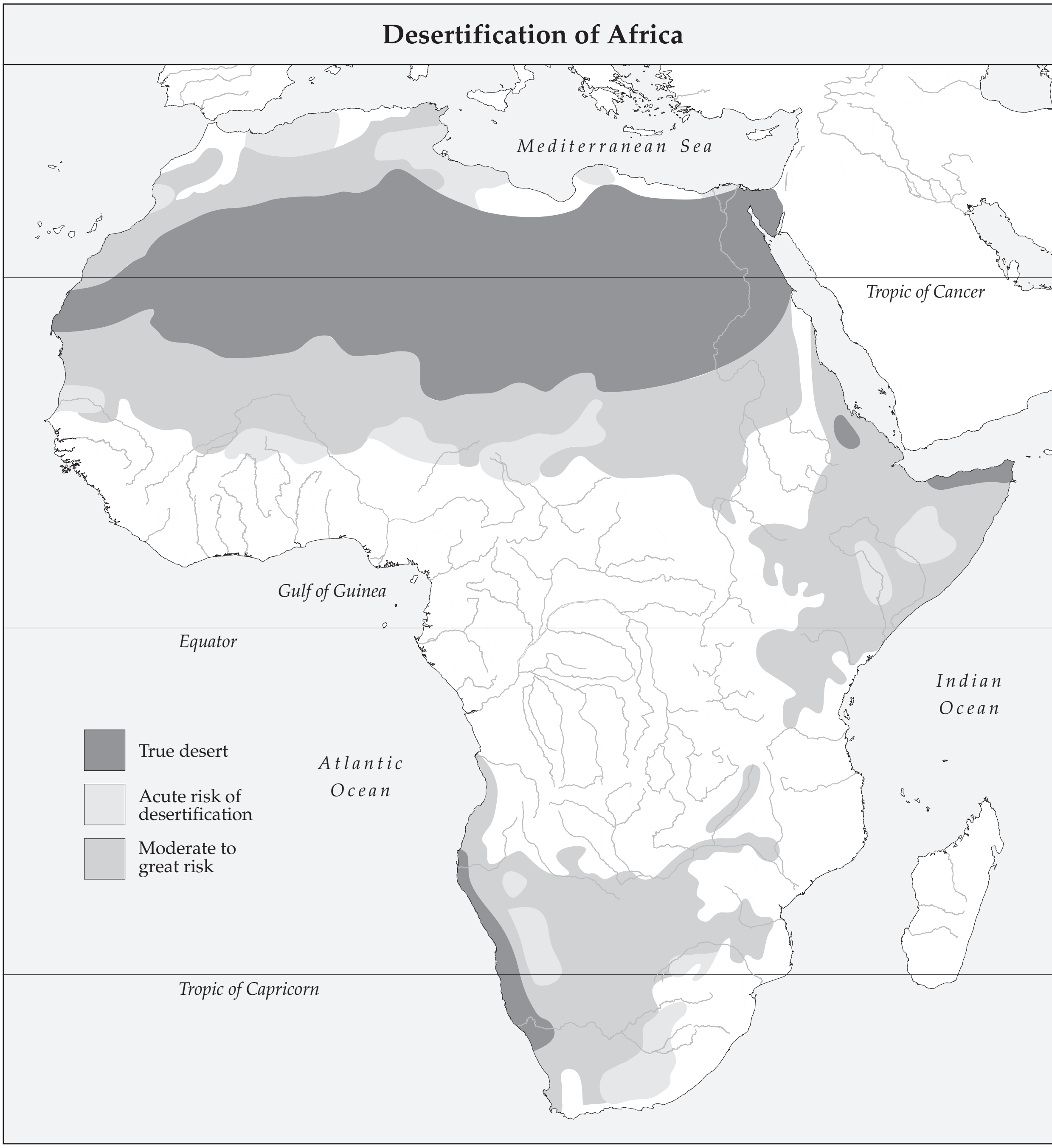
The largest deserts are in North Africa, Asia, Australia, and North America. Four thousand to six thousand years ago, these desert areas were less extensive and were occupied by prairie or savanna *grasslands*. Rock paintings found in the Sahara Desert show that humans during this era hunted buffalo and raised cattle on grasslands, where giraffes browsed. The region near the Tigris and Euphrates Rivers in the Middle East was also fertile. In the desert of northwest India, cattle and goats were grazed, and people lived in cities that have long since been abandoned. The deserts in the southwestern region of North America appear to have been wetter, according to the study of tree rings (*dendrochronology*) from that area. Ancient Palestine, which includes the Negev Desert of present-day Israel, was lush and was occupied by three million people.

Scientists use various methods to determine the historical climatic conditions of a region. These methods include studies of the historical distribution of trees and shrubs determined by the deposit patterns in lakes and bogs, patterns of ancient sand dunes, changes in lake levels through time, archaeological records, and tree rings.

The earth's creeping deserts supported approximately 720 million people, or one-sixth of the world's population, in the late 1970's. According to the United Nations, the world's *hyperarid* or *extreme deserts* are the Atacama and Peruvian Deserts (located along the west coast of South America), the Sonoran Desert of North America, the Takla Makan Desert of Central Asia, the Arabian Desert of Saudi Arabia, and the Sahara Desert of North Africa, which is the largest desert in the world. The *arid* zones surround the extreme desert zones, and the semiarid zones surround the arid zones. Areas that surround the semiarid zones have a high risk of becoming desert. By the late 1980's the expanding deserts were claiming about 15 million acres of land per year, or an area approximately the size of the state of West Virginia. The total area threatened by desertification equaled about 37.5 million square kilometers (14.5 million square miles).

Causes of Desertification

Desertification results from a two-prong process: climatic variations and human activities. First,



the major deserts of the world are located in areas of high atmospheric pressure, which experience subsiding dry air unfavorable to precipitation. Subtropical deserts have been experiencing prolonged periods of drought since the late 1960's, which causes these areas to be dryer than usual.

The problem of desertification was identified in the late 1960's and early 1970's as a result of severe drought in the Sahel Desert, which extends along the southern margin of the Sahara in West Africa. Rainfall has declined an average of 30 percent in the Sahel. One set of scientific studies of the drought focuses on changes in heat distribution in the ocean. A correlation has been found between sea surface temperatures and the reduction of rainfall in the Sahel. The Atlantic Ocean's higher surface temperatures south of the equator and lower temperatures north of the equator west of Africa are associated with lower precipitation in northern tropical Africa. However, the cause for the change in sea surface temperature patterns has not been determined.

Another set of studies is associated with land-cover changes. Lack of rain causes the ground and soils to get extremely dry. Without vegetative cover to hold it in place, thin soil blows away. As the water table drops from the lack of the natural recharge of the aquifers and the withdrawal of water by desert dwellers, inhabitants are forced to migrate to the grasslands and forests at fringes of the desert. *Overgrazing*, *overcultivation*, *deforestation*, and poor irrigation practices (which can cause salinization of soils) eventually lead to a repetition of the process, and the desert begins to encroach. These causes are influenced by changes in population, climate, and social and economic conditions.

The fundamental cause of desertification, therefore, is human activity. This is especially true when environmental stress occurs because of seasonal dryness, *drought*, or high winds. Many different forms of social, economic, and political pressure cause the overuse of these dry lands. People may be pushed onto unsuitable agricultural land because of land shortages, poverty, and other forces, while farmers overcultivate the fields in the few remaining fertile land areas.

Atmospheric Consequences

A reduction in vegetation cover and soil quality may impact the local climate by causing a rise in temperatures and a reduction in moisture. This can, in turn, impact the area beyond the desert by causing changes in the climate and atmospheric patterns of the region. It is predicted that by the year 2050 substantial changes in vegetation cover in humid and subhumid areas will occur and cause substantial regional climatic changes. Desertification is a global problem because it causes the loss of *biodiversity* as well as the pollution of rivers, lakes, and oceans. As a result of excessive rainfall and flooding in subhumid areas, fields lacking sufficient vegetation may be eroded by runoff.

Greenhouse Effect

Desertification and even the efforts to combat it may be impacting climatic change because of the emission and absorption of greenhouse gases. The decline in vegetation and soil quality can result in the release of carbon, while revegetation can influence the absorption of carbon from the atmosphere. The use of fertilizer to reclaim dry lands may cause an increase in nitrous oxide emissions. Although scientists involved in studies of rising greenhouse gases have not been able to gather evidence conclusive enough to support such theories, evidence of the impact of greenhouse gases on global warming continues to accumulate.

Policy Actions

As a result of the Sahelian drought, which lasted from 1968 to 1973, representatives from various countries met in Nairobi, Kenya, in 1977 for a United Nations conference on desertification. The conference resulted in the Plan of Action to Combat Desertification. The plan listed twenty-eight measures to combat land degradation by national, regional, and international organizations. A lack of adequate funding and commitment by governments caused the plan to fail. When the plan was assessed by the United Nations Environment Programme (UNEP), it found that little had been accomplished and that desertification had increased.

As a result of the 1977 United Nations conference, several countries developed national plans to combat desertification. One example is Kenya, where local organizations have worked with primary schools to plant five thousand to ten thousand seedlings per year. One U.S.-based organization promotes reforestation by providing materials to establish nurseries, training programs, and extension services. Community efforts to combat desertification have been more successful, and UNEP has recognized that such projects have a greater success rate than top-down projects. The Earth Summit, held in Rio de Janeiro, Brazil, in 1992, supported the concept of *sustainable development* at the community level to combat the problem of desertification.

Roberto Garza

See also: Agriculture: modern problems; Climate and resources; Deforestation; Deserts; Drought; Erosion and erosion control; Grazing and overgrazing; Greenhouse effect; Slash-and-burn agriculture; Soil conservation; Soil degradation; Soil salinization; Sustainable forestry.

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DESERTS

Categories: Biomes; ecosystems

Regions characterized by 10 inches or less of precipitation per year as considered deserts. Plants in desert biomes are typically specialized to endure the harsh conditions found there.

Deserts are regions, or biomes, too dry to support grasslands or forest vegetation but with enough moisture to allow specially adapted plants to live. In deserts, hot days alternate with cold nights. Ninety percent of incoming solar radiation reaches the ground during the day, and 90 percent of that is radiated back out into space at night, the result of the absence of clouds, low humidity, and sparse vegetation. The surface of the ground in desert areas is devoid of a continuous layer of plant litter and is usually rocky or sandy. Nutrient cycling in deserts is tight, with phosphorus and nitrogen typically in short supply.

How Deserts Form

Most large landmasses have interior desert regions. Air masses blown inland from coastal areas lose their moisture before reaching the interior. Examples include the Gobi Desert in Mongolia and parts of the Sahara Desert in Africa.

Another factor in the formation of deserts is the *rain-shadow effect*. If moisture-laden air masses bump up against a mountain range, the air mass is deflected upward. As the air mass rises, it cools, and moisture precipitates as rain or snow on the windward side of the mountain range. As the air mass passes over the mountain range, it begins to descend. Because it lost most of its moisture on the windward side, the air mass is dry. As it descends, the air heats up, creating drier conditions on the lee side of the mountain range. Sometimes these differences in moisture are so pronounced that different plant communities grow on the windward and leeward sides.

Latitude can also influence desert formation. Most deserts lie between 15 and 35 degrees north or south latitude. At the equator, the sun's rays hit the earth straight on. Moist equatorial air, warmed by intense heat from the sun, rises. As this air rises, it cools and loses its moisture, which falls as rain; this is why it usually rains every day in the equatorial rain forests. The *Coriolis force* causes the air masses to veer off, to the north in the Northern Hemisphere and to the south in the Southern Hemisphere. The now-dry air begins to descend and warm, reaching the ground between 15 and 35 degrees north and south latitude, creating the belt of deserts circling the globe between these latitudes.

Deserts can also form along coastlines next to cold-water ocean currents, which chill the air above them, decreasing their moisture content. Offshore winds blow the air above cold ocean waters back out to sea. In deserts, rain is infrequent, creating great hardships for the native plants and animals. The main source of moisture for the plants and animals of coastal deserts is fog.

Desert Vegetation

Many typical desert perennial plants, such as members of the *Cactaceae* (the cactus family), have thick, fleshy stems or leaves with heavy cuticles, sunken stomata (pores), and spiny defenses against browsing animals. The spines also trap a layer of air around the plant, retarding moisture loss. Desert plants, many of which photosynthesize using C_4 or CAM (crassulean acid metabolism), live spaced out from other plants. Many desert plants are tall and thin, to minimize the surface area exposed to the strongest light. For example, the entire stem of the Saguaro cactus is exposed to sunlight in the early morning and late afternoon; at noon, only the tops of the stems receive full sun. These traits allow the plants to cope with heat stress and competition for

DIGITAL STOCK

The Gobi Desert, much of which is in Mongolia, is one of the world's largest.

water and avoid damage from herbivores (plant-eating animals).

Where the mixture of heat and water stress is less severe, perennial bushes of the *Chenopodiaceae* (goosefoot family) or *Asteraceae* (sunflower family) form clumps of vegetation surrounded by bare ground. Numerous annuals, called *ephemerals*, can grow prolifically, if only briefly, following rainfall.

Unrelated plant families from different desert areas of the world show similar adaptations to desert conditions. This has resulted from a process called convergent evolution.

Types of Deserts

Deserts are not all alike. Hot deserts are found in lower latitudes, and cold deserts are found at higher latitudes. North America contains four different deserts, which are usually defined by their characteristic vegetation, which ecologists call *indicator species*.

In Mexico's Chihuahuan Desert, lechuguilla (*Agave lechuguilla*) is the indicator species of the Chihuahuan Desert. Fibers from lechuguilla can be made into nets, baskets, mats, ropes, and sandals. Its stems yield a soap substitute, and its pulp has been used as a spot remover. Certain compounds in lechuguilla are poisonous and were once used as arrows and fish poisons. Two of the most common plants in the Chihuahuan Desert are creosote bush (*Larrea divaricata*) and soaptree yucca (*Yucca elata*). Cacti in the Chihuahuan are numerous and diverse, especially the prickly pears and chollas.

The Joshua tree (*Yucca brevifolia*), is the indicator species of the Mojave Desert in Southern California. Nearly one-fourth of all the Mojave Desert plants are *endemics*, including the Joshua tree, Parry saltbush, Mojave sage, and woolly bur sage.

The Great Basin Desert, situated between the Sierra Nevada and the Rocky Mountains, is a cold desert, with fewer plant species than other North American deserts. Great Basin Desert plants are small to medium-size shrubs, usually sagebrushes or saltbushes. The indicator species of the Great Basin is big sagebrush (*Artemisia tridentata*). Other common plants are littleleaf horsebrush and Mormon tea. The major cactus species is the Plains prickly pear.

In the Sonoran Desert in Mexico, California, and Arizona, plants come in more shapes and sizes than in the other North American deserts, especially in the *Cactaceae*. The indicator species of the Sonoran Desert is the saguaro cactus (*Carnegiea gigantecus*).

The Sahara Desert of northern Africa is the world's largest, at 3.5 million square miles. The Northern Hemisphere also contains the Arabian, Indian, and Iranian deserts and the Eurasian deserts: the Takla Makan, Turkestan, and Gobi. Deserts in the Southern Hemisphere include the Australian, Kalahari, Namib, Atacama-Peruvian (the world's driest), and the Patagonian.

Environmental Considerations

Desert ecosystems are subject to disruption by human activities. Urban and suburban sprawl paves over desert land and destroys habitat for plants and animals, some of which are endemic to specific deserts. Farmers and metropolitan-area builders can tap into critical desert water supplies, changing the hydrology of desert regions. Off-road vehicles can destroy plant and animal life and leave tracks that may last for decades.

Carol S. Radford

See also: Biomes: definitions and determinants; Biomes: types; C_4 and CAM photosynthesis; Cacti and succulents; Desertification; Evolution: convergent and divergent; Photosynthesis.

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DEUTEROMYCETES

Categories: Fungi; taxonomic groups

Deuteromycetes are an artificial group of fungi, of which there exist approximately fifteen thousand species, often referred to as "fungi imperfecti" because their only known reproductive mechanism is asexual.

Deuteromycetes—also known as *Deuteromycota*, *Deuteromycotina*, fungi imperfecti, and mitosporic fungi—are fungi that are unable to produce sexual spores and are therefore placed in their own separate phylum. The deuteromycetes are commonly called fungi imperfecti, that is, "imperfect fungi," a term accepted by many mycologists.

Reproduction

Reproduction in the deuteromycetes occurs in several different forms. Spores, or *conidia*, may be produced directly on the mycelium (the mass of hyphae, or tubular filaments, forming the body of a fungus) or on a structure of specialized mycelial cell called a *condiophore*. Some of these fungi do not produce spores. Nonsporulating fungi are able to propagate themselves by fragmenting the hyphae or by producing a mass of hyphae called a *sclerotium*. Sclerotia can be microscopic in size or as large as several millimeters in diameter.

Conidia can vary in size and shape from small (2-3 microns long) to large (250-300 microns long). Colors can range from clear (hyaline) to a variety of earth tones. Conidia may consist of one to several cells. Shapes of conidia range from simple and oval to elongated and filamentous.

Classification

Classification of the fungi as deuteromycetes is based on the presence of conidia; the kind of conidia according to their shape, color, and size; and whether the conidia are produced in fungal structures called *conidiomata*. Conidiomata may have the shape of a flask made of fungal tissue, called a *pycnidium*; a pin cushion, called a *sporodochium*; or a mass of conidiophores located under either the epidermis or the cuticle of a plant host, called an *aecervulus*.

There are three classes. The *hyphomycetes* contain the fungi that produce conidia and conidiophores on hyphae or groups of hyphae. The *agonomycetes* do not produce conidia. The *coelomycetes* contain the fungi that produce conidia in distinct conidiomata.

Economic and Research Uses

The fungi in the deuteromycetes are extremely important for humanity. Several members of the deuteromycetes are used in industry. Antibiotics, such as penicillin and griseofulvin, are produced by these fungi, especially those of the genus *Penicillium*. These fungi are often found in the soil, and it is believed that they produce antibiotic substances in order to reduce competition with soil bacteria and other fungi.

Enzymes are produced by many of these fungi to enable them to degrade plant residues, from which they obtain nutrients. The enzymes they produce have been used by humans in the manufacture of laundry detergent, paper, and condiments such as soy sauce; the enzymes have also been used in scientific experiments. These enzymes are easily produced under industrial conditions.

Some of the fungi in the genus *Penicillium* are also used in the production of cheeses, including blue cheese and brie. After the cheese is processed and formed into wheels, spores of the fungus are injected into blue cheese, and cheese wheels of brie are dipped into a solution of spores. The cheeses are then allowed to age before entering the market.

Deuteromycetes as Pathogens

Several thousand species of deuteromycetes are pathogenic to plants and plant parts. Many are responsible for the degradation of foods, including decay from rots and molds on grains, vegetables, and fruits. All of the deuteromycetes, like other fungi, are *heterotrophic* (eat or get their food from other organisms) and therefore need to attach to an organic substrate (a living foundation). Food products are excellent substrates for fungi and, within short periods of time, the fungi will consume and destroy these foods. Some fungi produce toxic chemicals that are harmful to those who eat the rotting food. One example is aflatoxin, which is produced by the fungus *Aspergillus flavus*, found on peanuts. A general screening for the fungus can be done using a black light, under which the fungus fluoresces a yellow-green color.

Because all plants and plant parts that serve as food sources for people are affected by deuteromycetes, diseases of plants and animals are one of the more important effects of this fungal group. The fungi use their ability to produce enzymes to enter into growing plant tissue and then destroy the tissue. Annual crop losses caused by fungi in the United States can be measured in billions of dollars. In addition, the small spores of deuteromycetes can affect animals and humans directly. The spores are released into air currents and are blown from place to place. As humans breathe this air, the spores enter the nasal passages and lungs and react with the immune system, creating the allergies.

J. J. Muchovej

See also: Ascomycetes; *Basidiomycetes*; Basidiosporic fungi; Fungi; Lichens; Mitosporic fungi; Mycorrhizae; Yeasts.

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DIATOMS

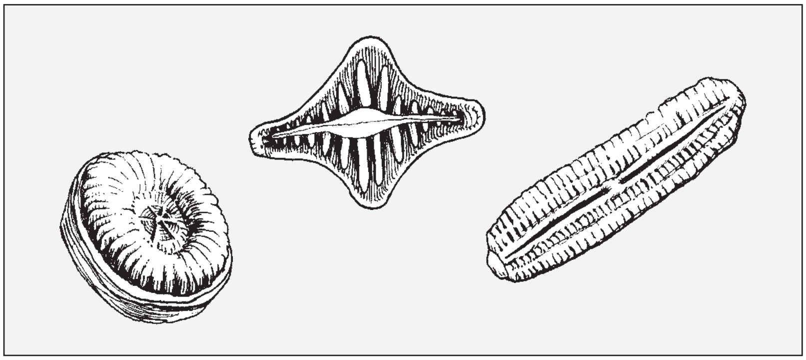
Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

Diatoms are unicellular microorganisms of the phylum Bacillariophyta *that are abundant in aquatic, semiaquatic, and moist habitats throughout the world, growing as solitary cells, chains of cells, or members of colonies.*

Diatoms, algal organisms of the phylum *Bacillariophyta*, have more than 250 genera and about 100,000 species. A distinctive siliceous cell wall called a *frustule* surrounds each vegetative cell. Diatoms have an extensive fossil record, going back some 100 million years to the Cretaceous period. Deposits of fossil diatoms, known as *diatomite* or *diatomaceous earth*, are mined commercially for use as abrasives and filtering aids. One subterranean marine deposit in Santa Maria, California, is about 900 meters in thickness. More than 270,000 metric tons of diatomaceous earth are quarried annually from a deposit in Lompoc, California. Analysis of fossil diatom assemblages provides important information on past environmental conditions. Although the ancestry of diatoms is obscure, they share similar pigments, food reserves, and plastid structure with the *chrysophytes* and complex, multicellular brown algae.

Classes

Diatoms are frequently separated into two classes based on differences in the symmetry of the cell wall. *Centric diatoms* (class *Centrobacillariophyceae*) may be circular, triangular, or rectangular but typically have surface markings that radiate from a cen-



Diatoms are unicellular or colonial algal marine organisms noted for their contribution to phytoplankton, contributing perhaps one-quarter of the world's primary photosynthetic production. They are noted for their frustules: cell walls made of silica and consisting of two halves that overlap each other, with a beautiful variety of ornamentation that makes these tiny organisms appear diverse and jewel-like.

tral area, an arrangement called radial symmetry. *Pennate diatoms* (class *Pennatibacillariophyceae*) are elongated with surface markings at right angles to the long axis, an arrangement called bilateral symmetry.

Cell Wall Components

The hallmark of the diatom is its distinctive and beautifully ornamented, boxlike cell wall, or frustule. The frustule is frequently highly differentiated and is almost always heavily impregnated with silica. An organic layer composed of carbohydrates and amino acids covers the siliceous frustule. The frustule is composed of two halves that fit together like the plates of a petri dish. The larger, overlapping half, the *epitheca*, sits atop the smaller *hypotheca*. The epitheca is composed of a relatively flat upper part (*valve face*) with downturned edges (*valve mantle*), called the *epivalve*, and one or more hooplike girdle bands called the *epicingulum*. Similarly, the hypotheca is composed of a *hypovalve* and a *hypocingulum*. The epicingulum and hypocingulum are collectively known as the *girdle*.

When viewed with the microscope, frustules may be seen in two very different perspectives, depending on the position in which they are lying. If the valve face and outline of the valve are visible, the frustule is said to be in valve view. If the valve mantle and girdle are visible, the frustule is said to be in girdle view.

The varied shapes and beautiful ornamentation of these walls give the diatom cell its intrinsic beauty and have long been used to classify diatoms. Many pennate diatoms possess a *raphe*, a slit along one or both valves, divided by a thickened bridge of silica (a central nodule) and terminated by polar nodules. Raphid pennate diatoms are capable of gliding movement that is caused by the secretion of mucopolysaccharides, derived from vesicles or crystalline bodies, through the raphe. Araphid pennate diatoms lack a raphe and posses a central, unornamented area known as the *sternum* or *pseudoraphe*. No centric diatom has a raphe.

Simple pores (*puncta*), more complex *areolae*, or chambers (*loculi*) are frequently arranged in regularly spaced lines (*striae*) which, in turn, may be strengthened by siliceous ribs (*costae*). Loculi and areolae open externally by a delicate pore plate and internally by a large, round hole. Because the protoplast is completely enclosed by the frustule, the flux of materials across the cell wall primarily occurs through these pores and slits. Additional processes and appendages may extend from the valves of different species.

Electron microscopical studies have revealed two additional openings in the valve: the *fultoportula* (strutted process) and the *rimoportula* (labiate process). The fultoportula consists of a tube that penetrates the wall and is supported internally by two or more buttresses. Fultoportulae are confined to a single order of centric diatoms. The rimoportula, found in centric and pennate diatoms, consists of a tube that opens to the outside by a simple aperture and internally by a longitudinal, liplike slit. Some researchers suggest that the raphe system may have evolved from one or more rimoportulae.

Reproductive Strategies

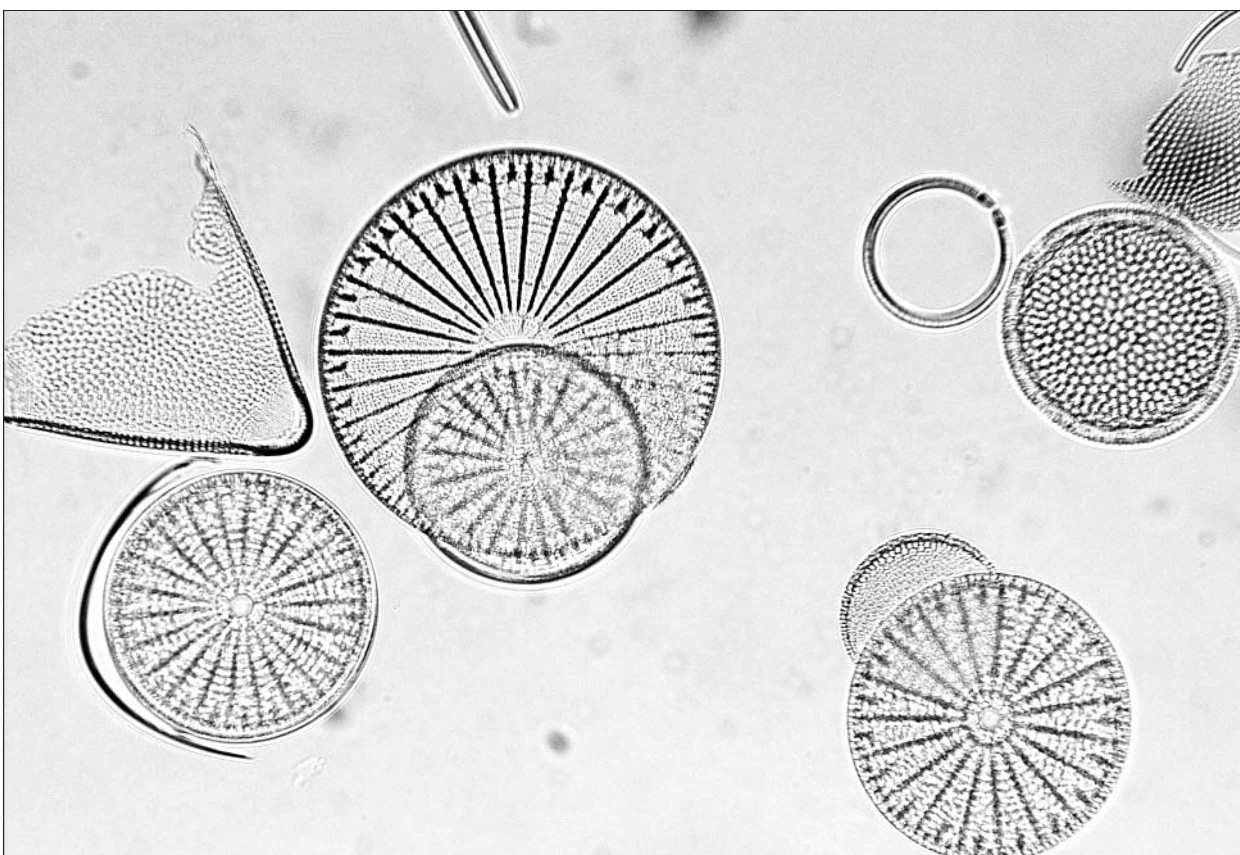
The most common mode of reproduction in diatoms is asexual by cell division of a diploid vegetative cell to produce two daughter cells. Following mitosis the protoplast expands, pushing apart the valves, and divides by furrowing. Each daughter cell receives the epitheca of the parent and forms a new hypotheca within a *silica deposition vesicle*. The daughter cell that receives the original epitheca remains the same size as the parent. However, the daughter cell that receives the original hypotheca forms a new hypotheca and is usually smaller than the parent cell. Thus, the average cell size of a population of diatoms may become progressively smaller during the growing season. The maximum size of the population is restored during sexual reproduction.

During sexual reproduction, diploid vegetative cells divide by meiosis to form haploid gametes (eggs and sperm in centric diatoms or amoeboid gametes in pennate diatoms). Fusion of the gametes results in a diploid zygote that enlarges to several times its original size by the uptake of water and forms valves. This enlarged zygote (*auxospore*) has a different valve morphology from that of the valves of vegetative cells. Auxospores, which do not serve as resting spores, divide by mitosis to form vegetative cells with the maximum size for the species.

Some centric diatoms form *resting spores* in response to the availability of various nutrients (especially nitrogen), temperature, light intensity, and pH. Resting spores are short cells with thick walls that differ from the walls of vegetative cells. Resting spores are usually formed within the frustule of a vegetative cell. A vegetative cell may give rise to one, two, or four resting spores. Resting spores germinate in light when environmental conditions improve.

Flagella

Flagellated cells are found only in the male gametes (*spermatazoids*) of some centric diatoms. Each spermatozoid bears a single flagellum covered with stiff tubular hairs (*mastigonemes*). Based on ultrastructural studies of two species, it appears that diatoms lack the normal 9 + 2 arrangement of microtubules in the shaft of the flagellum (*axoneme*). The two central microtubules are missing, leaving nine peripheral doublets (9 + 0). Further-



PhotoDisc

Micrograph showing diatoms in fresh water.

more, the basal body of these species consists of nine doublets of microtubules, instead of the normal nine triplets found in other eukaryotes.

Food Reserve

The most important carbohydrate food reserve is the *chrysolaminarin*, a beta-1,3-linked glucan, which is stored in special *vacuoles*. Chrysolaminarin (a water-soluble polysaccharide) is also the most important food reserve in the brown algae and chrysophytes. Diatoms may also accumulate various lipids. The fatty acid composition of these lipids differs somewhat from that found in the green algae and higher plants, notably in the absence of linolenic acid from most species. Lipids may be stored within or outside vacuoles.

Photosynthetic Pigments

All diatoms contain *chlorophylls a* and c_2. Chlorophylls c_1 and c_3 may also be present; however, chlorophyll *b* is never found in diatoms. Although the coloration of diatoms varies, living diatoms are frequently brown due to the presence of the accessory pigment *fucoxanthin*, which masks the green coloration of the chlorophylls. Diatoms also contain other *xanthophylls* (neofucoxanthin, diadinoxanthin, and diatoxanthin) and beta-carotene.

The photosynthetic pigments are stored within membrane-bound organelles called *plastids*. Many pennate diatoms have two large plastids, while centric diatoms generally have a large number of small discoid plastids. Four membranes surround the plastids of diatoms: a double-membrane envelope and a layer of endoplasmic reticulum that is continuous with the nuclear envelope. Each plastid contains more or less parallel lamellae composed of three stacked, flattened sacs (*thylakoids*) and at least one *pyrenoid*, which does not appear to be directly associated with any food reserve product.

Habitat

Diatoms are usually a major component of *benthic* and *planktonic* communities in all but the hottest and saltiest waters. While most diatoms live in water, a few species grow in damp soil and can tolerate extreme drought and heat for some time. Pennate diatoms are common members of the benthos and plankton in marine and freshwater habitats, while centric diatoms are more commonly found in the marine plankton. Some benthic diatoms grow attached to rocks, sand grains, other algae, aquatic plants, and even animals. Other benthic diatoms (usually raphid pennates) live freely on the surface of, or in, the substrate. Planktonic diatoms often produce spring and fall blooms in temperate lakes and oceans and summer blooms at higher altitudes. In coastal waters and lakes, they may produce resting spores to survive between growing seasons. One estimate suggests that 20-25 percent of the total primary production on earth is contributed by marine planktonic diatoms.

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See also: Algae; Aquatic plants; Brown algae; Chrysophytes; Marine plants; Phytoplankton; *Protista*.

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DINOFLAGELLATES

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

Dinoflagellates, phylum Dinophyta*, are unicellular and colonial algal organisms from the kingdom* Protista *named for the spinning motions that result from the movement of their flagella.*

The two thousand to four thousand species that make up the *Dinophyta* phylum typically have two flagella. Dinokonts (*Dinophyceae*) have one flagellum running in a groove that cuts transversely across the cell and another flagellum, the sulcus, that runs backward in a longitudinal groove and is more or less perpendicular to the transverse one. In desmokonts (*Desmophyceae*), both flagella arise from a point at the front of the cell. The motions of the flagella, which make dinoflagellates spin like a top, help give rise to the name, for *dinos* in Greek means "whirling," and *flagella* means "whip." Single-celled species are the most common, but colonial species exist. The largest dinoflagellate, *Noctiluca*, may grow as large as 2 millimeters in diameter.

In the active phase of their life cycles, dinoflagellates come in two forms, unarmored (naked) or armored (thecate). All species have a complex outer covering, consisting of an outer membrane, flattened vesicles in the middle, and a continuous inner membrane. In thecate forms, however, the vesicles contain plates made of cellulose or some other polysaccharide. The plates may form a structure as simple as a bivalve-type shell; however, in some species they form wings and other appendages that give the beholder the appearance of some fantastic alien spaceship.

Cell Characteristics

Dinoflagellates are not members of the kingdom *Plantae* but rather are protists, and they have both plant and animal characteristics. Some species are autotrophic—in other words, they have their own chloroplasts and can produce their own sugars and organic materials through photosynthesis. Other species are heterotrophic—they have no chloroplasts and typically must prey on or parasitize other organisms or consume organic detritus in order to obtain nourishment. Some of the heterotrophic species, however, can acquire the chloroplasts of prey and become photosynthetic themselves.

The chloroplasts in normally photosynthetic dinoflagellates are unique in that the plastids are enclosed within a triple membrane, rather than the double membrane of chloroplasts of most other organisms, and also in the fact that the chloroplasts in some cases have their own nuclei. These two characteristics, when considered with the large number of nonphotosynthetic dinoflagellates, have led some to argue that dinoflagellate chloroplasts have been secondarily acquired from a eukaryotic endosymbiont. Photosynthetic pigments include chlorophylls *a* and *c*, carotenoids, and xanthophylls.

Photosynthetic dinoflagellates often form symbioses with other aquatic organisms such as sponges, cnidarians (jellyfish, sea anemones, and corals), molluscs (bivalves, gastropods, octopuses, and squids), turbellarians, and tunicates. These symbiotic dinoflagellates, or *zooanthellae*, lack armor. They carry out most of the photosynthesis that fuels the productivity of coral reefs.

Although classified as protists, dinoflagellates have cellular nuclei with characteristics intermediate between those of prokaryotes and those of eukaryotes. As in eukaryotes, the nucleus is surrounded by a nuclear membrane and contains a nucleolus. However, the chromosomes are attached to the nuclear membrane in such a way that chromosomes remain attached to the inner wall of the cell membrane in prokaryotes. Dinoflagellates are also highly unusual in that they have permanently condensed chromosomes—and dinoflagellate deoxyribonucleic acid (DNA) does not form a complex with proteins, as in typical eukaryotic cells. There remains disagreement over whether dinoflagellate characteristics represent some ancient evolutionary lineage or more recent derivation.

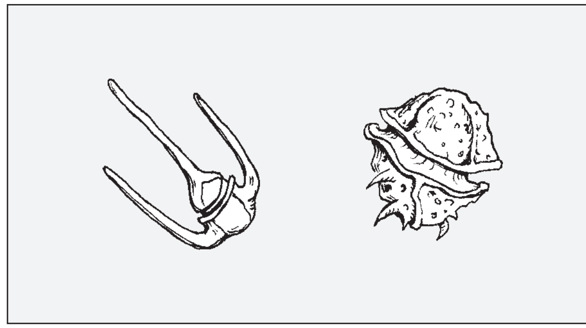
Life Cycle

Arguably the most accomplished shape shifters in the living world, dinoflagellates have incredibly complex life cycles. For example, *Pfiesteria* has at least twenty-four distinct stages in its life cycle, one of several reasons why scientists who work with the organism call it the "cell from hell." Dinoflagellate life cycles may include dormant cysts, cells without flagella (including amoeba-like stages), and more typical biflagellated cells.

Dinoflagellates may reproduce sexually or asexually. The cells are generally haploid, except for a zygote produced by the union of two gamete cells during sexual reproduction. The zygote undergoes meiosis shortly after fertilization. Dinoflagellate cells divide asexually in three ways: The parent cell of a naked dinoflagellate simply constricts and pinches off into two daughter cells; some armored types shed the theca prior to or during division; and other armored types split the parental theca, dividing the portions between the daughter cells. Unfavorable environmental conditions may trigger sexual reproduction as well as the formation of dormant cysts. Cysts may be transported large distances by currents, which in large part explains the dispersal of toxic dinoflagellate blooms up and down coastlines.

Pfiesteria exhibits all three forms, with the amoeboid and flagellated stages being toxic to fish. Encysted stages lie dormant in the bottom sediments of estuaries. The active amoeboid and flagellated stages are usually nontoxic. Amoeboid stages, which either inhabit the sediments or are free-swimming, consume bacteria, algae, small animals, or bits of fish tissues. Flagellated stages may ingest prey in a similar fashion but often siphon off the tissue of their prey through a cytoplasmic extension called the peduncle.

In the presence of an environmental trigger—such as substances given off by a school of live fish—amoeboid, flagellated, and encysted cells activate into toxic forms that swim toward the prey. The toxic forms then secrete toxins that immobilize and injure the prey with ulcerated, bleeding sores. *Pfiesteria* then feeds off materials that leak from the sores. Once the fish die, flagellated cells transform into amoeboid forms that feed on the carcass. If conditions suddenly become unfavorable, the active forms encyst and sink to the bottom. The entire cycle can take place in a matter of hours.



Kimberly L. Dawson Kurnizki

Dinoflagellates are unicellular or biflagellate algal organisms known for their whirling or spinning motion.

Red Tides and Toxins

Dinoflagellates are responsible for most of the *red tides* or *brown tides* that sicken and kill aquatic organisms and humans worldwide. Red tides are known from biblical times; one of the ten plagues reported to have been visited upon Egypt in the Book of Exodus (8:20-21) was most likely a red tide. Red tides were also known in ancient China and among Native Americans in Alaska and the Pacific Northwest.

Typically, the organisms that cause red and brown tides cause no harm until their populations explode or bloom. Adverse effects to other organisms result from oxygen depletion by irritation to skin and other organs, by the blocking of sunlight (in cases where the bloom is visible), or by the production of toxic substances, as in the case of *Pfiesteria*. In general, it is the toxic substances that sicken or kill humans and other vertebrates, such as manatees and birds. There is some controversy over whether human activities in estuarine and coastal waters have caused an increase in the frequency of these *algal blooms*.

In the mid-1990's a spate of horrific fish kills in the estuaries of North Carolina, Virginia, and Delaware began raising alarms up and down the East Coast of the United States. Ghastly lesions appeared on the affected fish, as if they were being eaten alive. People who spent a lot of time on or near the afflicted waters were affected, too, with symptoms ranging from memory loss to skin lesions. The single-celled culprit turned out to be *Pfiesteria piscicida*.

Several toxic syndromes that affect humans are caused by dinoflagellates: ciguatera fish poisoning, caused by toxins produced by *Gambierdiscus* and other species; paralytic shellfish poisoning, caused by toxins produced by *Alexandrium* and other species; neurotoxic shellfish poisoning, caused by toxins produced by *Gymnodinium breve*; diarrhetic shellfish poisoning, caused by toxins produced by *Dinophysis* species; and *Pfiesteria*-associated syndrome.

Bioluminescence

Dinoflagellates, besides being among the deadlier marine microorganisms, are also among the most beautiful. They are responsible for the *bioluminescence* of the sea that has enchanted mariners for millennia. The light is created through the reaction of oxygen with a substrate, luciferin (which has no relation to luciferins responsible for phosphorescence in other organisms such as lightning beetles), which is catalyzed by an enzyme, luciferase. Bioluminescence in dinoflagellates follows a circadian rhythm in which the maximum occurs at night.

David M. Lawrence

See also: Algae; Animal-plant interactions; Aquatic plants; Bioluminescence; Chloroplasts and other plastids; Chromosomes; Eukaryotic cells; Marine plants; Mitosis and meiosis; Phytoplankton.

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DISEASES AND DISORDERS

Categories: Diseases and disorders; pests and pest control

The science and study of plant diseases is known as plant pathology, which can be briefly defined as the study of the nature, cause and control of plant disease.

Plant disease is as old as land plants themselves, as shown by the fossil record. Several biblical accounts of plagues have been attributed to plant diseases, and in Roman times cereal rust was so serious that an annual ritual, the Robigalia, was performed to appease the Rust God, Robigo. In the mid-nineteenth century the Irish Potato Famine, a result of *potato late blight* disease, caused the deaths of some 800,000 persons and the emigration of about 1.5 million more, mostly to North America. Similarly, but to a lesser extent, *brown spot* disease of rice caused the Bengal famine of 1943 in India. Plant diseases continue to cost billions of dollars annually worldwide. The combined costs of lost yield, reduced quality, and costs of pesticides and other control measures are inevitably passed on to consumers. No type of plant is free from disease.

Causes and Types

Plant disease results from the continuing action of an irritant that can be either physical or biological. Physical, or abiotic, causes of disease include water stress (either from excess or insufficient

Symptoms of Plant Diseases

Symptom	*Injurious Effects, Sample Diseases*
Conversion of host	Fungal hyphae ramify and totally consume tissue into masses of host tissues, eventually replacing them with pathogen tissue: hard or powdery masses of fungal tissue. Includes rye ergot, cereal smuts.
Leaf mosaics, mottling	Irregular patterns of chlorophyll loss, malformations, localized leaf-cell death, and/or enhanced growth by other leaf cells. Includes tobacco mosaic virus, peach leaf curl disease.
Leaf spots, leaf blights	Death of leaf cells from parasitism and /or toxin release from the pathogen; limited to discrete, necrotic spots, or may coalesce into larger lesions covering most or all the leaf. Includes rose black spot, bean bacterial blight, potato late blight.
Overgrowths, galls	Localized overgrowth of host tissue, typically on stems, trunks, or roots, resulting in fleshy to woody galls. Includes root knot nematode, crown gall disease, pine rust galls.
Root rots	Debilitation or death of roots by soil-borne pathogens, reducing the plant's ability to absorb water and minerals. Includes common root rots of most plants.
Storage rots/molds	Ramification of fleshy storage tissue by fungi or bacteria, accompanied by release of wall-softening enzymes and sometimes by substances toxic to humans and animals. Includes potato soft rot, *Aspergillus* mold of peanut (with aflatoxin formation).
Stunted growth	Reduced activity of various meristematic tissues, resulting in dwarfed, often malformed plants. Includes peanut stunt virus.
Trunk and/or stem blight	Death of outer tissues of host stems; cankers on trunks resulting from parasitic and toxic action of the pathogen. Includes fire blight of pear, chestnut blight.
Wilts	Physical plugging of xylem vessels by the pathogen, with toxins that injure plant vascular tissue and/or formation of ballonlike extensions (tyloses) from adjacent host cells. Includes Dutch elm disease.

quantities), poor nutrition, improper soil acidity, and other environmental factors. Brief, damaging effects such as hail, wind, and lightning are considered injuries, not diseases.

Biological, biotic, causes of disease include bacteria, viruses, fungi, nematodes, and other microorganisms acting as disease-causing agents, or *pathogens*. Such pathogens infect plants, colonize tissues, and extract nutrients by living as *parasites*. Those actions often result in disruptions of normal physiological processes in plants, including photosynthesis, water uptake and movement, nutrient transport, and reproduction. In some instances anatomical abnormalities such as stunting, growth distortions, and gall formation are induced. The resulting physiological and anatomical abnormalities constitute disease *symptoms*.

Typically, and most important to producers and consumers, yield is reduced, both in quantity and in quality. In addition to diseases of growing plants, there are *postharvest diseases*. Those include fruit and vegetable rots and decay of stored grains. They may begin either before or after harvest, but in either case such diseases can continue long after harvest, further reducing the quality and value of food, fiber, and feed products. Some pathogens also produce toxins in plants they infect. Those toxins can be injurious, sometimes even fatal, to humans or animals that eat the contaminated plant materials.

Three interacting components are required for any plant disease to occur: (1) a susceptible host plant, (2) either a biotic pathogen or an abiotic, nonliving, causal agent, and (3) environmental conditions favorable for development of disease. Each of those components may vary in their contribution to overall severity of the resulting disease. The most important influences are the existing level of genetic resistance or susceptibility of the host plant; the existing level of *virulence*, or ability to cause disease, of the pathogen; for abiotic causes, the plant's degree of nutrient deficiency or water deficiency; and the degrees of favorable or unfavorable temperature, humidity, light intensity or other environmental factors that influence the health and vitality of both host and pathogen. A fourth component, a *vector*, may be required for some diseases. A vector is a second organism, most commonly an insect, that transmits the pathogen from a diseased plant to a healthy plant and injects or otherwise introduces the pathogen into the plant while feeding or laying eggs. Most pathogens do not require vectors.

Kinds of Plant Pathogens and Typical Diseases

Most fungi, bacteria, and nematodes are free-living organisms in nature. They generally contribute to the ecosystem and cause no deleterious effects on plants. Only a small percentage of microorganisms are plant-parasitic or pathogenic. The most important plant pathogens include fungi, bacteria and related forms, viruses, viroids, and nematodes; each group contains species that cause serious, economically important diseases. Fungi constitute the largest number of plant pathogens. By their very nature, viruses and viroids function only as parasites within plant or animal cells and cannot exist as free-living organisms. Nematodes are microscopic, wormlike animals that most commonly reside in soil and feed externally or internally on plant roots.

Plant Disease Control and Management

Plant pathology, in contrast to human and veterinary medicine, focuses very little on diseases of individuals but rather on large populations. Exceptions include certain high-value individuals, such as trees of historic or particular aesthetic or economic value. Emphasis is largely on prevention of plant diseases rather than curative therapy. Control of plant disease, in absolute terms, is usually impossible or economically impractical to achieve. The realistic goal is more commonly management of plant disease, with the goal of achieving a level of disease prevention or reduction that is both economically and environmentally sound. Briefly, most plant disease management practices fall within one of five broad categories: exclusion, eradication, resistance, protection or therapy, and adaptation to or modification of cultural conditions or practices.

Exclusion is the practice of keeping pathogens separated from their host plants and can be accomplished in several ways. Quarantines between countries are commonly used, with varying degrees of success, to prevent importation of pathogens into countries where they currently do not exist. Success of quarantines often depends on the extent and physical nature of the separation between the countries and whether the pathogen is wind-, soil-, or seed-borne. A variant of exclusion is *evasion* or *avoidance* of the pathogen: for example, growing plants susceptible to certain bacterial pathogens only in irrigated, semiarid regions unfavorable to the pathogen. The use of pathogen-free, certified seed or pathogen-free nursery stock are other examples of exclusion aimed at preventing or limiting introduction of pathogens into new areas.

Eradication is the practice of killing pathogens either in the environment or in and on the diseased plant. This limits infection, helps prevent further spread to healthy plants in the area, and helps prevent introduction of pathogens by shipment of diseased plant parts into regions where they currently are not present. Eradication practices such as chemical treatment of soil prior to planting, sanitation procedures such as removing infected crop debris, and long-duration crop rotations can all be successful to various degrees. Eradication and destruction of infected, living plants are often practiced for diseases of orchard crops and landscape trees, such as citrus canker and Dutch elm disease.

Resistance, resulting from innate genetic properties of plants or by directed plant breeding, is usually the most cost-effective means of managing plant diseases. Unfortunately, resistant cultivars may succumb to new, more virulent, or more aggressive strains of the pathogen that can arise by natural selection from populations of the pathogen in nature. Several examples also exist of successful application of *genetic modification* or genetic engineering to the development of resistant varieties, by introducing genes from other species, including nonrelated plants, viruses, or bacteria. Successful breeding of plants resistant or more tolerant to plant diseases provides billions of dollars' worth of benefit annually to producers of all types of plants.

Protection is the practice of treating susceptible plants in some manner, often chemically, to prevent infection once a pathogen reaches the plant surface by growth of the pathogen through the soil to seeds or roots, by deposition of windborne fungal spores, or by splash-drop dispersal of bacteria onto aerial plant surfaces. Protective fungicides or bactericides must be on the seed or plant surface prior to arrival of a pathogen to be effective. Protective fungicides do not kill pathogens; rather, they prevent spore germination, host penetration, or other early stages of infection, if spore germination does occur. Protective fungicides and bactericides are widely used throughout plant agriculture. Some recently developed protective fungicides also have limited eradicative activity. Those fungicides not only function as surface protectants but also enter plant tissue and kill pathogens already inside the plant—an example of therapeutic chemical action.

Adaptation to and *modification* of cultural conditions or practices are used to take advantage of conditions that benefit the plant but are also detrimental to development and spread of the pathogen. Examples include planting when soil temperatures are favorable for germination and subsequent growth of seedlings, altering soil pH by addition of lime or sulfur, not overfertilizing, increasing or lowering temperature, lowering humidity, and increasing airflow in greenhouses. The goal of such practices is to foster plant health and survival as well as prevent or reduce plant disease.

Often it is advantageous to use several of these approaches simultaneously. By combining natural host resistance, even if incomplete, with manipulation of environmental conditions unfavorable to the pathogen, by utilizing pathogen-free seed or nursery stock, or other practices, growers can often reduce significantly the amount of chemical pesticides required to manage a disease. Such a combined approach to disease and insect management is known as *integrated pest management* (IPM). Major goals of IPM are to reduce significantly the amount of pesticides going into the ecosystem while limiting plant disease at an economically acceptable level.

Larry J. Littlefield

See also: Acid precipitation; Agriculture: modern problems; Air pollution; Ascomycetes; Bacteria; Biopesticides; Endangered species; Fungi; Genetically modified bacteria; Genetically modified foods; Herbicides; Integrated pest management; Oomycetes; Pesticides; Resistance to plant diseases; Rusts; *Ustomycetes*; Viruses and viroids.

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DNA: HISTORICAL OVERVIEW

Categories: Cellular biology; genetics; history of plant science

The determination of the structure of DNA was preceded by years of research. Its discovery led to an avalanche of significant discoveries in molecular biology. The most important feature of the double-helix model was that it suggested how DNA might produce an exact copy of itself.

Deoxyribonucleic acid, or DNA, a molecule at the core of life itself, has existed for at least a few billion years. However, it was not until 1869 that Friedrich Miescher, a Swiss biochemist, was able to isolate it, though in a highly impure form. He discovered DNA in Tübingen, Germany, when he was a young postdoctoral student doing research on the chemistry of white blood cells. Through a series of chemical operations performed on pus cells, which have particularly large nuclei, he isolated a previously unobserved gelatinous substance. Analysis revealed that the new material contained phosphorus and nitrogen; Miescher named it *nuclein* because of its origin in cell nuclei. He recognized that the new substance's acidity was attributable to phosphoric acid.

Early Research

In the late nineteenth century, Albrecht Kossel, a German physiological chemist, discovered that nuclein contained *purines*, nitrogenous compounds with two rings, and *pyrimidines*, nitrogenous compounds with single rings. Furthermore, he showed that these nucleic acids were made of two different purines, adenine and guanine (A and G), and two different pyrimidines, thymine and cytosine (T and C). He also found a sugar among nucleic acid's decomposition products, but he was unable to identify it. Because nucleic acids were difficult to analyze, it was not until the first decade of the twentieth century that scientists realized that there are two types of *nucleic acid:* the thymus type, which is now known to be rich in DNA, and the yeast type, which is rich in *ribonucleic acid* (RNA).

Phoebus Levene, a Russian-American chemist who studied for a time with Kossel, was able to identify the sugar in yeast nucleic acid as ribose in 1908, but he did not definitively identify deoxyribose in thymus nucleic acid until 1929. He established that thymus nucleic acid contains the bases adenine, guanine, cytosine, and thymine and that yeast nucleic acid contains the bases adenine, guanine, cytosine, and uracil. He also isolated, from various nucleic acids, sugar-base fragments (called *nucleosides*) and base-sugar-phosphate groups (called *nucleotides*). In the 1920's he developed a theory that nucleic acids are linear chains of purines and pyrimidines joined to one another by means of the sugar-phosphate group. He took the simplest route and proposed that nucleic acids are composed of repeated sets of four nucleotides (the *tetranucleotide hypothesis*). Since this monotonous sequence could convey little information, most scientists believed that proteins, with their more than twenty amino acid building blocks, were more likely than nucleic acids to be the purveyors of the cell's genetic messages.

By World War II, scientists knew that DNA was an extremely long molecule, but most continued to believe that proteins were the sole carriers of genetic information and that nucleic acids played, at the most, a facilitating role. That DNA was the true source of genetic information was shown by Oswald T. Avery and his coworkers at the Rockefeller Institute for Medical Research. In a laboratory near Levene's, they discovered that protein-free DNA carried genetic information from a virulent form of *Pneumococcus* bacterial cells to a nonvirulent form. Avery stated that DNA is not merely structurally important but is also a functionally active substance in determining a cell's specific characteristics and biochemical activity. His discovery, which was published in a 1944 paper, greatly surprised those geneticists and biochemists who had long believed that genes, in order to perform their complex tasks, had to be made of proteins. Many of them continued to believe that protein contaminants in Avery's experiments must be the transforming agents, not the DNA itself.

The experiments of Alfred D. Hershey and Martha Chase in 1952 finally convinced most scientists that DNA, not protein, is the genetic material. They experimented with a *bacteriophage* (a virus that infects bacteria). The outer surface of a bacteriophage, or phage, consists of protein, but DNA exists within its head. Phages were known to multiply, in part, by injecting their genetic material into bacterial cells.

Hershey and Chase prepared two populations of phages. They labeled the phage protein in one group with a radioactive isotope. In the other group, it was the phage DNA that they radioactively labeled. The scientists then allowed the phages to attack cells of *Escherichia coli*, a colon bacteria. Afterward, their analysis showed that the phage protein had remained outside the bacteria, but the phage DNA had been injected into the bacteria. This research showed that the phages' genetic material was in the DNA rather than in the protein.

Research into DNA Structure

Only by understanding how covalent bonds link together the atoms of DNA and then by establishing their three-dimensional arrangement in space could scientists learn how this molecule carries genetic information. The British organic chemist Alexander Todd decided to clarify the chemical bonding of the nucleic acids by starting with the simplest units, the nucleosides. By the early 1950's he was able to show that the nucleic acids are linear, rather than branched, polymers and to specify exactly how the sugar ring (ribose or deoxyribose) is bonded to the various bases and to the phosphate group.

During the 1940's, while Todd was working out the detailed bonding of the nucleic acids, Erwin Chargaff, a biochemist at the College of Physicians and Surgeons in New York, was exploring the chemical differences in the base compositions of DNA from different sources. By 1950 his careful analyses of the base compositions of DNA samples from many plants and animals had revealed that the compositions varied widely, but his data also yielded the significant result that the ratios of adenine to thymine, and guanine to cytosine, were always close to one. Chargaff's work disproved the theory that DNA was made of repeating tetranucleotide units, but he did not attach any meaning to the one-to-one base ratios (now known as *Chargaff's rules*) because, along with other scientists, he continued to think of DNA as a single polynucleotide chain.

Linus Pauling, along with many other American chemists, was slow to accept DNA as the genetic material. Beginning in the 1930's, Pauling had done important work on hemoglobin and the structure of proteins. In 1948 he discovered the structure of the protein alpha keratin by using only a pen, a ruler, and a piece of paper: the alpha helix held together in its twisting turns by hydrogen bonds.

Moving Toward a Helical Model

In the early 1950's James Watson and Francis Crick, both of whom had become interested in DNA, were deeply impressed by Pauling's work, not so much because of the helical structure he had discovered ("helices were in the air," according to Crick) but because Pauling had the correct approach to biological problems. He believed that the chemists' knowledge of atomic sizes, bond distances, and bond angles would allow biologists to build accurate models of the three-dimensional structures of the complex molecules in living things. Crick, then in his mid-thirties, was a physicist working on the theory of the X-ray diffraction of proteins. Watson, in his early twenties, was a biologist whose interest in genes had led him to the Cavendish Laboratory of Cambridge University. At first glance, Watson and Crick made an odd team: Crick had expertise in crystallography and Watson in genetics, but neither had much knowledge of chemistry. Nevertheless, they were determined to discover the structure of DNA.

The work that ultimately led to the formulation of DNA's three-dimensional structure was performed by three different groups: Pauling and Robert Corey at the California Institute of Technology; Maurice Wilkins and Rosalind Franklin in John Randall's laboratory at King's College, London; and Watson and Crick at the Cavendish Laboratory. Particularly important were Franklin's X-ray studies of DNA. She showed that DNA existed in two forms, each with a distinctive X-ray picture: The wetter form (called the *B form*) gave an X-shaped pattern, and the slightly drier form (the *A form*) gave a more detailed array of spots. From these X-ray pictures, the workers in Randall's laboratory found that DNA had two periodicities in its B form: a major one of 3.4 angstroms and a secondary one of 34 angstroms. Gradually, their studies also began to suggest that DNA had a helical structure.

Watson and Crick decided to approach DNA's structure using Pauling's model-building approach. It was known that DNA's chemical formula, with its many single bonds that allowed free rotation of various groups, meant that the molecule could assume many different configurations. In their early research, Watson and Crick had to make some assumptions. For example, they assumed that the polynucleotide chain was coiled in a helix, somewhat like a vine winding around a cylinder. They reasoned that the different sizes and shapes of the bases probably led to their irregular sequence along the chain, whereas the orderly sugar-phosphate backbone must be responsible for the regular molecular features predicted from the X-ray photographs. Because of the high density of DNA, Watson and Crick proposed, as their first model, a triple helix. The three polynucleotide strands were arranged with the sugar-phosphate groups on the inside of the molecule and the bases on the outside. Wilkins, Franklin, and others came to Cambridge to see this model, but they thought it was ridiculous. Watson and Crick had understood neither the X-ray data nor the water content of the various forms of DNA.

In late 1952 Pauling, relying on poor X-ray photographs of DNA and faulty information about the density of its two forms, also proposed a triple helix. He had decided that packing the extremely bulky bases in the center of the molecule would be too difficult, and so, like Watson and Crick, he situated them on the periphery of his three-strand model. Before this work, Pauling had speculated, in some of his papers and talks, that the genetic material in living things had to be composed of two complementary strands. In studying the actual density determinations and X-ray photographs, however, he was led to the conclusion that this DNA, the product of laboratory manipulations, must be a triple helix.

Watson and Crick quickly abandoned their triple helix. Their search for another model of DNA was aided by a visit to Cambridge in the summer of 1952 by Erwin Chargaff. After talking with them, he was shocked that neither had precise knowledge of the chemical differences among the four bases. He explained to them his findings about the base ratios, which eventually suggested to them that these bases might be paired in the DNA structure. Watson, in fact, started manipulating paper models of the bases, in an attempt to mate them, but he did not understand which base forms actually existed in DNA. (Chemists had found that these nitrogenous bases could exist, depending on conditions, in two forms, the keto and the enol.)

Fortunately, an American crystallographer and Pauling protégé, Jerry Donohue, had an excellent knowledge of these base forms, which he communicated to Watson, who was still mired in like-with-like schemes. At Donohue's insistence, Watson began matching adenine with thymine and guanine with cytosine. This proved to be the key to the structure, for when these base pairs were joined with hydrogen bonds, their combinations were almost identical in size and shape. Thus, these base pairs could be fit into the interior of the helix, whereas the regular sugar-phosphate backbone at the molecule's exterior could account for its acidity and its interactions with water.

Watson-Crick Model

In the Watson-Crick model, DNA's structure consists of two strands, which may contain several million nucleotide units, that run in opposite directions (because of the asymmetry of the sugar-phosphate linkage). Although the hydrogen bonds that hold the chains together are much weaker than normal chemical bonds, they are so numerous that the union is tight. The two strands are not straight; rather, they wind around an imaginary axis in a helical fashion, as if wrapped around a cylinder. The sugar-phosphate groups form the coil, with their attached bases extending inward toward the axis of the helix.

In this double helix (which represents the B form of DNA), a single turn repeats itself every ten base

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pairs. More specifically, the space between one base pair and the next is 3.4 angstroms, and the helix makes one complete turn every 34 angstroms. Scientists later determined that the A form has eleven base pairs per turn.

The double helix is a right-hand helix, which means that an observer looking down the axis of the helix sees each strand, as it goes away from him, moving in a clockwise direction. This helix, which is about 20 angstroms in diameter, has a deep groove on its surface, winding parallel to a much shallower groove. The structure is stabilized by the hydrogen bonding of the complementary base pairs. The purine adenine (A) is always hydrogen-bonded to the pyrimidine thymine (T), while the purine guanine (G) is always hydrogen-bonded to the pyrimidine cytosine (C).

Because of this base-pairing scheme, each chain's sequence determines its partner's sequence. For example, if one strand has the first following sequence, then the other strand would have the second sequence.

TACGCAT

ATGCGTA

The complementary nature of these opposing sequences accounts for Chargaff's rules and, as Watson and Crick noted in their famous 1953 paper in *Nature*, provides a natural explanation for the replication of the molecule. Because of the specific phosphodiester bonding between the sugars, each strand has a top and bottom end, making the two strands antiparallel—that is, positioned relative to each other like two swimmers heading in opposite directions.

In the decades after the discovery of the double helix, scientists found that DNA could exist in structures other than the B-form double helix. For example, the chromosomes of some small viruses have single-stranded DNA molecules. Furthermore, some DNA molecules from living organisms turned out to be circular, which means that the polynucleotide chain formed a closed loop. In fact, the DNA molecules of some viruses interconvert between linear and circular forms, the linear being present inside the virus particle, the circular form existing in the host cell. While studying the conversion of the linear to the circular form of DNA, Jerome Vinograd, a physical chemist, discovered that the axis of the double helix can be twisted to form a superhelix, which can be right- or left-handed.

In the late 1970's and early 1980's, Alexander Rich at the Massachusetts Institute of Technology discovered a left-handed double helix containing about twelve nucleotides per turn. Because the backbones follow a zigzag path, this left-handed structure was called Z-DNA. Instead of the major and minor grooves of B-DNA, only a single groove winds around Z-DNA. Scientists have found the Z form of DNA in nature, specifically in regions of the DNA molecule where G and C bases form an extended, alternating sequence.

Implications of DNA Structure

DNA has been called the master key of life, and the discovery of its structure has been called the most influential event in modern biology. Watson and Crick's discovery of the double helix led to an avalanche of significant discoveries in molecular biology. The most important feature of their model was that it suggested how DNA might produce an exact copy of itself.

Because the model consists of two chains, each the complement of the other, either chain may act as a mold or template on which a complementary chain can be synthesized. As the two chains of DNA unwind and separate, each strand begins to construct a new complement onto itself. When the process is finished, two pairs of double helices exist where there was one before. Thus, the Watson-Crick model helped lead to an explanation, at the molecular level, of how genes duplicate themselves with great fidelity.

The Watson-Crick model also contributed to the solution of the pivotal problem of genetics: how genes control the making of proteins in cells. Though this problem was not solved directly by the double helix, the study of the interactions between DNA and the proteins it indirectly produces revealed that its structure contains, in the sequences of its bases, an intricate code that supervises the construction of the thousands of proteins used by cells. In working out this genetic code, scientists discovered little similarity between DNA's three-nucleotide sequences that code for particular amino acids and the structures of the amino acids themselves. Indeed, the transfer of information from DNA to the cellular mechanisms overseeing protein construction turned out to be quite complex, involving various types of RNA.

Watson and Crick, the originators of the revolution in molecular biology, also played important parts in its evolution. Their work was the catalyst for the development of its "central dogma," which explains how genetic information passes from DNA to the cell's proteins. In the first part of the process, DNA serves as the template for its *self-replication* (duplication). Then, RNA molecules are made on a DNA template (*transcription*). Finally, RNA templates determine all proteins (*translation*). Although DNA can therefore act on itself, the processes of transcription and translation were seen as moving in one direction only: DNA sequences are never made on protein templates, and DNA sequences are never made on RNA templates. In the course of time, some exceptions to these rules have been discovered, but the central dogma remains essentially valid, as does the double helix. Watson and Crick, along with many other scientists, solved, by means of ideas drawn from physics and chemistry, the basic mysteries of the gene.

Robert J. Paradowski

See also: Chromosomes; DNA in plants; DNA replication; Genetic code; Nucleic acids.

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DNA IN PLANTS

Categories: Cellular biology; genetics

DNA is the hereditary or genetic material, present in all cells, that carries information for the structure and function of living things.

In the plant kingdom, DNA, or deoxyribonucleic acid, is contained within the membrane-bound cell structures of the nucleus, mitochondria, and chloroplasts. DNA has several properties that are unique among chemical molecules. It is universal to all living organisms, having the same structure and function in each. It is capable of reproducing itself in a process known as self-replication. This property allows cell division, and thus continuity, growth, and repair. It carries in its structure the genetic code, or set of instructions, for cellular development and maintenance. Finally, it undergoes changes in chemical structure, from both environmental and internal causes, called mutations, which contribute to evolution, diversity, and disease.

Chemical Structure

DNA is a simple molecule, consisting of four nucleotides. Each nucleotide has a five-carbon sugar (deoxyribose), a phosphate, and one of four possible nitrogenous bases: the double-ringed purines of *adenine* (A) and *guanine* (G) and the single-ringed pyrimidines of *thymine* (T) and *cytosine* (C). Most of the properties of DNA relate to the unique bonds that form among the nucleotides: The sugar-phosphate components align themselves linearly, while the nitrogen rings bond perpendicularly. The nitrogen rings further bond in a very specific fashion: A always pairs with T, and G always pairs with C. The DNA molecule thus appears as a ladder, the sides being sugar-phosphate; the rungs, the A-T and G-C pairs.

Further bonding and folding produces a structure shaped like a spiral ladder, known as a *double helix*. This double helix is compactly packaged in ropelike structures known as *chromosomes*, which are visible under a light microscope before and during cell division. During the daily life of the cell, the DNA appears as an indistinguishable dark mass call chromatin (an inclusive term referring to DNA and the proteins that bind to it, located in the nuclei of eukaryotic cells).

The Watson and Crick Model

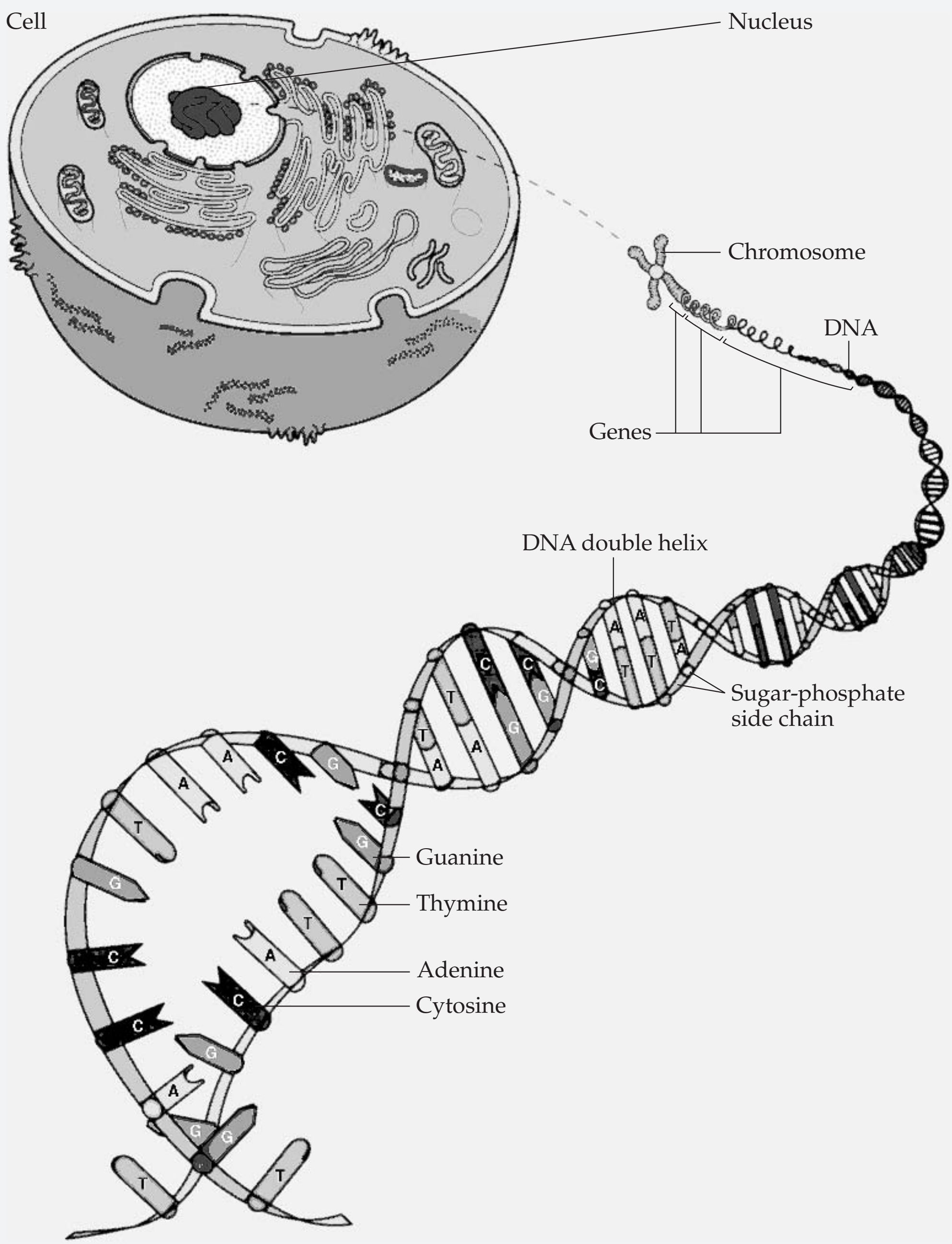
In the mid-1800's Gregor Mendel, an Austrian monk, postulated that genetic material existed. He discovered the laws of heredity using the pea and other plants in his garden to study the inheritance of such traits as flower color. Nearly seventy years passed before scientists James Watson and Francis Crick, in 1953, proposed the double helix as the most plausible model for each of the unique properties of the molecule. Their model was verified by X-ray diffraction techniques soon afterward.

Several researchers, working at Columbia University and elsewhere in the United States, had led the way prior to Watson and Crick by discovering the chemical composition of this genetic material and the nitrogenous base pairing: The amount of adenine always equaled that of thymine and likewise with guanine and cytosine. The Watson and Crick model also suggested that the two sides, or strands, of DNA run in opposite directions: That is, the phosphate sugar of one side points upward, while the other strand points downward. This property is known as *antiparallel bonding*. The Watson and Crick model could easily explain how DNA replicates during cell division and how genetic information is encoded in its structure.

Self-Replication

Self-replication, which allows the continuity of generations and the growth and repair of individual organisms, occurs during cell division. DNA must be able to produce exact copies of itself. The molecule is uniquely designed for this: A series of enzyme-mediated steps allows the double helix to unwind or unzip, like a zipper, separating the two strands. Next, nucleotides from digested food enter first the cell and then the nucleus. They bind to a corresponding nucleotide: A with T and G with C. The process continues until two new double-stranded molecules of DNA have formed, each a copy of the other and each going into the new cells that resulted from cell division.

The Structure of DNA



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Protein Synthesis

The information encoded in DNA allows for all the development and maintenance of the cell and the organism. The language of this code lies in a linear reading of adjacent nucleotides on each strand. Every three nucleotides specify or fit a particular amino acid, the individual units of proteins. A second molecule, *ribonucleic acid* (RNA), copies the molecular structure of DNA and brings the information outside the nucleus into the surrounding cytoplasm of the cell, where the amino acids are assembled, in specified order, to produce a protein. Postproduction modifications of these proteins, such as the addition of sugars, fats, or metals, allow a vast array of functional and structural diversity. Plant DNA codes for a variety of substances that are unique to plants. These products sustain not only the plants themselves but also entire ecological niches, as well as humankind.

Mitochondrial and Chloroplastic DNA

A second, independently functioning set of DNA exists in two organelles outside the cell's nucleus, the mitochondria and the chloroplast. It is in the *mitochondria*, the power sources of cells, where carbohydrates, fats, and proteins are broken down to their raw elements with the release of stored chemical bond energy in the form of heat (calories).

The second region in which DNA is housed outside the nucleus is in the *chloroplast*, a structure unique to plant cells. In chloroplasts, photosynthesis occurs, the process by which plants are able to transform carbon dioxide, water, and solar energy to produce sugars and, later, fats and proteins, with the release of oxygen. This critical process undertaken by plants sustains most life on earth.

Both mitochondrial and chloroplastic DNA replicate separately from nuclear DNA during cell division. It is postulated that these organelles once, billions of years ago, may have been independently living organisms that were incorporated into other cells to form the eukaryotic cells that make up nonbacterial life-forms such as fungi, protists, plants, and animals.

Plant Proteins

A large array of proteins that are unique to plants are encoded on plant DNA. A group that has received much attention are the so-called *phytochemicals*, substances with powerful health benefits. Well-studied classes are few, including the flavonoids, phytosterols, carotenoids, indoles, coumarins, organosulfurs, terpenes, saponins, lignans, and isothiocyanates. Each group contains specific proteins that are both antioxidants and anticarcinogens—protecting animal cells from cancer-causing agents. The carotenoids, such as beta-carotene, found in orange and yellow fruits and vegetables, and lycopenes, found in tomatoes, appear to protect animals against heart disease and stroke as well as cancer. The phytosterols, like those found in soybeans, are estrogenlike compounds that mimic female hormones. These appear to protect female organs from cancers and also appear to lower cholesterol.

Plant Hormones

Large segments of plant DNA are devoted to coding for specialized plant hormones. Hormones are substances that are produced by one group of cells, circulate to another site, and affect the DNA of the target cells. In plants, these hormones control cell division, growth, and differentiation.

There are five well-described classes of plant hormones: the auxins, gibberellins, cytokinins, ethylene, and abscisic acid. Among the auxins' functions is allowing phototropism, the property that makes plants bend toward the light. Produced in the roots, auxins travel to stems, making cells elongate on the dark side of plant tissue. Ethylene is a gaseous substance that ripens fruits and causes them to drop from the plant. Abscisic acid contributes to the aging and falling of leaves.

Genetically Modified Plants

Because plants are easy to manipulate, plant DNA is second only to bacterial DNA as a primary experimental subject for bioengineers. The direct modification of DNA by adding or removing a particular segment of genes that code for specific traits is the focus of bioengineering and biotechnology. Because plants provide the major food source for human and livestock populations, *genetically modified foods* have been developed that resist insects, bacteria, viruses, and other pests and decrease the need for external pesticides.

Genetically modified plant crops are designed to enhance a variety of characteristics, from looking and tasting good to growing faster or ripening more slowly to having no seeds. The introduction of genes from other kingdoms, such as the animal kingdom, into plant DNA is allowing scientists to develop future crops that may contain human vaccines, human hormones, and other pharmaceutical products. A tomato was the first federally approved bioengineered food to be sold in the United States. Today, dozens of produce items and livestock feed are in some way genetically modified.

Connie Rizzo

See also: Biotechnology; Chloroplast DNA; Chromatin; Chromosomes; DNA: recombinant technology; DNA replication; Genetic code; Genetically modified bacteria; Genetically modified foods; Genetics: mutations; Hormones; Mitochondrial DNA; Nucleic acids; Nucleus; Plant biotechnology; Proteins and amino acids; RNA.

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DNA: RECOMBINANT TECHNOLOGY

Categories: Biotechnology; cellular biology; economic botany and plant uses; genetics

Recombinant DNA technology makes use of science's understanding of the molecular structure of DNA, the nucleic acid that encodes genetic information, to alter DNA in order to manipulate genetic traits. Such technology has immense implications for agriculture, horticulture, and the generation of medicinal compounds from plants.

Recombinant DNA technology has been essential for understanding DNA sequences. Because of their large, complex genomes, it was difficult to study one gene in eukaryotes, but recombinant DNA technology has allowed the isolation and amplification of specific DNA fragments facilitating the molecular analysis of genes. In addition, the tools of recombinant DNA technology have been used to create genetically modified plants. Such modifications include the introduction of resistance to insects, herbicides, viruses, and bacterial and fungal diseases into plants. Plants have also been made to produce antibodies so that plants can serve as edible vaccines.

DNA Structure

Organisms contain two kinds of nucleic acids: ribonucleic acid, or RNA, and deoxyribonucleic acid, or DNA. DNA is made of a double chain, or helix. The structure of one chain, or strand, is a backbone made up of repetitions of the same basic unit. That unit is a five-carbon sugar molecule called 2′-deoxyribose attached to a phosphate residue. RNA contains a ribose sugar instead. Also attached to the sugar part of the backbone are other molecules called bases. The four bases are adenine (A), guanine (G), cytosine (C), and thymine (T). DNA molecules are double strands that are held together because each base in one strand is paired to (hydrogen-bonds with) a base in the other strand. Adenine always pairs with the base thymine, and guanine always pairs with cytosine. A and T are called complementary bases. Likewise, G and C are complementary bases.

DNA is shaped much like a helical ladder, with the sugar and phosphate backbones being the sides of a ladder and the base pairs that hold the two strands together being the rungs of a ladder. DNA is often represented as a string of letters, with each letter representing a base. The order of A's, T's, G's, and C's (the rungs of the ladder) along a DNA double helix is the sequence of that DNA which contains the genetic information.

Restriction Enzymes

In recombinant DNA technology, scientists are able to use molecules called *restriction enzymes* to make cuts at specific sequences. Some restriction enzymes make cuts straight across the two strands of DNA in the double helix, creating blunt ends. Other restriction enzymes cut the two strands in a staggered pattern, leaving short, specific single strands at the cut sites. These single-stranded regions, called *sticky ends* or cohesive ends, can base-pair (hydrogen-bond) with complementary base sequences from other, similarly cut DNAs. These sticky ends allow joining of DNA from any source cut with restriction enzymes that create the same ends.

Cutting with restriction enzymes creates fragments of DNA with sequence-specific ends that can be spliced into small, self-replicating vehicle, or vector, molecules and introduced into a host cell where the vector molecules with the added DNA

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fragments replicate to produce a large amount of specific DNA for analyses. This process is *recombinant DNA cloning*.

DNA Cloning

One way to clone a specific gene is to clone all the DNA fragments generated from cutting with a restriction enzyme and then screen for the clone containing the desired gene. This method of cloning random DNA segments into a vector is called *shotgunning*. The entire collection of such cloned fragments, which together represent the entire genome of the organism, is called a gene library. Genomic DNA libraries are made by cloning the total genomic DNA of an organism.

Another way to clone a specific gene is to begin with messenger RNA (mRNA) from the organism. (Messenger RNA is a molecule that functions to create complementary copies of DNA strands. At a ribosome the messenger RNA then determine the order of amino acids that are joined to make a protein.) Using *reverse transcriptase* (an enzyme encoded by some RNA viruses that uses RNA as a template for DNA synthesis), scientists can make a DNA copy of the mRNA. The complementary strand is also synthesized to create a double-stranded DNA called cDNA (complementary DNA) that is complementary to the mRNA. These cDNAs are then cloned to create a complementary DNA library. Individual cloned cDNAs can be used to trap the corresponding mRNA on a nitrocellulose filter. At this point, the mRNA can be used in a cell-free protein synthesis system to allow identification of the protein encoded by that cDNA clone. Alternatively, the cDNA can be used to find sequences complementary to it in a genomic library to obtain a clone of the specific gene.

Nucleic Acid Hybridization

The ability to hybridize nucleic acids to find sequences complementary to a particular DNA is another essential tool that offers another way to identify cloned genes. This method is called *nucleic acid hybridization* or Southern blotting (named after E. M. Southern, who developed the method). In this procedure, DNA is cut with restriction endonucleases, and the resulting DNA fragments are separated by size using agarose gel electrophoresis. The DNA in the gel is denatured (made single-stranded) by high pH and transferred to a nitrocellulose filter. The DNAs are immobilized on the nitrocellulose in the same pattern as on the gel (a Southern blot). Aprobe—a specific DNA or RNA—is hybridized to the nitrocellulose. The probe is "labeled" with a radioactive or fluorescent (nonradioactive) tag so it can be detected. The probe is denatured by heat so it is single-stranded and able to anneal (hybridize) with its complementary sequence among the single-stranded DNAs tethered to the nitrocellulose. The probe is then detected to reveal the position of the DNAs that hybridized with the probe.

Polymerase Chain Reactions

Another tool of molecular biology is to use a *polymerase chain reaction* (PCR) to amplify specific segments of DNA in vitro (in the test tube). PCR requires a pair of sequences, called primers, about twenty base pairs long that are complementary to the ends of the region of DNA to be amplified. High temperature is used to denature the double-stranded DNA. At a lower temperature, the primers anneal (base-pair) to their complementary sequences, and a thermal-stable DNA polymerase copies the single-stranded templates. After the replication of the segment between the two primers (one cycle), the newly synthesized double-stranded DNA molecules are denatured by high temperature, the temperature is lowered, primers anneal, and a second cycle of replication occurs. The number of DNA molecules produced doubles with each cycle of replication. As a result, a million copies of a single DNA molecule can be produced in only a few hours, if the appropriate sequences for the two primers are known. PCR is a very sensitive method: Even a single DNA molecule can be amplified. PCR is much faster than recombinant DNA cloning and can produce a large amount of a specific piece of DNA.

Developing ways to determine DNA sequences (the sequences of adenine, thymine, guanine, and cytosine base pairs on the DNA "rungs") has led to the identification of the complete DNA sequences of the genomes of a number of organisms, including the model plant *Arabidopsis* as well as the much more complex human genome.

Susan J. Karcher

See also: Biotechnology; Chromosomes; Cloning of plants; DNA in plants; DNA replication; Electrophoresis; Environmental biotechnology; Gene regulation; Genetic code; Genetically modified bacteria; Genetically modified foods; Genetics: mutations; Genetics: post-Mendelian; Plant biotechnology; RNA.

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MAGILL'S ENCYCLOPEDIA OF SCIENCE

PLANT LIFE

Volume 2

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DNA Replication–Metabolites: Primary vs. Secondary

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PUBLISHER'S NOTE

Magill's Encyclopedia of Science: Plant Life is designed to meet the needs of college and high school students as well as nonspecialists seeking general information about botany and related sciences. The definition of "plant life" is quite broad, covering the range from molecular to macro topics: the basics of cell structure and function, genetic and photosynthetic processes, evolution, systematics and classification, ecology and environmental issues, and those forms of life—archaea, bacteria, algae, and fungi—that, in addition to plants, are traditionally studied in introductory botany courses. A number of practical and issue-oriented topics are covered as well, from agricultural, economic, medicinal, and cultural uses of plants to biomes, plant-related environmental issues, and the flora of major regions of the world. (Readers should note that, although cultural and medicinal uses of plants are occasionally addressed, this encyclopedia is intended for broad information and educational purposes. Those interested in the use of plants to achieve nutritive or medicinal benefits should consult a physician.)

Altogether, the four volumes of *Plant Life* survey 379 topics, alphabetically arranged from *Acid precipitation* to *Zygomycetes*. For this publication, 196 essays have been newly acquired, and 183 essays are previously published essays whose contents were reviewed and deemed important to include as core topics. The latter group originally appeared in the following Salem publications: *Magill's Survey of Science: Life Science* (1991), *Magill's Survey of Science: Life Science, Supplement* (1998), *Natural Resources* (1998), *Encyclopedia of Genetics* (1999), *Encyclopedia of Environmental Issues* (2000), *World Geography* (2001), and *Earth Science* (2001). All of these previously published essays have been thoroughly scrutinized and updated by the set's editors. In addition to updating the text, the editors have added new bibliographies at the ends of all articles.

New appendices, providing essential research tools for students, have been acquired as well:

- a "Biographical List of Botanists" with brief descriptions of the contributions of 134 famous naturalists, botanists, and other plant scientists
- a Plant Classification table
- a Plant Names appendix, alphabetized by common name with scientific equivalents
- another Plant Names appendix, alphabetized by scientific name with common equivalents
- a "Time Line" of advancements in plant science (a discursive textual history is also provided in the encyclopedia-proper)
- a Glossary of 1,160 terms
- a Bibliography, organized by category of research
- a list of authoritative Web sites with their sponsors, URLs, and descriptions

Every essay is signed by the botanist, biologist, or other expert who wrote it; where essays have been revised or updated, the name of the updater appears as well. In the tradition of Magill reference, each essay is offered in a standard format that allows readers to predict the location of core information and to skim for topics of interest: The title of each article lists the topic as it is most likely to be looked up by students; the "Category" line indicates pertinent scientific subdiscipline(s) or area(s) of research; and a capsule "Definition" of the topic follows. Numerous subheads guide the reader

through the text; moreover, key concepts are italicized throughout. These features are designed to help students navigate the text and identify passages of interest in context. At the end of each essay is an annotated list of "Sources for Further Study": print resources, accessible through most libraries, for additional information. (Web sites are reserved for their own appendix at the end of volume 4.) A "See also" section closes every essay and refers readers to related essays in the set, thereby linking topics that, together, form a larger picture. For example, since all components of the plant cell are covered in detail in separate entries (from the *Cell wall* through *Vacuoles*), the "See also" sections for these dozen or so essays list all other essays covering parts of the cell as well as any other topics of interest.

Approximately 150 charts, sidebars, maps, tables, diagrams, graphs, and labeled line drawings offer the essential visual content so important to students of the sciences, illustrating such core concepts as the parts of a plant cell, the replication of DNA, the phases of mitosis and meiosis, the world's most important crops by region, the parts of a flower, major types of inflorescence, or different classifications of fruits and their characteristics. In addition, nearly 200 black-and-white photographs appear throughout the text and are captioned to offer examples of the important phyla of plants, parts of plants, biomes of plants, and processes of plants: from bromeliads to horsetails to wheat; from Arctic tundra to rain forests; from anthers to stems to roots; from carnivorous plants to tropisms.

Reference aids are carefully designed to allow easy access to the information in a variety of modes: The front matter to each of the four volumes includes the volume's contents, followed by a full "Alphabetical List of Contents" (of all the volumes). All four volumes include a "List of Illustrations, Charts, and Tables," alphabetized by key term, to allow readers to locate pages with (for example) a picture of the apparatus used in the *Miller-Urey Experiment*, a chart demonstrating the genetic offspring of *Mendel's Pea Plants*, a map showing the world's major zones of *Desertification*, a cross-section of *Flower Parts*, or a sampling of the many types of *Leaf Margins*. At the end of volume 4 is a "Categorized Index" of the essays, organized by scientific subdiscipline; a "Biographical Index," which provides both a list of famous personages and access to discussions in which they figure prominently; and a comprehensive "Subject Index" including not only the personages but also the core concepts, topics, and terms discussed throughout these volumes.

Reference works such as *Magill's Encyclopedia of Science: Plant Life* would not be possible without the help of experts in botany, ecology, environmental, cellular, biological, and other life sciences; the names of these individuals, along with their academic affiliations, appear in the front matter to volume 1. We are particularly grateful to the project's editor, Bryan Ness, Ph.D., Professor of Biology at Pacific Union College in Angwin, California. Dr. Ness was tireless in helping to ensure thorough, accurate, and up-to-date coverage of the content, which reflects the most current scientific knowledge. He guided the use of commonly accepted terminology when describing plant life processes, helping to make *Magill's Encyclopedia of Science: Plant Life* easy for readers to use for reference to complement the standard biology texts.

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DNA REPLICATION

Categories: Cellular biology; genetics; reproduction and life cycles

DNA, deoxyribonucleic acid, is the hereditary material of most living creatures. It carries genetic information that determines all types of plant lives. DNA replication is a process by which a single DNA molecule is copied, resulting in two identical molecules prior to the cell division. The accuracy and precision in DNA replication has ensured the continuity of life from generation to generation.

Following James Watson and Francis Crick's landmark proposal for the structure of the deoxyribonucleic acid (DNA) molecule in 1953, many scientists turned their attention to how this molecule is replicated. The process of replication is the key to continuity of plant as well as other forms of life. The DNA molecule consists of two polymer chains (strands) forming a *double helix*. Each strand is made up of a five-carbon sugar (2'-deoxyribose), phosphoric acid, and four nitrogen-containing bases. Two bases are *purines*, which have a double-ring structure; the other two are *pyrimidines*, which contain a single ring. The purine bases are adenine (A) and guanine (G), while the pyrimidine bases are thymine (T) and cytosine (C). The two strands of a DNA molecule running in opposite directions are held together by hydrogen bonding between the A-T and G-C base pairs, which form the "rungs" of the ladder that makes the double helix. Such complementary *base pairing* is the foundation for the DNA double helix as well as its replication.

Semiconservative Replication

The replication mechanism first proposed by Watson and Crick was that the strands of the original (*parental*) duplex separate, and each individual strand serves as a pattern or template for the synthesis of a new strand (*daughter*). The daughter strands are synthesized by the addition of successive nucleotides in such a way that each base in the daughter strand is complementary to the base across the way in the template strand. This is called *semiconservative replication*.

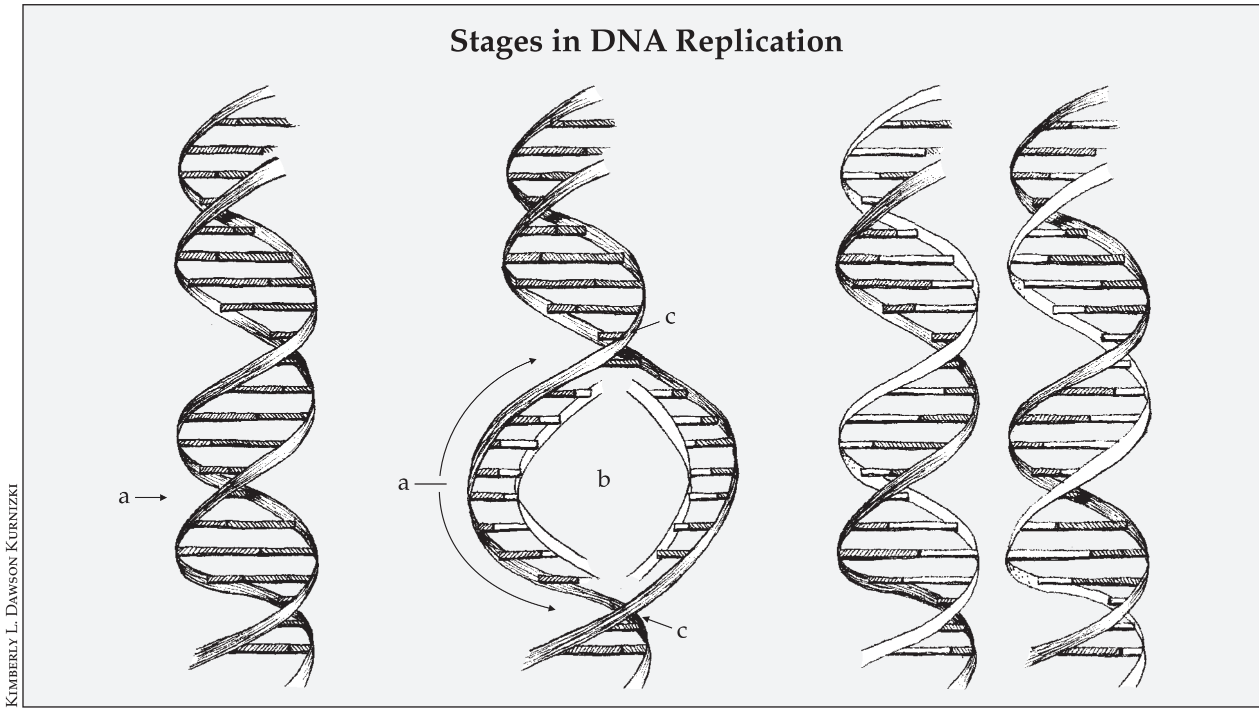
Although the mechanism is simple in principle, replication is a complex process, with geometric problems requiring energy, a variety of enzymes, and other proteins. The end result, nevertheless, is that a single double-stranded DNA is replicated into two copies having identical sequences. Each of the two daughter double-stranded DNA copies is made up of one parental strand and one newly synthesized strand, hence the name semi-conservative (literally, "half conserving") replication.

DNA Synthesis

DNA replication in plant cells occurs in three basic steps, each catalyzed by at least one enzyme. First, the two original, or parental, DNA strands of the double helix unwind and separate. Then each parental strand is used as a template for the formation of a new daughter strand. Finally, one parental strand and its newly synthesized daughter strand wind together into one double helix, while the other parental strand and its daughter strand wind together into a second double helix.

The process begins with the separation and unwinding of segments of the parental double helix. To accomplish this, an enzyme named *DNA helicase*, powered by adenosine triphosphate (ATP), works its way between the two strands. As this enzyme "plows" its way through the double helix, it breaks the hydrogen bonds that hold together the "rungs" of the ladder, formed by the base pairs. DNA helicase then "walks" along one strand, nudging the other strand out of its way as it goes. The result is that the two DNA strands separate, thus exposing their bases, as though the ladder had been split vetically, down through the rungs.

The second step of DNA synthesis requires the enzyme *DNA polymerase*, which performs a dual function during the replication. First, it recognizes bases exposed in a parental strand and matches them up with free nucleotides that have complementary bases. Second, DNA polymerase bonds to-



At left, a double-stranded DNA molecule, with the sides made of sugar-phosphate molecules and the "rungs" of base pairs. Replication begins at a point (a), with the separation of a base pair, as a result of the action of special initiator proteins (b). The molecule splits, or "unzips," in opposite directions (c) as each parental strand is used as a template for the formation of a new daughter strand (new bases pair with their appropriate "mate" bases to form new ladder "rungs"). Finally (right), one parental strand and its newly synthesized daughter strand form a new double helix, while the other parental strand and its daughter strand form a second double helix.

gether the sugars and phosphates of the complementary nucleotides to form the backbone of the daughter strand. Because the DNA polymerase can travel in only one direction on a DNA strand, from the 3′ end to 5′ end, the two DNA polymerase molecules, one on each parental strand, move in opposite directions. Only one daughter strand is synthesized continuously, while the duplication of another is done piece by piece. As the DNA helicase molecule continues to separate the parental strands, one polymerase simply follows behind it, synthesizing a long, continuous complementary daughter strand as it goes. The polymerase on the second parental strand travels away from the DNA helicase. As the helicase continues to separate the parental strands, this polymerase cannot reach the newly separated segment of the second strand. Hence a new DNA polymerase attaches to the second strand close behind the helicase to synthesize another small piece of DNA. These pieces are "sewn" together by another enzyme called *DNA ligase*. This process is repeated many times until the copying of a second parental strand is completed.

Proofreading and End-Sealing

Hydrogen bonding between complementary base pairs makes DNA replication highly accurate. However, the process is not perfect. This is a result partly of the fast pace (fifty to five hundred nucleotides added per second) and partly to the chemical flip-flops in the bases occurring spontaneously. DNA polymerase occasionally matches bases incorrectly, making on average one mistake in every ten thousand base pairs. Even this low rate of errors, if left uncorrected, would be devastating to the continuity of life. In reality, replicated DNA strands contain only one mistake in every billion base pairs. This incredible accuracy is achieved by several DNA repair enzymes, including DNA polymerase. Mismatches and errors are corrected through "proofreading" by DNA polymerase or other repair enzymes.

A separate problem in DNA replication lies at the end of a linear DNA molecule, which is not suitable for replication by polymerase. Yet another enzyme, *DNA telomerase*, is involved in solving this problem. It attaches a long stretch of repeating sequence of nucleotide 5′-TTGGGG-3′ to the strand already synthesized by polymerase. This ending sequence (called the *telomere*) offers protection and provides stability for plant DNA molecules.

Plant Propagation

Overall, the faithful replication and the amazing stability of each DNA molecule ensure the continuity and survival of species from generation to generation. DNA replication precedes every cycle of mitosis, so that two daughter cells derived from cell division can inherit a full complement of genetic material. The replication is also an essential prerequisite for plant sexual reproduction, a process by which the two sexual cells (pollen and egg) produced via meiosis are united to start a new generation.

The faithful DNA replication and subsequent cell divisions (mitosis) form the basis for plant growth as well as for vegetative propagation in many plant species. Growth in size and volume of the plant results from a combination of mitosis, cell enlargement, and cell differentiation. Mitosis is also essential in wound healing through the production of a mass of cells called callus. Vegetative propagation, an asexual process through mitosis, plays an important role in agriculture. Through vegetative propagation, individual plants of the progeny population are genetic copies both of the original source plant and of one another. Such plants are known as *clones*, and the process is called cloning. Examples of cloning include grafting hardwood cuttings of grapevines and apple trees and rapid propagation of liriope by crown division. The best-known example of vegetative propagation is probably the production of Macintosh apples via grafting. More recently, micropropagation via direct cell cultures and related biotechnology has played a critical role in agriculture.

Ming Y. Zheng

See also: Biotechnology; Cell cycle; Chromatin; Chromosomes; Cloning of plants; DNA in plants; DNA: recombinant technology; Gene regulation; Genetic code; Genetics: Mendelian; Genetics: mutations; Genetics: post-Mendelian; Mitosis and meiosis; Nucleic acids; Nucleus; Plant biotechnology; RNA.

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DORMANCY

Categories: Gardening; physiology

Dormancy is the state in which a plant or plant part exhibits little or no growth and in which most, if not all, metabolic activity ceases for a period of time.

The vast majority of plant life functions best when there is ample water and temperatures are well above freezing throughout the year. Except for those in moist, tropical regions, however, plants are exposed to dry periods and temperatures below freezing for varying lengths of time during the year. Plants, unlike animals, do not have the luxury of body insulation or locomotion. Hence, plants cannot seek shelter or use other active ways to survive water shortages and cold weather. Consequently, many plants become dormant to avoid unfavorable environmental conditions. In dormancy, their *metabolic activity* either ceases or is drastically reduced.

Dormancy evolved as a means of surviving unfavorable environmental conditions. In the temperate zones, buds normally form from spring to midsummer. While there may be a little growth in the late summer, growth virtually ceases in the fall in preparation for winter. Entering a dormant state protects the buds from freezing temperatures.

Mature seeds contain a complete embryo along with a reserve food supply—and mature seeds are formed within ripened fruit. If it were not for germination inhibitors present in the fruit or seed, the seeds would begin to germinate while still in the fruit. In addition, the seeds of plants in temperate regions most often reach the soil in late summer or early fall, when the plants are most often faced with low moisture and imminent cold weather. Were the seeds to germinate at this time, survival would be unlikely.

Patterns of Growth and Death

The type of dormant response depends on the plant's pattern of growth and death. *Perennials* are plants that live year after year, undergoing a period of dormancy during the cold season. In *herbaceous* species, the aboveground portions die, but the plants survive as specialized underground stems. Woody shrubs and trees remain alive aboveground. *Deciduous* species shed their leaves in winter, while many nondeciduous species, often called *evergreens*, keep their leaves year-round but dramatically reduce their metabolic rates.

Biennial species live for two years. The first year is devoted to vegetative growth and the formation of underground storage tissues. After the plant lies dormant through the winter months, its second year of growth results in the stored food supply being used to produce flowers and seeds. *Annuals* are plants that complete an entire life cycle in one growing season. The plants die, producing seeds, which normally remain dormant until the following growing season.

Most perennial trees and shrubs in temperate regions produce buds in the summer. These buds, which can eventually develop into leaves, stems, or flowers, exhibit reduced metabolic activity even before leaves begin to *senesce* (age). As temperatures decrease in the fall, complete dormancy sets in. Specialized leaves called bud scales cover the dormant tissue. These scales block the diffusion of oxygen into the bud; they also prevent the loss of water from the tissue.

Almost all flowering plants produce seeds. The seeds develop as ovules within a structural component of the flower called the *ovary*. As the ovary ripens to form the fruit, the ovules mature into seeds. Each seed is composed of a reserved food supply and a new plant with embryonic root, leaf, and stem tissue. The embryonic plant and reserve food supply are surrounded by a tough seed coat. The seeds of many species, especially trees in the temperate zones, do not germinate immediately after maturing even under ideal moisture, temperature, and nutritional conditions because there is a built-in period of dormancy.

Although seasonal dormancy is most often correlated with temperature changes, variation in precipitation is the primary factor in regions where pronounced wet and dry seasons alternate. Some deciduous trees and shrubs drop their leaves and remain dormant during the dry season and grow new leaves when the rains return. Herbaceous perennials die back and go dormant at the beginning of the dry season, then regrow their aboveground biomass. Many desert annuals have seeds that will only break dormancy when sufficient rains come, which in some regions may be only every few years. Some particularly specialized seeds germinate only after they have been tumbled in the waters of a flash flood, which scrapes their seed coats.

Bud and Seed Dormancy

A number of environmental factors appear to induce bud dormancy. In many species, bud dormancy occurs in response to low temperatures; among other species, the proper short-day *photoperiod* is responsible for initiating dormancy. In still other species, both low temperature and short days are required to trigger the onset of dormancy. Hence, dormancy is generally initiated with the onset of the short or cold days of winter. In addition, dormancy in buds has been shown to occur under situations of limited supply of nutrients or drought conditions. Dormancy can therefore be seen as a survival mechanism. When temperature, water, or nutritional conditions are no longer favorable, the buds become dormant.

Seed dormancy can also be caused by a number of different factors. For several reasons, the presence of a hard *seed coat* will very often result in dormancy of the seed. In many cases, the seed coat is impermeable to water. Because water is required for the *germination* process, the impermeable nature of the seed coat will serve as an effective inducer of dormancy. In some instances, the seed coat may be impermeable to certain gases. Both carbon dioxide and oxygen are required for germination; some seed coats prevent the diffusion of oxygen into the seed, while others are impermeable to carbon dioxide. In a few species, the seed coat physically restricts the growth of the embryo. A growing embryo must develop sufficient thrust to break through a seed coat, and in some instances the seed coat prevents this from happening.

Seed germination is also dependent on temperature. The seeds of almost all species have a minimal temperature below which they will not germinate. The exact mechanism by which low temperature causes dormancy is poorly understood, but it appears that the temperature alters membrane structure, which somehow prevents the seed from germinating.

Light is also a factor in the dormancy of many seeds. In many species, light is required for germination; in some cases, however, the exposure to light will induce dormancy. Also, some species exhibit a sensitivity to the photoperiod. Certain species are dormant during short-day cycles and germinate during long-day cycles, while others remain dormant when exposed to long-day cycles and germinate under short-day cycles. The light apparently activates a plant regulator that blocks the metabolic reactions necessary for germination.

Genetic and Chemical Control

Numerous studies show that bud dormancy is induced in some varieties of certain species but not in other varieties of the same species. This difference suggests there may be genetic variation in the control mechanism. The exact mechanisms of genetic control are not clearly understood, but there are some clues about chemical control.

The plant hormone *abscisic acid* may be associated with bud dormancy, but the evidence is inconclusive. With seed dormancy, however, the involvement of abscisic acid is fairly certain. A number of studies have shown that abscisic acid, when applied to the seed, will block the activity of enzymes necessary for germination.

A number of germination-inhibiting substances are present in dormant seeds. *Respiratory inhibitors*, such as cyanide, are produced in some seeds. High concentrations of various inorganic salts prevent germination in some species, while an assortment of phenolic compounds are known to prevent the process in others. A compound known as *coumarin* is particularly widespread in seeds and is known to be an effective inhibitor of germination. A number of these germination-inhibiting substances are present in both fruit and seed and prevent the seeds from germinating within the fruit. In addition, the substances will cause the seeds to lie dormant in nature until sufficient rain has fallen to leach the substances from the seeds. This adaptation ensures that sufficient moisture will be available to support the young seedlings.

Breaking Dormancy

It is often desirable to break dormancy artificially in order to obtain faster growth or increase plant production. Treatments to release bud and seed dormancy can be categorized by their use of temperature, light, chemicals, or mechanical means. Artificial exposure to low temperatures, warmth, and altered photoperiods, either singly or in combination, mimics the natural environmental factors that break dormancy.

A number of chemicals break bud dormancy. Ethylene chlorohydrin has been used for years to release dormancy in many fruit trees, and natural hormones known as *gibberellins* will break dormancy in most cold-requiring plants when applied directly to the buds. Gibberellins, *cytokinins*, and *ethylene*, all natural plant hormones, have been shown to be involved in breaking seed dormancy, and the gibberellins and other substances, such as thiourea, are used to germinate seeds commercially. The *scarification* (mechanical breaking) of the seed coat has proven to be an effective means of overcoming dormancy in many seeds. The broken seed coats allow the seeds to take up the water and gases necessary for germination.

D. R. Gossett, updated by Bryan Ness

See also: Germination and seedling development; Hormones.

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DROUGHT

Categories: Agriculture; environmental issues

Drought is a shortage of precipitation that results in a water deficit for some activity. Droughts occur in both arid and humid regions.

One problem in analyzing and assessing the impacts of drought, as well as in delimiting drought areas, is simply defining "drought" itself. Conditions considered a drought by a farmer whose crops have withered during the summer may not be seen as a drought by a city planner. There are many types of drought: *agricultural*, *hydrological*, *economic*, and *meteorological*. The Palmer Drought Severity Index is the best known of a number of indexes that attempt to standardize the measurement of drought magnitude. Nevertheless, there still is much confusion and uncertainty on what defines a drought.

Roger G. Barry and Richard J. Chorley, in *Atmosphere, Weather, and Climate* (1998), have noted that drought conditions tend to be associated with one or more of four factors: increases in extent and persistence of subtropical high-pressure cells; changes in the summer monsoonal circulation patterns that can cause a postponement or failure of the incursion of wet maritime tropical air onto the land; lower ocean surface temperatures resulting from changes in ocean currents or increased upwelling of cold waters; and displacement of midlatitude storm tracks by drier air.

Effects of Drought

Drought can have wide-ranging impacts on the environment, communities, and farmers. Most plants and animals in arid regions are adapted to dealing with drought, either behaviorally or through specialized physical adaptations. Humans, however, are often unprepared or overwhelmed by the consequences of drought. Farmers experience decreased incomes from crop failure. Low rainfall frequently increases a crop's susceptibility to disease and pests. Drought can particularly hurt small rural communities, especially local business people who are dependent on purchases from farmers and ranchers.

Drought is a natural element of climate, and no region is immune to the drought hazard. Farmers in humid areas grow crops that are less drought-resistant than those grown in arid regions. In developing countries the effects of drought can include malnutrition and famine. A prolonged drought struck the Sahel zone of Africa from 1968 through 1974. Nearly 5 million cattle died during the drought, and more than 100,000 people died from malnutrition-related diseases during just one year of the drought.

Subsistence and traditional societies can be very resilient in the face of drought. American Indians either stored food for poor years or migrated to wetter areas. The !Kung Bushmen of southern Africa learned to change their diet, find alternate water sources, and generally adapt to the fluctuation of seasons and climate in the Kalahari Desert.

More than any other event, the Dust Bowl years of the 1930's influenced Americans' perceptions and knowledge of drought. Stories of dust storms that turned day into night, fences covered by drifting soil, and the migration of destitute farmers from the Great Plains to California captured public and government attention. The enormous topsoil loss to wind erosion, continuous crop failures, and widespread bankruptcies suggested that the United States had in some way failed to adapt to the drought hazard.

Federal Drought Response in the United States

Beginning in the 1930's, the federal government took an increasing role in drought management and relief. In 1933 the federal government created the Soil Erosion Service, known today as the Natural Resources Conservation Service. No other single federal program or organization has had a greater impact on farmers' abilities to manage the drought hazard. President Franklin D. Roosevelt's Prairie States Forestry Project (1934-1942) planted more than 230,000 acres of shelterbelts in the Plains states for wind erosion control. The federal government purchased nearly 1 million acres of marginal farmland for replanting with grass. Federal agencies constructed water resource and irrigation projects.

Post-Dust Bowl droughts still caused hardships, but the brunt of the environmental, economic, and social consequences of drought were considerably lessened. Fewer dust storms ravaged the Plains. New crop varieties and better farming practices decreased crop losses during drought years. Government programs and better knowledge have enabled families and communities to cope better with drought.

Coping with Future Droughts

Numerous attempts have been made to predict droughts, especially in terms of cycles. However, attempts to predict droughts one or more years into the future have generally been unsuccessful. The

PhotoDisc

Low rainfall is one factor that can lead to drought, leaving the soil too parched for plants to grow. Drought is a natural element of climate, and no region is immune to drought hazard.

Impacts of Drought

While a farmer is aware of drought conditions in the course of his or her day-to-day activities, an urban dweller first knows about drought conditions only when he or she reads a newspaper article or views a television news item. However, droughts become important to urban inhabitants when they are affected directly.

Droughts affect urban and rural users whose water comes from wells when the water table lowers and the water supply either diminishes or becomes more expensive to pump. Redrilling wells to pump from lowered water levels can be expensive. Users hooked up to a water utility receive notices about drought from their water supplier.

In dry climates, California for example, drought is classified into five levels, depending on the severity of a drought and projected availability of water supplies. The classifications and penalties for excess use have been defined by the California State Water Resources Control Board. Drought levels increase as the projected severity increases. In the lowest level (Level 1), voluntary conservation measures are encouraged, and water conservation information is published by the supplier. As the anticipated severity increases, conservation measures become mandatory and more restrictive. The water utility imposes cutback goals. Fines for overuse may be imposed and, in egregious instances, water service can be terminated until corrective action is taken. To encourage conservation even when plentiful water supplies are projected, water rates have been implemented to include inverted rate blocks (the more one uses, the higher unit price one pays).

shorter the prediction interval has been, the more accurate the prediction has been. Nevertheless, progress has been made in estimating drought occurrence and timing. For example, the El Niño/Southern Oscillation may be a precursor of drought in some areas. Possibly with time, the physical mechanics of climate and drought will be understood adequately for long-term predictions to have value.

Perhaps of greater value is the current capacity to detect and monitor drought in its early stages (usually meaning within one to twelve months). Early recognition of potential drought conditions can give policymakers and resource managers the extra time needed to adjust their management strategies. Information on soil moisture conditions aids farmers with planting and crop selection, seeding, fertilization, irrigation rates, and harvest decisions. Communities that have a few months' warning of impending drought can increase water storage, implement water conservation measures, and obtain outside sources of water.

Unfortunately, the progress made in the world's developed countries has not always been available to the developing nations. Overpopulation and overuse of agricultural lands have resulted in regional problems of *desertification* and impeded the ability of developing nations to respond. Monitoring equipment can be costly. Furthermore, drought adjustments used in the United States may not be applicable to other countries' drought situations.

David M. Diggs

See also: Agriculture: modern problems; Cacti and succulents; Climate and resources; Deserts; Desertification; Erosion and erosion control; Human population growth; Hydrologic cycle; Irrigation; Leaf anatomy.

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ECOLOGY: CONCEPT

Categories: Disciplines; ecology; ecosystems; forests and forestry

Ecology is the scientific study of ecosystems, which are generally defined as local units of nature, consisting of the aggregate of plants, animals, the physical environment, and their interactions.

Ecosystems consist of both *biotic* (living) and *abiotic* (nonliving) components. Biotic components include plants, animals, and microorganisms. The abiotic components are the physical factors of the ecosystem. The roots of ecology can be traced to the writings of early Greek philosophers such as Aristotle and Theophrastus, who were keen observers of plants and animals in their natural habitats. During the nineteenth century, German biogeographer Alexander von Humboldt and English naturalist Charles Darwin wrote detailed descriptions of their travels. They recognized that the distribution of living things is determined by such factors as rainfall, temperature, and soil.

The word "ecology" was first proposed in 1869 by the German biologist Ernst Haeckel. It soon came to be defined as "environmental biology," or the effect of environmental factors on living things. At the beginning of the twentieth century, American botanist Henry Cowles established *plant succession* as a major concept of ecology. During the next few decades, F. E. Clements helped establish plant ecology as a recognized branch of biology. Animal ecology developed separately and slightly later. Reflecting the independent development of plant and animal ecology, most ecological studies in the early twentieth century were concerned with either plant or animal communities but not both. Furthermore, most were descriptive rather than being involved with explanations of fundamental ecological processes.

However, other lines of research during this time increasingly emphasized interrelationships among all life-forms, especially those within lakes. From such beginnings emerged the concept of the ecosystem. The term, first used by British ecologist Arthur G. Tansley in the 1930's, is now considered the foundation stone of ecology.

Ecosystems at Work

Ecologists place all the organisms of an ecosystem into three categories: *producers*, *consumers*, and *decomposers*. Producers include algae and green plants that, because of their ability to generate biochemical energy by means of *photosynthesis*, produce all the food for the ecosystem. Consumers (herbivores, omnivores, and carnivores) are animals that feed directly on the producers. Decomposers are bacteria and fungi that break the large organic molecules of dead plants and organisms down into simpler substances. Ecosystems are dynamic. Each day, matter (nutrients) cycles through ecosystems as consumers eat producers, then moves to decomposers, which release nutrients into the soil, air, and water. Producers absorb nutrients as they photosynthesize, thus completing the cycle. Energy flows from the sun to producers, then consumers, and finally to decomposers.

Other changes in ecosystems occur over longer periods of time. Large-scale disturbances such as fire, logging, and storms initiate gradual, long-term changes known as *ecological succession*. Following a major disturbance, an ecosystem of pioneer species exists for a while but is soon replaced by a series of other temporary ecosystems. Eventually a permanent, or climax, ecosystem is formed, the nature of which is primarily determined by climate. Although generally considered to be stable, climax communities are subject to gradual changes caused by climatic fluctuations or subsequent disturbances.

Classifying Systems and Study

Ecologists attempt to name and classify ecosystems in a manner similar to the way that taxonomists name and classify species. Ecosystems may be named according to their dominant plants, such as deciduous forests, prairies, and evergreen forests. Others, such as coral reefs, are named according to their dominant animals. Physical factors are used to name deserts, ponds, tidal pools, and other ecosystems.

The science of ecology has developed a few major branches as well as several areas of specialization, with theoretical, or academic, ecology on one hand and applied, or practical, ecology on the other. Among the specialties that have developed from *theoretical ecology* are *autecology* (study at the level of individuals or species), *synecology* (study at the community level), and the *ecosystems approach*, which is largely concerned with the flow of energy and the cycling of nutrients within ecosystems. As one might expect, theoretical ecologists are generally associated with universities, where their basic research contributes to the understanding of a great diversity of ecosystems.

Applied ecologists are employed by a variety of governmental and environmental agencies as well as by universities. Their primary objective is to apply fundamental principles of ecology and related disciplines to the solution of specific problems. *Forestry*, although it developed independently from ecology, may be considered a specialty within the field of *applied ecology*. Foresters must be knowledgeable of a wide range of factors that influence the accumulation of tree biomass. Wildlife management, once concerned with only game species, has been extended to include a wide range of nongame animal species as well. Another branch of applied ecology is *conservation biology*. Concerned with biodiversity in all its aspects, conservation biologists attempt to prevent the extinction of threatened species around the globe. Disturbed ecosystems are rehabilitated by scientists working in a related field called *restoration ecology*.

The efforts of ecologists, whether theoretical or applied, represent attempts to understand and solve the many environmental challenges that humankind faces. Climate change, pollution, and other global and local problems contribute to a loss of biodiversity. All are made worse by increasing human activities.

Thomas E. Hemmerly

See also: Animal-plant interactions; Biomass related to energy; Biomes: types; Coevolution; Community-ecosystem interactions; Ecology: history; Ecosystems: overview; Ecosystems: studies; Food chain; Paleoecology; Population genetics; Succession; Trophic levels and ecological niches.

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ECOLOGY: HISTORY

Categories: Disciplines; ecology; ecosystems; history of plant science

Ecology is the science that studies the relationships among organisms and their biotic and abiotic environments. The term "ecology" is commonly, but mistakenly, used by people to refer to the environment or to the environmental movement.

The study of ecological topics arose in ancient Greece, but these studies were part of a catch-all science called natural history. The earliest attempt to organize an ecological science separate from natural history was made by Carolus Linnaeus in his essay *Oeconomia Naturae* (1749; *The Economy of Nature*), which focused on the balance of nature and the environments in which various natural communities existed. Although the essay was well known, the eighteenth century was dominated by biological exploration of the world, and the science of ecology did not develop.

Early Ecological Studies

The study of fossils led some naturalists to conclude that many species known only as fossils must have become extinct. However, Jean-Baptiste Lamarck argued in his *Philosophie zoologique* (1809; *Zoological Philosophy*, 1914) that fossils represented the early stages of species that evolved into different species that were still living. In order to refute this claim, geologist Charles Lyell mastered the science of biogeography and used it to argue that species do become extinct and that competition from other species seemed to be the main cause. English naturalist Charles Darwin's book *On the Origin of Species by Means of Natural Selection* (1859) blends his own researches with the influence of Linnaeus and Lyell in order to argue that some species do become extinct, but existing species have evolved from earlier ones. Lamarck had underrated and Lyell had overrated the importance of competition in nature.

Although Darwin's book was an important step toward ecological science, he and his colleagues mainly studied evolution rather than ecology. However, German evolutionist Ernst Haeckel realized the need for an ecological science and coined the name *oecologie* in 1866. It was not until the 1890's that steps were actually taken to organize this science. Virtually all of the early ecologists were specialists in the study of particular groups of organisms, and it was only in the late 1930's that some efforts were made to write textbooks covering all aspects of ecology. Since the 1890's, most ecologists have viewed themselves as *plant ecologists*, *animal ecologists*, *marine biologists*, or *limnologists*. Limnology is the study of freshwater aquatic environments.

Nevertheless, general ecological societies were established. The first was the British Ecological Society, which was founded in 1913 and began publishing the *Journal of Ecology* in the same year. Two years later ecologists in the United States and Canada founded the Ecological Society of America, which began publishing *Ecology* as a quarterly journal in 1920; in 1965 *Ecology* began appearing bimonthly. Other national societies have since been established. More specialized societies and journals also began appearing. For example, the Limnological Society of America was established in 1936 and expanded in 1948 into the American Society of Limnology and Oceanography. It publishes the journal *Limnology and Oceanography*.

Although Great Britain and Western Europe were active in establishing the study of ecological sciences, it was difficult for their trained ecologists to obtain full-time employment that utilized their expertise. European universities were mostly venerable institutions with fixed budgets; they already had as many faculty positions as they could afford, and these were all allocated to the older arts and sciences. Governments employed few, if any, ecologists. The situation was more favorable in the United States, Canada, and Australia, where universities were still growing. In the United States, the universities that became important for ecological research and the training of new ecologists were mostly in the Midwest. The reason was that eastern universities were similar to European ones in being well established, with scientists in traditional fields.

Ecology After 1950

Ecological research in the United States was not well funded until after World War II. With the advent of the Cold War, science was suddenly considered important for national welfare. In 1950 the U.S. Congress established the National Science Foundation, and ecologists were able to make the case for their research along with that of the other sciences. The Atomic Energy Commission had already begun to fund ecological researches by 1947, and under its patronage the Oak Ridge Laboratory and the University of Georgia gradually became important centers for radiation ecology research.

Another important source of research funds was the International Biological Program (IBP), which, though international in scope, depended upon national research funds. It got under way in the United States in 1968 and was still producing publications in the 1980's. Even though no new funding sources were created for the IBP, its existence meant that more research money flowed to ecologists than otherwise would have.

Ecologists learned to think big. Computers became available for ecological research shortly before the IBP got under way, and so computers and the IBP became linked in ecologists' imaginations. Earth Day, established in 1970, helped awaken Americans to the environmental crisis. The IBP encouraged a variety of studies, but in the United States, studies of biomes (large-scale environments) and ecosystems were most prominent. The biome studies were grouped under the headings of desert, eastern deciduous forest, western coniferous forest, grassland, and tundra (a proposed tropical forest program was never funded). Although the IBP has ended, a number of the biome studies continued at a reduced level.

Ecosystem studies are also large-scale, at least in comparison with many previous ecological studies, though smaller in size than a biome. The goal of ecosystem studies was to gain a total understanding of how an ecosystem—such as a lake, river valley, or forest—works. IBP funds enabled students to collect data, which computers processed. However, ecologists could not agree on what data to collect, how to compute outcomes, and how to interpret the results. Therefore, thinking big did not always produce impressive results.

Plant Ecology

Because ecology is enormous in scope, it was bound to have growing pains. It arose at the same time as the science of genetics, but because genetics is a cohesive science, it reached maturity much sooner than ecology. Ecology can be subdivided in a wide variety of ways, and any collection of ecology textbooks will show how diversely it is organized by different ecologists. Nevertheless, self-identified professional subgroups tend to produce their own coherent findings.

Plant ecology progressed more rapidly than other subgroups and has retained its prominence. In the early nineteenth century, German naturalist Alexander von Humboldt's many publications on plant geography in relation to climate and topography were a powerful stimulus to other botanists. By the early twentieth century, however, the idea of plant communities was the main focus for plant ecologists. Henry Chandler Cowles began his studies at the University of Chicago in geology but switched to botany and studied plant communities on the Indiana dunes of Lake Michigan. He received his doctorate in 1898 and stayed at that university as a plant ecologist. He trained others in the study of community succession.

Frederic Edward Clements received his doctorate in botany in 1898 from the University of Nebraska. He carried the concept of plant community succession to an extreme by taking literally the analogy between the growth and maturation of an organism and that of a plant community. His numerous studies were funded by the Carnegie Institute in Washington, D.C., and even ecologists who disagreed with his theoretical extremes found his data useful. Henry Allan Gleason was skeptical; his studies indicated that plant species that have similar environmental needs compete with one another and do not form cohesive communities. Although Gleason first expressed his views in 1917, Clements and his disciples held the day until 1947, when Gleason's individualistic concept received the support of three leading ecologists. Debates over plant succession and the reality of communities helped increase the sophistication of plant ecologists and prepared them for later studies on biomes, ecosystems, and the degradation of vegetation by pollution, logging, and agriculture.

Marine Ecology

Marine ecology is viewed as a branch of either ecology or oceanography. Early studies were made either from the ocean shore or close to shore because of the great expense of committing oceangoing vessels to research. The first important research institute was the Statione Zoologica at Naples, Italy, founded in 1874. Its successes soon inspired the founding of others in Europe, the United States, and other countries. Karl Möbius, a German zoologist who studied oyster beds, was an important pioneer of the community concept in ecology. Great Britain dominated the seas during the nineteenth century and made the first substantial commitment to deep-sea research by equipping the HMS *Challenger* as an oceangoing laboratory that sailed the world's seas from 1872 to 1876. Its scientists collected so many specimens and so much data that they called upon marine scientists in other countries to help them write the fifty large volumes of reports (1885-1895). The development of new technologies and the funding of new institutions and ships in the nineteenth century enabled marine ecologists to monitor the world's marine fisheries and other resources and provide advice on harvesting marine species.

Limnology is the scientific study of bodies of fresh water. The Swiss zoologist François A. Forel coined the term and also published the first textbook on the subject in 1901. He taught zoology at the Académie de Lausanne and devoted his life's researches to understanding Lake Geneva's characteristics and its plants and animals. In the United States in the early twentieth century, the University of Wisconsin became the leading center for limnological research and the training of limnologists, and it has retained that preeminence. Limnology is important for managing freshwater fisheries and water quality.

Frank N. Egerton

See also: Animal-plant interactions; Botany; Community-ecosystem interactions; Ecosystems: studies; Food chain; History of plant science; Trophic levels and ecological niches.

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ECOSYSTEMS: OVERVIEW

Categories: Ecology; ecosystems

An ecosystem is made up of the complex interactions of a community of organisms of different species with one another and with their abiotic (nonliving) environment.

A *biological community* consists of a mixture of populations of individual species; a *population* consists of potentially interbreeding members of a species. Individual organisms interact with members of their own species as well as with other species. An ecosystem is formed by this web of interactions among species, along with the physical, chemical, and climatic conditions of the area.

Abiotic and Biotic Interactions

Abiotic environmental conditions include temperature, water availability, soil nutrient content, and many other factors that depend on the climate, soil, and geology of an area. Living organisms can alter their environment to some degree. A canopy formed by large forest trees, for example, will change the light, temperature, and moisture available to herbaceous plants growing near the forest floor. The environmental conditions in a particular area can also be affected by the conditions of neighboring areas. The disturbance of a stream bank can lead to erosion, which will affect aquatic habitat for a considerable distance downstream. It can be difficult to anticipate the wide-ranging affects of ecosystem disturbance.

Species and individuals within an ecosystem may interact directly with one another through the exchange of energy and material. *Predators*, for example, obtain their energy and meet their nutritional needs through consumption of prey species. Organisms also interact indirectly through modification of their surrounding environment. Earthworms physically modify soil structure, affecting aeration and the transport of water through the soil. These alterations of the physical environment, in turn, affect plant root growth and development as well as the ability of plants to secure nutrients.

Ecosystems are not closed systems: Energy and material are transferred to and from neighboring systems. The flow of energy or material among the components of an ecosystem, and exchanges with neighboring ecosystems, are governed by functions of the abiotic and biotic ecosystem components. These ecological processes operate simultaneously on many different temporal and spatial scales. At the same time that a microorganism is consuming a fallen leaf, the process of soil formation is occurring through chemical and physical weathering of parent material; plants are competing with one another for light, water, and nutrients.

Boundaries and Temporal Scales

Because of the exchange of energy and material, it is not possible to draw clear boundaries around an ecosystem. A *watershed*, for example, is formed by topographic conditions that create physical barriers guiding the gravitational flow of water, yet

NOAA/National Estuarine Research Reserve Collection

Wetlands ecosystem on Bear Island, South Carolina.

wind carries seeds and pollen over these barriers, and animals can move from watershed to watershed. The strength of the interactions among neighboring systems is the basis on which humans delineate ecosystem boundaries. In truth, all ecosystems around the world interact with one another to some degree.

Ecological processes operate on many different time scales as well. Some operate over such long time scales that they are almost imperceptible to human observation. The process of soil formation occurs over many human life spans. Other processes operate over extremely short time intervals. The reproduction of soil bacteria, the response of leaves to changing temperature over the length of a day, and the time required for chemical reactions in the soil are all very short when compared to a human life span.

Ecosystem Disturbances

Ecosystems are subject to disturbance, or perturbation, when one or more ecosystem processes are interrupted. Disturbance is a natural ecological process, and the character of many ecosystems is shaped by natural disturbance patterns. There are species that require disturbance in order to regenerate themselves. These species may be present in great abundance following a disturbance. Their abundance then decreases over time, and if there is no disturbance to renew the population, they will eventually die out and no longer be present in the ecosystem.

The successful reproduction of many prairie species may be dependent on periodic fires. Suppression of fire as a means of protecting an ecosystem may lead to the local extinction of small plants, which depend on periodic fires to increase light availability by removing larger grasses and providing nutrients to the soil. The formation of sandbars in streams may be controlled by periodic flood events that remove great amounts of sediment from stream banks. Protection of existing ecosystems can depend on the protection or simulation of *natural disturbances*. This is even true of old-growth forests; the natural disturbance interval due to fire or windstorm may be centuries, and yet interruption of the natural disturbance pattern may lead to shifts in species composition or productivity.

Increasing the frequency of disturbance can also affect ecosystem structure and function. Repeated vegetation removal will favor species that take advantage of early-successional conditions at the expense of species that are more adapted to late-successional conditions. In order to ensure continued functioning of ecosystem processes and the survival of all species, it is necessary to have a mix of systems in early-successional and late-successional stages in a landscape. Human resource utilization must be managed within this context in order to ensure the long-term sustainability of all ecosystem components and to reduce the chances of extinction of some species due to human alteration of natural disturbance intervals.

Ecosystem Stability

A system is stable, or in *equilibrium*, if it can return to its previous condition at some time after disturbance. The length of time required to return to the original condition is the *recovery time*. The reestablishment of a forest following harvesting and the renewed production of forage following grazing both depend on the inherent stability of the affected ecosystem. The stability of an ecosystem is dependent on its components and their interrelationships. Disturbance may primarily affect one component of an ecosystem, as with salmon fishing in the Pacific Ocean. The ability of the entire ecosystem to adjust to this disturbance depends on the complexities of the interrelationships between the salmon, their predators and prey, and their competitors.

The length of the recovery time varies with the type of system, the natural disturbance interval, and the severity of the disturbance. A system is usually stable only within some bounds. If disturbed beyond these recovery limits the system may not return to its previous state but may settle into a new equilibrium. There are examples in the Mediterranean region of systems that were overgrazed in ancient times that have never returned to their previous species composition and productivity. Forest managers, farmers, fishermen, and others must understand the natural resiliency of the systems within which they work and stay within the bounds of stability in order to ensure sustainable resource utilization into the future.

Matter and Energy Cycles

Ecological processes work through the cycling of matter and energy within the system. *Nutrient cycling* consists of the uptake of nutrients from the soil and the transfer of these nutrients through plants, herbivores, and predators until their eventual return to the soil to begin the cycle anew. Interruption of these cycles can have far-reaching consequences in the survival of different ecosystem components.

These cycles also govern the transport of toxic substances within a system. It took many years before it was realized that persistent pesticides such as DDT would eventually be concentrated in top predators, such as raptors. The decline in populations of birds of prey because of reproductive failure caused by DDT was a consequence of the transport of the chemical through ecosystem food webs. Likewise, radionucleides from the 1986 explosion at the Chernobyl nuclear reactor have become concentrated in certain components of the ecosystems where they were deposited. This is particularly true of fungi, which take radionucleides and heavy metals from their food sources but do not shed the substances. Humans eating mushrooms from these forests can receive larger than expected doses of radiation, because the concentration in the fungi is much greater than in the surrounding system.

A basic understanding of ecosystem properties and processes is critical in designing management methods to allow continued human utilization of systems while sustaining ecosystem structure and function. With increasing human population and advancing living standards, more and more natural ecosystems are being pushed near their limits of stability. It is therefore critical for humans to understand how ecosystems are structured and function in order to ensure their sustainability in the face of continued, and often increasing, utilization.

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See also: Animal-plant interactions; Biomass related to energy; Biomes: types; Coevolution; Community-ecosystem interactions; Ecology: history; Ecosystems: studies; Food chain; Forest fires; Paleoecology; Population genetics; Succession; Trophic levels and ecological niches.

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ECOSYSTEMS: STUDIES

Categories: Ecology; ecosystems; history of plant science

The study of ecosystems defines a specific area of the earth and the attendant interactions among organisms and the physical-chemical environment present at the site.

Ecosystems are viewed by ecologists as basic units of the *biosphere*, much as cells are considered by biologists to be the basic units of an organism. Ecosystems are self-organized and self-regulating entities within which energy flows and resources are cycled in a coordinated, interdependent manner to sustain life. Disruptions and perturbations to, or within, the unit's organization or processes may reduce the quality of life there or cause its demise. Ecosystem boundaries are usually defined by the research or management questions being asked. An entire ocean can be viewed as an ecosystem, as can a single tree, a rotting log, or a drop of pond water. Systems with tangible boundaries—such as forests, grasslands, ponds, lakes, watersheds, seas, or oceans—are especially useful to ecosystem research.

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Research Principles

The ecosystem concept was first put to use by American limnologist Raymond L. Lindeman in the classic study he conducted on Cedar Bog Lake, Minnesota, which resulted in his article "The Trophic Dynamic Aspect of Ecology" (1942). Lindeman's study, along with the publication of Eugene P. Odum's *Fundamentals of Ecology* (1953), converted the ecosystem notion into a guiding paradigm for ecological studies, thus making it a concept of theoretical and applied significance.

Ecologists study ecosystems as integrated components through which energy flows and resources cycle. Although ecosystems can be divided into many components, the four fundamental ones are *abiotic* (nonliving) *resources*, *producers*, *consumers*, and *decomposers*. The ultimate sources of energy come from outside the boundaries of the ecosystem (solar energy or chemothermo energy from deep-ocean hydrothermal vent systems). Because this energy is captured and transformed into chemical energy by producers and translocated through all biological systems via consumers and decomposers, all organisms are considered as potential sources of energy.

Abiotic resources—water, carbon dioxide, nitrogen, oxygen, and other inorganic nutrients and minerals—primarily come from within the boundaries of the ecosystem. From these, producers utilizing energy synthesize biomolecules, which are transformed, upgraded, and degraded as they cycle through the living systems that comprise the various components. The destiny of these *bioresources* is to be degraded to their original abiotic forms and recycled.

The ecosystem approach to environmental research is a major endeavor. It requires amassing large amounts of data relevant to the structure and function of each component. These data are then integrated among the components, in an attempt to determine linkages and relationships. This holistic ecosystem approach to research involves the use of systems information theory, predictive models, and computer application and simulations. As ecosystem ecologist Frank B. Golley stated in his book *A History of the Ecosystem Concept in Ecology* (1993), the ecosystem approach to the study of ecosystems is "machine theory applied to nature."

Research Projects

Initially, ecosystem ecologists used the principles of Arthur G. Tansley, Lindeman, and Odum to determine and describe the flow of energy and resources through organisms and their environment. Fundamental academic questions that plagued ecologists included those concerning controls on ecosystem productivity: What are the connections between animal and plant productivity? How are energy and nutrients transformed and cycled in ecosystems?

Once fundamental insights were obtained, computer-model-driven theories were constructed to provide an understanding of the biochemophysical dynamics that govern ecosystems. Responses of ecosystem components could then be examined by manipulating parameters within the simulation model. Early development of the ecosystem concept culminated, during the 1960's, in defining the approach of ecosystem studies.

Ecosystem projects were primarily funded under the umbrella of the International Biological Program (IBP). Other funding came from the Atomic Energy Commission and the National Science Foundation. The intention of the IBP was to integrate data collected by teams of scientists at research sites that were considered typical of wide regions. Although the IBP was international in scope, studies in the United States received the greatest portion of the funds—approximately $45 million during the life of IBP (1964-1974).

Five major IBP ecosystem studies, involving *grasslands*, *tundra*, *deserts*, *coniferous forests*, and *deciduous forests*, were undertaken. The Grasslands Project, directed by George Van Dyne, set the research stage for the other four endeavors. However, because the research effort was so extensive in scope, the objectives of the IBP were not totally realized. Because of the large number of scientists involved, little coherence in results was obtained even within the same project. A more pervasive concern, voiced by environmentalists and scientists alike, was that little of the information obtained from the ecosystem simulation models could be applied to the solution of existing environmental problems.

An unconventional project partially funded by the IBP was called the Hubbard Brook Watershed Ecosystem. Located in New Hampshire and studied by F. Herbert Bormann and Gene E. Likens, the project redirected the research approach for studying ecosystems from the IBP computer-model-driven theory to more conventional scientific methods of study. Under the Hubbard Brook approach, an ecosystem phenomenon is observed and noted. A pattern for the phenomenon's behavior is then established for observation, and questions are posed about the behavior. Hypotheses are developed to allow experimentation in an attempt to explain the observed behavior. This approach requires detailed scrutiny of the ecosystem's subsystems and their linkages. Since each ecosystem functions as a unique entity, this approach has more utility. The end results provide insights specific to the activities observed within particular ecosystems. Explanations for these observed behaviors can then be made in terms of biological, chemical, or physical principles.

Utility of the Concept

Publicity from the massive ecosystem projects and the publication of Rachel Carson's classic *Silent Spring* (1962) helped stimulate the environmental movement of the 1960's. The public began to realize that human activity was destroying the bioecological matrices that sustained life. By the end of the 1960's, the applicability of the IBP approach to ecosystem research was proving to be purely academic and provided few solutions to the problems that plagued the environment. Scientists realized that, because of the lack of fundamental knowledge about many of the systems and their links and because of the technological shortcomings that existed, ecosystems could not be divided into three to five components and analyzed by computer simulation.

The more applied approach taken in the Hubbard Brook project, however, showed that the ecosystem approach to environmental studies could be successful if the principles of the scientific method were used. The Hubbard Brook study area and the protocols used to study it were clearly defined. This ecosystem allowed hypotheses to be generated and experimentally tested. Applying the scientific method to the study of ecosystems had practical utility for the management of natural resources and for testing possible solutions to environmental problems. When perturbations such as diseases, parasites, fires, deforestation, and urban and rural development disrupt ecosystems from within, this approach helps define potential mitigation and management plans. Similarly, external causative agents within airsheds, drainage flows, or watersheds can be considered.

The principles and research approach of the ecosystem concept are being used to define and attack the impact of environmental changes caused by humans. Such problems as human population growth, apportioning of resources, toxification of biosphere, loss of *biodiversity*, global warming, acid rain, atmospheric ozone depletion, land-use changes, and eutrophication are being holistically examined. Management programs related to woodlands (the New Forestry program) and urban and rural centers (the Urban to Rural Gradient Ecology, or URGE, program), as well as other governmental agencies that are investigating water and land use, fisheries, endangered species, and exotic species introductions, have found the ecosystem perspective useful.

Ecosystems are also viewed as systems that provide the services necessary to sustain life on earth. Most people either take these services for granted or do not realize that such natural processes exist. Ecosystem research has identified seventeen naturally occurring services, including water purification, regulation, and supply, as well as atmospheric gas regulation and pollination. A 1997 article by Robert Costanza and others, "The Value of the World's Ecosystem Services and Natural Capital," placed a monetary cost to humanity should the service, for some disastrous reason, need to be maintained by human technology. The amount is staggering, averaging $33 trillion per year. Humanity could not afford this; the global gross national product is only about $20 trillion.

Academically, ecosystem science has been shown to be a tool to dissect environmental problems, but this has not been effectively demonstrated to the public and private sectors, especially decision makers and policymakers at governmental levels. The idea that healthy ecosystems provide socioeconomic benefits and services remains controversial. In order to bridge this gap between academia and the public, Scott Collins of the National Science Foundation suggested to the Association of Ecosystem Research Centers that ecosystem scientists be "bilingual"; that is, they should be able speak their scientific language and translate it so that the nonscientist can understand.

Richard F. Modlin

See also: Animal-plant interactions; Biomass related to energy; Biomes: types; Coevolution; Community-ecosystem interactions; Ecology: history; Ecosystems: overview; Food chain; Forest fires; Paleoecology; Population genetics; Succession; Trophic levels and ecological niches.

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ELECTROPHORESIS

Category: Methods and techniques

Electrophoresis is a biochemical technique used to separate charged molecules in an electric field. Gel electrophoresis is one of the most common forms of this method, used to separate DNA, proteins, enzymes, and other molecules from the cell for laboratory investigation and manipulation.

Electrophoresis is widely used to separate, visualize, or purify charged biological molecules such as deoxyribonucleic and ribonucleic acids (DNA and RNA) and proteins, including enzymes. It is also used to estimate the size of DNA fragments and the molecular weight of proteins. Most biological molecules are electrically charged in solution; hence, when subjected to an electric field, they migrate as zones toward an electrode (a terminal source of electricity) of opposite electrical polarity. Positively charged molecules migrate to the negative electrical terminal, known as the cathode, and negatively charged molecules migrate toward the positive electrical terminal, known as the anode. The rate of migration depends on the size, shape, and charge of the molecules to be sorted as well as the strength of the electric field (voltage).

Types of Supporting Matrix

Electrophoresis is conducted in a sievelike *supporting matrix*, such as filter paper, cellulose acetate membrane, or, more commonly, a gel. Gels are made primarily of starch, agarose, or polyacrylamide. Starch and agarose are carbohydrates. *Gel electrophoresis* typically uses agarose, a purified form of agar-agar, extracted from seaweeds (marine red algae). Agarose gels have large pores, which allow large molecules to pass through.

Polyacrylamide is a synthetic polymer made of acrylamide and bisacrylamide. Acrylamide is a suspected human carcinogen (cancer-causing agent) and a potent neurotoxin (a compound that causes damage to the brain). Extreme caution is therefore required when handling polyacrylamide or its components. Polyacrylamide gels have smaller pores than agarose, therefore allowing only small molecules to pass through.

Separation of Nucleic Acids

The method of choice for separating nucleic acids, typically pieces of DNA, is agarose gel electrophoresis. The DNA fragments migrate through the agarose gel at a rate that is inversely proportional to their size. In other words, smaller fragments migrate faster through the gel than larger fragments.

In the laboratory, an agarose gel is prepared by dissolving agarose powder in a buffer solution (a salt solution) and heating to boiling. The viscous solution formed is then cooled and poured into a casting tray. A plastic-toothed comb is inserted in the melted agarose at the top. The agarose is allowed to solidify in the tray into a gelatinous slab and is then submerged into a buffer solution in a horizontal chamber. The buffer functions as a conductor of electricity through the agarose gel. After the gel is submerged, the comb is carefully removed, thereby creating a row of wells in the gel slab. The wells are then loaded with a sample consisting of a mixture of DNA fragments, sucrose or glycerol, and a blue dye. Sucrose sinks the DNA sample into the wells, while the dye marks the migration of the invisible DNA fragments through the gel. In order to establish an electric field in the chamber, a constant electric current from a power supply is generated between the electrodes at both ends of the gel. DNA is negatively charged because of its phosphate groups; therefore, the electric current drags the DNA fragments out of the wells toward the anode through a path known as a lane. Greater voltages result in faster migration of DNA fragments through the gel. The current is switched off when the blue dye moves about three-fourths of the way.

Upon completion of electrophoresis, the separated DNA fragments are made visible by staining the gel with ethidium bromide or methylene blue. Ethidium bromide is a fluorescent dye, a potent mutagen, and possible carcinogen. The stained gel is viewed with the aid of an ultraviolet box called the transilluminator. The separated DNA fragments appear as fluorescent orange bands. Each band corresponds to DNA fragments of equal length that have migrated to the same position in the gel. Methylene blue dye stains DNA bands blue under visible light.

Separation of Proteins

The principle behind the separation of proteins is similar to that of nucleic acids. Proteins can be separated by paper or cellulose acetate electrophoresis by simply placing a protein sample on a strip of filter paper or cellulose acetate saturated with a buffer, dipping the ends of the strip into chambers of buffer, and subject the strip to an electric field. The separation of most proteins, however, is performed in a polyacrylamide gel. The gel is cast and submerged in a vertical chamber of buffer.

Proteins can be separated on the basis of size (molecular weight) alone, net charge alone, or size and charge together. A common technique for separating proteins by size only is *sodium dodecyl sulfate-polyacrylamide gel electrophoresis* (SDS-PAGE). In this type of separation, a protein mixture is treated with the detergent sodium dodecyl sulfate. The detergent binds and causes the proteins to dissociate into polypeptides and become negatively charged. The proteins thereafter separate into bands according to their sizes alone. Bands are then visualized by staining with silver stain or a protein dye called coomassie blue.

Proteins can be separated on the basis of charge alone, using a method called *isoelectric focusing*. The separation is performed in a glass tube of polyacrylamide gel in which a pH gradient has been established. When a current is applied, each protein migrates until it reaches its characteristic pH (acidity or alkalinity level). At this point, the net charge on the protein becomes zero, and migration stops. The pH at which the net charge is zero is called the isoelectric focusing.

Complex mixtures of proteins of similar sizes are separated based on size and charge using the *two-dimensional gel electrophoresis*. In this technique, proteins are separated in two sequential steps. First, they are separated in a tube gel by isoelectric focusing based on their charges alone. Then the proteins migrate into a gel slab and separate by SDS-PAGE, based on their size alone. The proteins are visualized as spots in the gel slab.

Applications

Every species of organism examined by researchers has revealed immense genetic variation or polymorphism (many forms), an indication of the presence of different genotypes (genetic makeup) in the population. It is however, impossible to infer the genotypes of plants simply by observing their visible characteristics or phenotypes. In many plant science laboratories, researchers employ electrophoresis to determine the mode of reproduction of plant species, to detect genetic variation within and between plant populations, and to identify plant genotypes. Also, researchers establish genetic relatedness in plants, that is, establish the most probable paternal parent or pollen donor within and outside a study site that sired seeds collected from a known maternal plant. To accomplish these tasks, researchers rely upon protein and DNA markers generated by gel electrophoresis.

Protein markers known as *allozymes* have been used extensively in a number of genetic analyses. Allozymes are electrophoretically distinct forms of an enzyme produced by different alleles (alternate forms of a gene). (An enzyme is a protein that speeds up the rate of a chemical reaction in an organism, without being consumed in the process.) Allozymes catalyze the same chemical reactions but have slightly different sequences of amino acids, the building blocks of proteins.

To analyze allozymes, researchers extract enzymes from plants and separate them on starch or polyacrylamide gels. Gels made up of potato starch are most commonly used because of their low cost and ease of use. After electrophoresis, the gel is submerged in a solution containing a dye and a substrate appropriate for the enzyme studied. The enzyme reacts with the substrate to produce a colored band on the gel. If the gel yields one colored discrete band in a lane, then that particular plant contains just one form of the enzyme, therefore the genotype of the plant must be *homozygous* (having two identical alleles of a gene). If the gel yields two colored bands, then the plant contains two forms of the enzyme and is therefore *heterozygous* (having two different alleles of a gene). Allozyme electrophoresis enables researchers to learn about the mode of reproduction of plants. For example, plant populations with high numbers of heterozygotes indicate a high level of cross-pollination, that is, the transfer of pollen (plant male gamete) by wind, insects, birds, bats, or other animals from one flowering plant to another. High numbers of homozygotes within a plant population indicate a high level of self-pollination, the transfer of pollen within a flower or between flowers of the same plant.

In many plant laboratories today, protein markers have been superseded by DNA markers, which are fragments of DNA that are distinguished from one another because of the differences in their base sequences. To generate DNA markers, DNA is extracted from plants and cut into fragments with special enzymes known as *restriction enzymes*. The fragments are then separated by electrophoresis on an agarose gel and analyzed.

Some of the widely used DNA markers in many laboratories are different lengths of DNA fragments, known as *restriction fragment polymorphisms* (RFLPs) or short sequences of DNA bases that are repeated many times in tandem (head to tail), called variable number of tandem repeats (VNTR), a type of RFLP. RFLP analysis distinguishes between heterozygous and homozygous genotypes. Heterozygotes yield two fragments on a gel, while homozygous genotypes yield a single fragment. Another DNA marker, known as *random amplified polymorphic DNAs* (RAPDs), have become extremely popular DNA markers with plant scientists. They are DNA fragments amplified by a technique known as polymerase chain reaction (PCR) using a short primer consisting of ten nucleotides chosen randomly and then separated by size by agarose gel electrophoresis. Polymorphisms are revealed when a DNA fragment is amplified in one plant and fails to amplify in another. On a gel, the researcher checks for the presence or absence of the marker.

Many studies involving parentage of seeds and seed pods have been done using DNA markers. The DNA profiles of seeds or seed pods are compared to maternal and paternal plants. If seeds were produced by cross-pollination, then half of the DNA bands of the seeds would be found in the maternal plant and the other half from the paternal plant.

Oluwatoyin O. Osunsanya

See also: Autoradiography; Chromatography; DNA in plants; Nucleic acids; Proteins and amino acids.

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ENDANGERED SPECIES

Categories: Ecology; environmental issues

The International Union for the Conservation of Nature-World Conservation Union (IUCN) defines endangered species as those in immediate danger of extinction. Extinction means that the species is no longer known to exist. The IUCN defines threatened species as those at a high risk of extinction but not yet endangered. Vulnerable species are considered ones that are likely to become extinct at some point in the foreseeable future. Rare species are at risk but not yet at the vulnerable, threatened, or endangered levels.

Worldwide, the number of endangered plant species was estimated at more than 33,400 in 1999. This number is much higher than that of all of the endangered or threatened animal species combined. Although extinction is a natural process, and all species will eventually be extinct, human activities threaten the existence of plant and animal life worldwide.

Humans use plants for food; medicine; building materials; energy; to clean water, air, and soil of pollutants; to control erosion; and to convert carbon dioxide to oxygen. The process of extinction increased dramatically during the nineteenth and twentieth centuries because of habitat destruction or loss, deforestation, competition from introduced species, pollution, global warming, and plant hunting, collecting, and harvesting. Over time, pollutants and contaminates accumulate in the soil and remain in the environment, some for many decades. Pollution in the atmosphere also contributes to long-term changes in climate.

Habitat Loss

By far the most significant threat to plant species is habitat loss or destruction. Habitat loss can occur because of resource harvesting for food, medicine, and other products, deforestation, and the conversion of wilderness for agricultural, industrial, or urban uses. Wood consumption and tree clearing for agriculture and development threaten the world's forests, especially the tropical forests, which may disappear by the mid-twenty-first century if sufficient preventive action is not taken. Natural disasters, such as climatic changes, meteorites, floods, volcanic eruptions, earthquakes, drought, hurricanes, and tornados, also can be devastating to a habitat.

In Europe and Asia, the plant distribution is complex, with isolated populations of plants spread across a large area. The plants are greatly influenced by the cold climate and by humans. Plant species are disappearing, especially in Europe and the Mediterranean, because of habitat destruction and disturbances including urbanization, road construction, overgrazing, cultivation, forest plantation, fire, pollution, and overexploitation of resources, or for use in horticulture.

The mountain plants are threatened by development for industry and tourism, pollution, strip mining, walkers, and skiers. The wetlands are threatened by removal of peat for fuel, water extraction which lowers the water table, and increased drainage for building or agriculture or fear of malaria. Recreational use and susceptibility to pollution such as acid rain or fertilizer run-off present further threats.

In North America, the major causes of endangerment include loss of habitat, overexploitation of resources, introduction of invasive species, and pollution. A massive loss of wilderness has occurred through the clearing of forests, plowing of prairies, and draining of swamplands. For example, in the northeastern United States there are only 13 square miles of alpine habitat, an area in which grow thirty-three at-risk species. This area is heavily used by hikers and mountain bikers. The Florida Everglades are threatened because the water supply is diverted to supply cities, industries, and agriculture.

In California, the Channel Islands are home to seventy-six flowering plants which do not exist on the mainland. Eighteen species are located on just one island. These plants, including the San

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Clemente broom, bush mallow (*Malacothamnus Greene*), a species of larkspur, and the San Clemente Island Indian paintbrush (*Castilleja grisea*), have been devastated by introduced grazers, browsers, and by invasive other plants. In Hawaii, more than 90 percent of native plants and almost all land birds and invertebrates are found nowhere else in world. The Hawaiian red-flowered geranium (*Geranium arboreum*) is threatened by introduced feral pigs, agricultural livestock, and competition by nonnative plants.

In developing or highly populated nations in Asia, Africa, Central and South America, the Caribbean, the Pacific Ocean islands, Australia, and New Zealand, habitat loss occurs because of population needs. Land is cleared for agriculture, develop-

A Sampling of the World's Endangered Plant Species

Common Name	*Scientific Name*	*Habitat*
African teak	*Pericopsis elata*	Semideciduous forests of Central and West Africa
Almug or red sandalwood	*Pterocarpus santalinus*	Forests of India
Atlas or Moroccan cypress	*Cupressus atlantica*	Dry woodland on steep slopes of the Atlas Mountains, Morocco
Bastard quiver tree or Basterkokerboom	*Aloe pillansii*	Hot and arid areas of Namibia and South Africa
Camphor tree	*Dryobalanops aromatica*	Peninsular Malaysia and Sumatra
Carossier palm	*Attalea crassispatha*	Haiti's southwestern peninsula in scrub forest and agricultural land
Clay's hibiscus	*Hibiscus clayi*	Dry forests in a few locations on some of the Hawaiian Islands
Commoner lignum vitae or guaiac tree	*Guaiacum officinale*	Lowland dry forests and coastland areas of Caribbean, Colombia, Venezuela
Cook's holly	*Ilex cookii*	Puerto Rican cloud forests on ridgetops of Monte Javuya in Toro Negro State Park and Cerro de Punta
Dall's pittosporum	*Pittosporum dallii*	Rocky creeks in the mountains of New Zealand
Dragon's blood tree	*Dracaena cinnabari*	Woodland areas in the center and east of Socotra Island near Saudi Arabia and the Red Sea
Ebony	*Diospyros mun*	Limestone mountains in the Lao People's Democratic Republic and Vietnam
Egyptian papyrus	*Cyperus papyrus hadidii*	Shallow, freshwater marshes in Egypt
Fiddlewood or yax-nik	*Vitex gaumeri*	Damp forests with limestone or pine ridges in Belize, Guatemala, Honduras, Mexico
Four-petal pawpaw	*Asimina tetramera*	Scrub vegetation near the Atlantic coast in Florida
Gigasiphon	*Gigasiphon macrosiphon*	Tropical forests on the coastal plains of Kenya and Tanzania
Ginkgo	*Ginkgo biloba*	Temperate forests in southern China
Hainan sonneratia	*Sonneratia hainanensis*	Mangrove forests in Wenchang County, Hainan, China

ment, and population resettlement. In Central America and the Caribbean, the Swietenia mahogany is found only in a few protected or remote areas. The Caoba tree (*Persea theobromifolia*) was newly identified as a species as recently as 1977. The lumber is commercially important, and habitat loss has occurred as a result of the conversion of forests to banana and palm plantations. In Ecuador, only 6 percent of the original rain forest remains standing, because the rest has been converted to farmland. In Asia, including the Philippines, population pressures bring about deforestation and the clearing of land for agriculture.

In southern Africa, land is used for crops, livestock, and firewood production. Overgrazing and the introduction of agriculture have caused the Sahara Desert area to grow rapidly. The island of Madagascar has between ten thousand and twelve

Common Name	*Scientific Name*	*Habitat*
Hawaiian gardenia	*Gardenia brighamii*	Dry forest on the island of Kauai, Hawaii
Horseshoe fern	*Marattia salicina nov*	Lord Howe Island, Australia
Ley's whitebeam	*Sorbus leyana*	Carboniferous limestone cliffs in southern Breconshire, Wales
Madeira net-leaf orchid	*Goodyera macrophylla*	Cliffs and ravines in humid, maritime climate of Madeira, Portugal
Mellblom's spider orchid	*Caladenia hastata*	Coastal areas near Portland, Victoria, Australia
Millionaire's salad	*Deckenia nobilis*	Lowland forests of the Seychelles Islands off the east coast of Africa
Mongarlowe mallee	*Eucalyptus recurva*	Near Mongarlowe in New South Wales, Australia
Nubian dragon tree	*Dracaena ombet*	Tropical forests near the Red Sea Hills in Egypt, Saudi Arabia, East Africa
Saharan cypress	*Cupressus dupreziana*	Tassili N'Ajjer National Park, Algeria
Taiwan trident maple	*Acer buergerianum ssp. formosanum*	Lowland evergreen forest of Taiwan
Tennessee purple coneflower	*Echinacea tennesseensis*	Red cedar glades and dry environments in forest openings of Tennessee
Virginia round-leaf birch	*Betula uber*	Second-growth forest along Cressy Creek in Virginia
West Himalayan elm	*Ulmus walliciana*	Temperate areas near streams, rivers, and wetlands in Afghanistan, Nepal, Pakistan, India
None	*Anthoceros neesii*	Clay-loam soils in Austria, Czech Republic, Germany, Poland
None	*Diplocolea sikkimensis*	Tropical rain forests in India (Sikkim) and Nepal
None	*Distichophyllum carinatum*	Temperate mixed forests of Austria, Germany, Switzerland, China (Sichuan), Japan
None	*Andrewsianthus ferrugineus*	Coniferous forest of Bhutan, Nepal

Source: Compiled from the International Union for Conservation of Nature, World Conservation Union (IUCN) Red List of endangered species at the web site www.redlist.org (homepage www.iucn.org), and *Encyclopedia of Endangered Species*, edited by Bill Freedman, volume 2 (Detroit: Gale Research, 1999).

thousand plant species, of which 80 percent grow nowhere else in the world. Because of conversion to grassland through farming methods, only about one-fifth of the original species survive. In Australia there are 1,140 rare or threatened plants, and logging, clearing for grazing animals and crops, building developments, and mining have threatened many native species.

Plant Hunting, Collecting, and Harvesting

Habitat damage, the construction of facilities, and the opening of remote areas for human population have made many plants vulnerable to gathering and collecting. Some plants have been overharvested by gardeners, botanists, and horticulturists. One species of lady's slipper orchid (*Cypripedium calceolus*) is rare over much of its natural range except in parts of Scandinavia and the Alps because of collecting. Additionally, many mountain flowers or bulbs such as saxifrages, bellflowers, snowdrops, and cyclamen are endangered. In France and Italy, florulent saxifrage (*Saxifraga florulenta*), an alpine plant, has been overcollected by horticulturists and poachers.

Parts of the southeastern United States have poor soil that is home to the carnivorous or insectivorous plants—those that eat insects. These plants include sundews, bladderworts, Venus's flytrap, and pitcher plants. Collectors or suppliers have stripped many areas of all of these plants. In the Southwest, rare cacti are harvested for sale nationwide and worldwide. Endangered cacti include the Nellie Cory cactus (which has one remaining colony), *Epithelantha micromeres bokei*, *Ancistrocactus tubuschii*, saguaro cactus (*Carnegiea gigantea*), and *Coryphantha minima*. Near the Sierra Madre, two tree species—Guatemalan fir, or Pinabete, and the Ayuque—are endangered because of harvesting for use as Christmas trees or for the making of hand looms. Additionally, sheep eat the seedlings. In New Mexico, the gypsum wild buckwheat habitat is limited to one limestone hill, and the plants are threatened by cattle, off-road vehicles, and botanists.

In southern Mexico, there are 411 species of *epiphytes* (air plants or bromeliads in the genus *Tillandsia*), of which several are extremely rare. These plants are threatened by overcollection for the houseplant trade or conservatories. The African violet (*Saintpaulia ionantha*) of Tanzania may soon be extinct in the wild because of the horticultural trade and habitat loss due to encroaching agriculture.

Worldwide, orchids are overcollected for horticulture. Several species have been collected to extinction, are extremely rare, or have been lost because of habitat destruction. Examples include the extremely rare blue vanda (*Vanda caerulea*); *Paphiopedilum druryi*, believed extinct in its native habitat; *Dendrobium pauciflorum*, endangered and possibly extinct—only a single plant was known to exist in the wild in 1970; and the Javan phalaenopsis orchid, *Phalaenopsis javanica*. The latter was believed extinct. When it was rediscovered in 1960's, it was overcollected by commercial orchid dealers and thereby exterminated. There are no other known wild populations.

About 80 percent of the human populations in developing countries rely on traditional medicine, for which 85 percent of ingredients come from plant extracts. In Western medicine, one in four prescription medicines contain one or more plant products. Some at-risk species contain chemicals used in treating medical conditions, such as the African *Prunus africana* tree, whose bark has chemicals used to treat some prostate gland conditions, and the *Strophanthus thollonii*, a root parasite with chemicals used in heart drugs.

The Madagascan periwinkle (*Catharanthus roseus*) is commonly cultivated (its close relative *Catharanthus coriaceus* is rare and its medicinal importance unknown) and produces about seventy chemicals, some of which are useful in the treatment of cancer. The Indian podophyllum (*Podophyllum hexandrum*), a threatened species, is used to treat intestinal worms, constipation, and cancer. Rauwolfia (*Rauvolfia serpentina*), also a threatened species, is used to treat mental disorders, hypertension, and as a sedative. The lily *Amorphopahllus campanulatus* is used to treat stomachaches, and a fig, *Ficus sceptica*, is used to treat fever; both of these species are vulnerable because of habitat destruction.

The Micronesian dragon tree is believed to have magical and medicinal properties. It has been overharvested and is now extinct on several islands. In the United States' Appalachian Mountains, American ginseng is being overcollected because of an escalating demand for this plant's health benefits.

Conservation

The conservation of endangered plant species employs several compelling arguments: Plants enhance the world's beauty, have the right to exist, and are useful to people. The most persuasive argument may be that the survival of the human species depends on a healthy worldwide ecosystem. Three major goals of conservation are recovery, protection, and reintroduction.

Conservation methods depend on increasing public awareness by providing information about endangered or threatened species so that people can take action to reverse damage to the ecosystems. Other important strategies include achieving a widespread commitment to conservation and obtaining funding to protect rare or endangered species. Conservation efforts include setting aside protected areas, such as reserves, wilderness areas, and parks, and recognizing that humans must integrate and protect biodiversity where they live and work. Many countries are actively conserving species through protected areas, endangered-species acts, detailed studies of species and habitat, and information campaigns directed to the public.

Virginia L. Hodges

See also: Biological invasions; Competition; Deforestation; Ecology: history; Ecosystems: overview; Ecosystems: studies; Grazing and overgrazing; Human population growth; Invasive plants; Logging and clear-cutting.

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ENDOCYTOSIS AND EXOCYTOSIS

Categories: Cellular biology; physiology; transport systems

Endocytosis is used by cells to move water, macromolecules, or larger objects, such as cell fragments or even whole cells, from outside a cell to the inside of the cell. Exocytosis is the reverse of endocytosis, that is, the movement of materials from the inside to the outside of the cell. Both types of transport move the materials using membrane-bound vesicles.

Endocytosis

In endocytosis, during which materials are moved into a cell, the cell's plasma membrane engulfs material and packs it into saclike structures called *vesicles*. The vesicles then detach from the plasma membrane and move into the cell. Once the vesicle is in the cytoplasm, it will typically fuse with some other membrane-bound organelle, such as a vacuole or the endoplasmic reticulum, and release its contents into the organelle. There are three types of endocytosis: *phagocytosis* (transport of actual particles), *pinocytosis* (transport of water, along with any solutes in the water), and *receptor-mediated endocytosis* (explained in detail below).

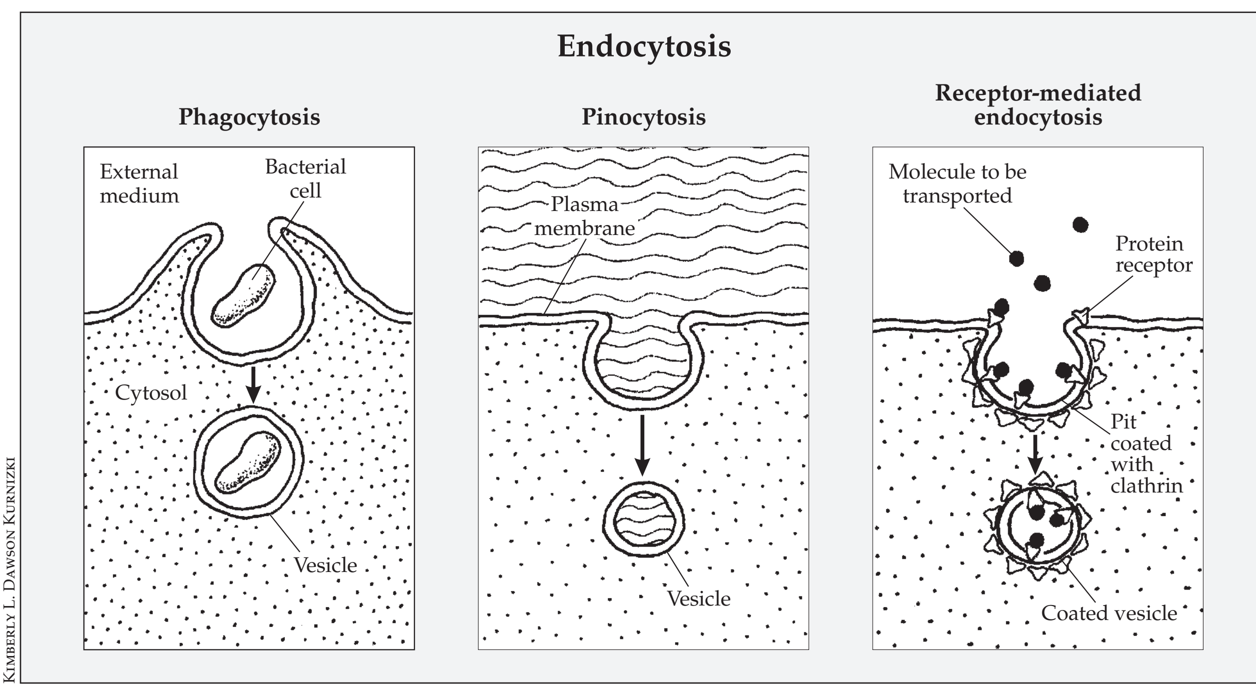
In receptor-mediated endocytosis, specific macromolecules outside the cell attach to the binding sites of receptor proteins. These receptors are embedded in the plasma membrane in specialized regions called *coated pits*. The macromolecules contact and bind with receptor proteins in the pit. The coated pit deepens inward to the cytosol and eventually is pinched off as a *coated vesicle* inside the cell. Coated vesicles contain the receptor proteins and whatever molecules they are importing and are coated on the outside by a protein called *clathrin*. After the contents of the vesicle are released inside the cell, the receptor proteins are reused to form new coated pits. Receptor-mediated endocytosis is especially useful for importing specific molecules, even when they are present at low concentrations.

Endocytosis is more difficult in plants than in animals because the plasma membrane of a plant cell is usually pressed against the rigid cell wall by turgor pressure, which hinders the plasma membrane from invaginating into the cytosol. Nevertheless, plant cells do have coated pits, and experiments with isolated *protoplasts* (plant cells without their cell walls) suggest that receptor-mediated endocytosis works in plant cells much as it does in animal cells.

In a special form of phagocytosis, symbiotic nitrogen-fixing bacteria (*rhizobia*) colonize root cells in legumes. First, root hairs surround rhizobia cells in a ball-like mass. Next, *infection threads*, composed of an extended portion of the cell membranes of the cell being invaded, are formed. The bacteria multiply inside the thread, which extends inwardly and penetrates through and between cortex cells. In the inner cortex cells, portions of the thread wrap around groups of bacteria in vesicles, which pinch off into the cytosol. A membrane which forms around a group of bacteria is called a *bacteroid*.

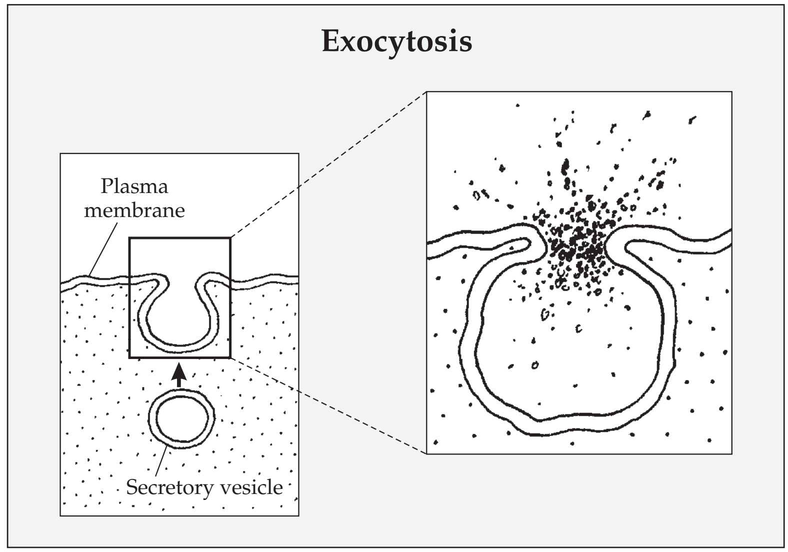
Exocytosis

Exocytosis, the transport of macromolecules and large particles outside the cell, is the reverse of endocytosis. In exocytosis, materials inside the cell are packed in a vesicle, which fuses to the plasma membrane. Some vesicles contain structural proteins and polysaccharides, whereas other



Three types of endocytosis: phagocytosis, in which the plasma membrane extends outward to engulf and draw in a particle to be taken into the cell; pinocytosis, in which the plasma membrane pouches inward, surrounding water and solutes, and then pinches off inside the cell; and receptor-mediated endocytosis, in which the molecules to be taken into the cell first bind to protein receptors in coated pits in the plasma membrane, which then form coated vesicles that pinch off and move into the cell.

vesicles, such as vacuoles, contain digestive enzymes. Each vesicle attaches to the plasma membrane. The site where it attaches opens, and the materials in the vesicle are dumped out of the cell. The vacated vesicle straightens and becomes a part of the plasma membrane. A problem arises if vesicles continually fuse with the plasma membrane, because large amounts of new membrane being added can double the amount of plasma membrane every thirty minutes, and the plasma membrane has little room to expand in cells with rigid cell walls. Nevertheless, plants cells regularly recycle excess plasma membrane via endocytosis.



The reverse of endocytosis, exocytosis is the process of moving materials outside the cell by packing them in a vesicle that fuses to the plasma membrane and then opens to dump out its contents.

Roles of Endocytosis and Exocytosis

Both exocytosis and endocytosis occur within seeds. Starch-digesting enzymes, such as alpha-amylase, move from cell to cell in cereal grains. In the cells of the *aleurone* layer, the endoplasmic reticulum manufactures these enzymes and packs them into vesicles. The enzymes are exuded from vesicles by exocytosis through the plasma membrane and must then be transported into the cells of the endosperm by endocytosis. Inside the endosperm cells, the enzyme-containing vesicle fuses with an *amyloplast*, a plastid specialized for storage of starch, where the enzymes hydrolyze starch into glucose.

Exocytosis of macromolecules plays other important roles in plants. For example, polysaccharides and proteins that are exported become structural components of cell walls. After cell division, exocytosis by secretory vesicles builds primary cell walls between newly divided nuclei. Epidermal cells of leaves extrude waxy substances onto leaf surfaces to minimize transpiration. Root-tip cells exude slimy polysaccharides to lubricate their movement as they grow and penetrate the soil.

Exocytosis of other substances by specialized cells also plays many roles in plants. For example, exocytosis is involved in the secretion of nectar by flower cells to attract pollinators. Exocytosis is also the process whereby oils are emitted by aromatic flowers, herbs, and spices. Such oils function both as attractants for pollinators and as defenses. For example, oils emitted by mustard plants irritate many animals, thus preventing many herbivores from eating them. Lignin, which is more rigid than cellulose and strengthens woody tissue, is expelled via exocytosis in woody plants and then accumulates in the middle lamella and cell walls. Enzymes that digest insects are released by the leaf cells of carnivorous plants, such as Venus's flytrap. Root exudates are released by some plants in response to environmental stress or to deter the growth of other plant species nearby.

Phytoremediation

Phytoremediation uses plant roots to clean polluted soil and water. They can remove, by endocytosis, and degrade both small organic molecular pollutants (ammunition wastes, chlorinated solvents, and herbicides) and large organic molecular pollutants (crude oil and polyaromatic hydrocarbons) in the environment. The degraded products can then be incorporated in the plant's tissues.

Domingo M. Jariel

See also: Active transport; Cell wall; Cells and diffusion; Cytosol; Endomembrane system and Golgi complex; Membrane structure; Microbodies; Osmosis, simple diffusion, and facilitated diffusion; Peroxisomes; Plasma membranes; Vacuoles; Vesicle-mediated transport.

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ENDOMEMBRANE SYSTEM AND GOLGI COMPLEX

Categories: Anatomy; cellular biology

The endomembrane system is a collective term applied to all of the membranes in a cell that are either connected with or are derived from the endoplasmic reticulum (ER), including the plasma membrane but not the membranes of chloroplasts or mitochondria. The membrane-bound organelles considered to be part of the endomembrane system are the vacuole, nuclear envelope, endoplasmic reticulum, Golgi complex, and various types of vacuoles.

Some components of the endomembrane system have direct, permanent connections with the endomembrane system (such as between the endoplasmic reticulum and the nuclear envelope), whereas other components share membrane and contents by trafficking *vesicles* (membrane-bound packages) from one component to another (for example, the ER sends numerous vesicles to the Golgi complex) across the *cytosol*. The endomembrane system is responsible for processing, sorting, and packaging membrane material, proteins embedded in membranes, and large water-soluble molecules (such as proteins or carbohydrates), either for export from the cell (called *exocytosis*) or for use within the cell. The endoplasmic reticulum is the ultimate source of all the membranes of the endomembrane system.

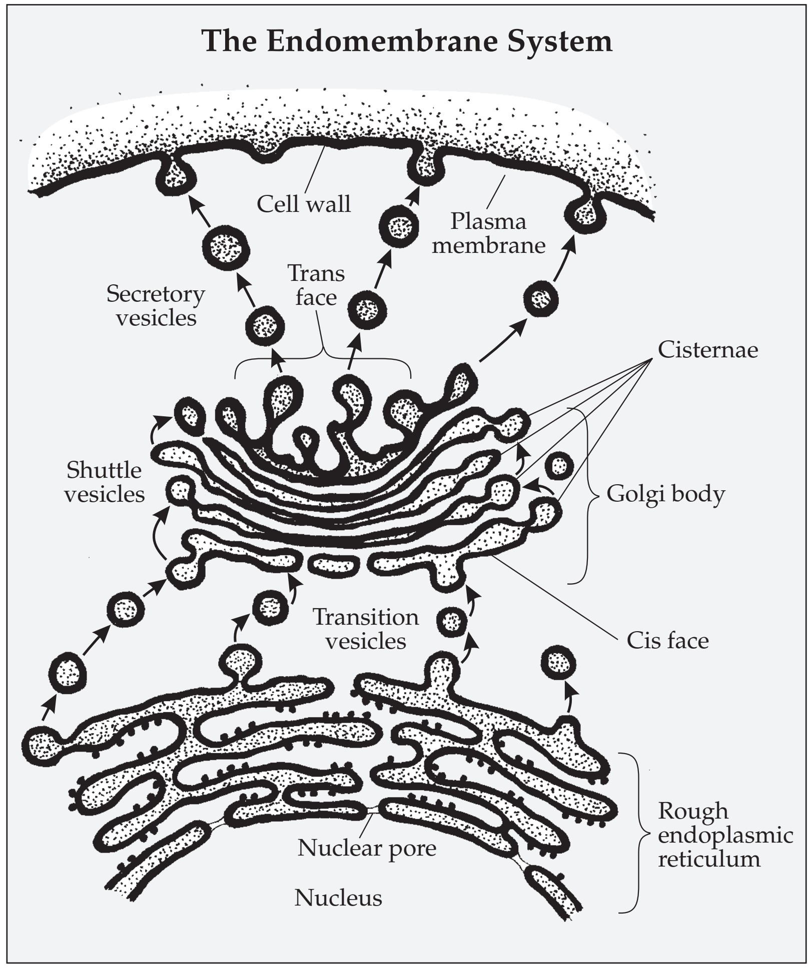
Golgi Complex

The Golgi complex is a major component of the endomembrane system and, in most cells, its primary role is secretion. The term "Golgi complex" refers collectively to all the *Golgi bodies* (once commonly called *dictyosomes* in plants) in a cell. It is named after Camillo Golgi (1843-1926), an Italian scientist who first described the structures in 1878. Golgi won the 1906 Nobel Prize in Physiology or Medicine for his contributions to the understanding of the structure of the nervous system.

When viewed through an electron microscope, a single Golgi body is composed of a series (of typically four to eight) round, flattened membranous sacs called *cisternae*. This "stack of sacs" has two sides; the cisterna on the *cis* side often faces the ER, while the cisterna on the *trans* side often faces away from the ER. The *medial cisternae* are in between. The *trans-Golgi network* is the collection of vesicles seen leaving the *trans* face of the Golgi body. *Intercisternal elements* are protein fibers that span the space between cisternae. They may help anchor the Golgi enzymes in the individual cisternae so they are not transported away and lost with the *shuttle vesicles*, described below. The intercisternal elements may also help stabilize the entire Golgi body.

An individual Golgi body is surrounded by a very faint, filamentous structure called the *Golgi matrix*. The matrix (along with the intercisternal elements) probably helps hold the Golgi body together as it is moved around the cell. The matrix also appears to exclude ribosomes and other cytosolic components from the immediate vicinity of the Golgi bodies and keeps the cytoplasm from interfering with the functioning of the complex. There are apparently no direct membrane connections among the individual cisternae in a Golgi body. Rather, membrane and contents move between cisternae via shuttle vesicles that pinch off of one cisterna, move in a trans direction, and fuse with an adjacent cisterna. The number of Golgi bodies in a plant cell can vary widely, from several dozen to more than ten thousand, depending on the size and function of the cell.

Entire Golgi bodies are transported around the cell via the *cytoskeleton*. They show a stop-and-go type of movement that may be associated with a need to approach a segment of the *rough ER*, or RER, to pick up proteins and then move closer to the plasma membrane or vacuole to deliver those proteins to the proper destination. Golgi bodies divide by fission, with new stacks pinching off of existing ones.



The endomembrane system, including the rough endoplasmic reticulum outside the cell's nucleus, transports materials to and from the cell's plasma membrane by means of vesicles transported through the Golgi complex (composed of flattened sacs called cisternae). The Golgi complex is responsible for the processing and packaging of proteins and other molecules for secretion from the cell or use within the cell.

KIMBERLY L. DAWSON KURNIZKI

Golgi Functioning

The Golgi complex is responsible for the processing and packaging of proteins and other molecules for secretion from the cell or use within the cell. A typical pathway for the secretion of a protein to the cell exterior (that is, exocytosis) would be as follows. A ribosome bound to the RER translates a piece of messenger RNA into a protein, and that protein is inserted into the lumen (the aqueous space enclosed by the RER membrane) of the RER. A vesicle forms by enclosing the protein and pinching off of the RER.

This *transition vesicle* travels across the cytosol (the traffic being directed by the *microtubules* and *microfilaments* of the cytoskeleton), fuses with the cisterna on the *cis* face of a Golgi body, and delivers the protein to the *lumen* of that cisterna. Enzymes in the lumen of the cisterna modify the protein by adding sugars (called "glycosylation") to produce a *glycoprotein*. A vesicle of Golgi membrane pinches off, forms a shuttle vesicle, and delivers the glycoprotein to the next cisterna in the stack, where the protein may be further glycosylated. The protein moves its way through the Golgi body and, eventually, leaves the *trans* face in a *secretory vesicle* that fuses with the plasma membrane. The contents of the secretory vesicle are moved out of the cell by exocytosis, while the membrane of the vesicle becomes incorporated into the plasma membrane.

In a similar fashion, the Golgi complex delivers matrix polysaccharides to the cell wall, large molecules and membrane lipids to the vacuole, or *integral* membrane proteins to the vacuolar membrane. In contrast to proteins (which are synthesized on the RER and merely modified during their transit through the Golgi body), cell wall matrix polysaccharides are synthesized from the ground up in the Golgi.

Surface-exposed proteins in the membrane of the vesicle contain the information needed to direct the vesicle to either the plasma membrane or some other place in the cell. Vesicles destined for the vacuole are visibly coated (as seen using an electron microscope) with protein, the major coat protein being *clathrin*. Vesicles destined for the plasma membrane appear smooth but undoubtedly have protein information on the exterior that directs them to the plasma membrane.

A single Golgi body can be involved in processing and packaging both glycoproteins and polysaccharides for delivery to the plasma membrane or intracellular locations at the same time. They also can be "retailored" to suit changing needs over the lifetime of a cell. That is to say, the enzymes in the cisternal lumen can be degraded and replaced with other enzymes that direct the synthesis of different molecules.

Other Endomembrane System Components

From the above, it can be seen how the ER and Golgi complex interact to deliver proteins and carbohydrates to the plasma membrane and vacuoles. In addition, the electron microscope often shows the ER to be physically connected to the nuclear envelope. Thus, the nuclear envelope is almost always included in a discussion of the endomembrane system. However, the exact functional nature of this nuclear connection remains unknown. The nuclear envelope is composed of two membranes, the outermost of which can be studded with ribosomes, much like the RER. The outer membrane of the nuclear envelope may, in some ways, be functionally similar to the RER, producing proteins which are passed across the outer membrane to the space between the two envelope membranes.

The fate of those membranes remains unclear. Whether they cross the inner membrane of the nuclear envelope as well and are delivered to the interior of the nucleus or diffuse to the lumen of a nearby section of ER and are processed through the Golgi complex is not known. The ER/nuclear envelope connection may be better understood by investigating the evolution of the eukaryotic cell.

Evolutionary Significance

According to the *endosymbiotic theory*, the ancestor of today's eukaryotic cells was a primitive prokaryote that engulfed a respiratory prokaryote (which eventually became established as mitochondria) and a photosynthetic prokaryote (which became chloroplasts). The other membrane-bound organelles of the cytoplasm were derived from infoldings of the plasma membrane. Thus the entire endomembrane system (plasma membrane, ER, Golgi complex, vacuoles, and nuclear envelope) probably has a common evolutionary background. Over time, the individual compartments became more specialized.

Robert R. Wise

See also: Active transport; Cell-to-cell communication; Chloroplasts and other plastids; Cytoplasm; Cytoskeleton; Endocytosis and exocytosis; Endoplasmic reticulum; Eukaryotic cells; Genetic code; Liquid transport systems; Microbodies; Microscopy; Mitochondria; Nucleus; Osmosis, simple diffusion, and facilitated diffusion; Plasma membranes; Vacuoles; Vesicle-mediated transport.

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ENDOPHYTES

Categories: Animal-plant interactions; fungi; microorganisms

Fungi that spend at least a part of their lives within the aboveground parts of living plants—in leaves, stems, and in some cases reproductive organs—but cause no outward signs of infection are called endophytes. Some endophytes protect the host plant by deterring grazing animals or pathogenic fungi.

In the 1980's scientists began to realize that a great variety of microscopic fungal species live benignly within plants, as endophytes (from the Greek words *endos*, meaning "inside," and *phyton*, for "plant"), in contrast to fungi living on the surfaces of plants, as *epiphytes* (from the Greek *epi*, meaning "upon," plus *phyton*). Most endophytic fungi are *ascomycetes*. Many appear to be close relatives of plant pathogens.

Most endophytic fungi live and feed between the host plant's cells. Those endophytes that provide a benefit to the plant in return for their keep are considered to be partners with their host, in a symbiotic relationship called *mutualism*. Endophytic mutualism is well developed in some grasses, in which the fungal partner produces alkaloid substances that deter herbivores and pathogens.

Some fungi live within a plant benignly or mutualistically for a time, and then, if environmental stress or senescence afflicts the host or conditions otherwise change, the fungi turn pathogenic. For example, in a drought-weakened tree, previously benign fungi may initiate disease symptoms. Such fungi are said to have both an endophytic and a pathogenic phase. Other fungi may have a dormant, endophytic phase, then eventually become dependent on dead organic matter for sustenance.

Two Growth Patterns

The endophytes of grasses differ in growth habit from those of woody plants (both coniferous and angiospermous). Grass endophytes have been found to grow systemically, throughout the stems and leaves, of the mature plant, producing substantial fungal biomass. Hyphae, or filaments, of the fungal body even penetrate the grass ovule, which is the reproductive structure that develops into the seed. Via the infected seed, the fungus is transmitted to the next generation and thus is perpetuated down a plant's lineage.

In contrast, in most of the woody plants that have been investigated, individual endophytes are not systemic but instead are localized within leaves or stems, where they may be confined to specific plant tissues, such as bark or xylem (wood). Woody-plant endophytes typically propagate not by invading the host's ovule but rather via spores, which are carried to other plants by air, water, or animals. Presumably, the spores are able to disperse because they are not produced inside the plant host but rather on plant parts that have dropped off or are dying. This subject has been little investigated, however.

Abundance and Diversity

Endophytic fungi are common and widespread. Although research has focused mainly on grasses and woody plants, endophytes have also been found in mosses, ferns, and herbaceous angiosperms (flowering plants). Scientists have suggested that endophytic fungi may be as widespread among plants as are *mycorrhizae* (associations between certain fungi and plant roots), which characterize the vast majority of vascular plants. In mycorrhizae, part of the fungal body is external to the plant, whereas endophytes are wholly internal.

Endophytes are diverse, especially in trees and shrubs. Individual woody species and even individual plants typically harbor scores of fungal species, as has been shown for alder, oak, beech, maple, birch, ash, pine, spruce, fir, and other plants. Nevertheless, just one or a few species or genera of fungi usually dominate the fungal community of each woody plant species. These dominants commonly do not occur in plants other than the host species or closely related species.

Tropical trees are only beginning to be investigated for endophytes, but indications are that they are particularly rich in endophytic species. Given the high diversity of tropical trees, the endophytes still awaiting discovery may represent an enormous reservoir of biodiversity. In contrast to the wide variety of endophytes in woody plants, endophytes in grasses seem to be of low diversity. Grass endophytes are all closely related species, and each grass species seems to host only one or a few of them. Grasses, however, have been little examined for the nonsystemic kinds of endophytes that woody plants harbor in such variety.

Mutualisms and Ecology

Endophytic fungi that are mutualistic, or protective of the plant, are particularly well known in the pasture grasses tall fescue (*Festuca arundinacea*) and perennial ryegrass (*Lolium perenne*). The endophytes produce alkaloid toxins that defend these plants against insect attack and also cause serious illness in grazing livestock. Some endophytes, especially in grasses, increase host tolerance of other environmental stresses, such as drought. Many of the diverse endophytic species in woody plants have no known protective function, and some seem to be latent pathogens. Among those that are protective is one in the needles of Douglas fir (*Pseudotsuga menziesii*). It produces substances toxic to midges that form galls on the needles.

The ecological effects of endophytes in natural populations seem to be very complex. Endophytes sometimes are actually antagonistic to the host plant rather than mutualistic with it. The ecological role of endophytes and their host plants in natural environments has been little studied, however.

Economic Importance

The chemical substances produced by endophytic fungi are of considerable commercial interest to the pharmaceutical and food-processing industries and as potential biocontrol agents for plant diseases and pests. Endophytic fungi may eventually help farmers grow crops with minimal use of water, fertilizers, and pesticides.

Jane F. Hill

See also: Animal-plant interactions; Ascomycetes; Biopesticides; Community-ecosystem interactions; Drought; Fungi; Mycorrhizae; Resistance to plant diseases.

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ENDOPLASMIC RETICULUM

Categories: Anatomy; cellular biology

The endoplasmic reticulum is a network of sacs in the cytosol of eukaryotic cells that manufactures, processes, transports, and stores chemical compounds for use inside and outside of the cell.

The endoplasmic reticulum (ER) is an extensive, complex system of a more or less continuous distribution of convoluted membrane-bound cavities that take up a sizable portion of the cytosol. The internal space of the ER is called the *lumen*. The ER is attached to the double-layered nuclear envelope and provides a connection, or bridge, between the nucleus and the cytosol. In addition, it provides living bridges between cells by way of the *plasmodesmata*, small tubes that connect plant cells. The ER is a dynamic structure, constantly changing. It accounts for 10 percent or more of the volume of the cytosol.

In general, there are two kinds of endoplasmic reticulum, rough and smooth. *Smooth ER* is quite varied in appearance and most likely in function as well. Through a microscope, it appears as numerous nearly circular blotches, indicating that it consists of interlocking tubes of membranes. On the other hand, *rough ER* almost always appears as stacks of double membranes that are heavily dotted with *ribosomes*. Based on the consistent appearance of rough ER, it most likely consists of parallel sheets of membrane, rather than the tubular sheets that characterize smooth ER. These flattened, interconnected sacs are called *cisternae*, or cisternal cells. The cisternal cells of rough ER are also referred to as luminal cells. Rough ER and the *Golgi complex* are both composed of cisternal cells.

Smooth and Rough ER Functions

Because rough ER is covered with ribosomes, it has a bumpy appearance when viewed with an electron microscope. Rough ER is primarily involved in the production of proteins that will be exported from the cell to help with other functions of building the plant. Such proteins include antibodies, digestive enzymes, and certain hormones. Amino acid chains are assembled into proteins by the ribosomes. The protein units needed outside the manufacturing cell are transported into the rough ER for further processing. Once inside, they are shaped into the correct three-dimensional configuration that will be useful outside the cell. Necessary chemicals, such as carbohydrates or sugars, are then added to complete the proteins. The ER then transports these proteins to other areas of the ER, called *transitional ER*, where they are packed in vesicles to be sent to the Golgi complex for export, or secretion, to other parts of the plant. Occasionally, some of the completed proteins are transported to areas of the manufacturing cell where they are needed.

Because the smooth ER does not have attached ribosomes, it appears relatively smooth when viewed through an electron microscope. It also appears to bud off from vesicles that contain material from the lumen of the ER. Using the many different enzymes that are anchored to its walls, the smooth ER is involved with the synthesis, secretion, and storage of lipids as well as the manufacture of new membranes and the metabolism of carbohydrates.

Lipids are a group of fatty substances needed for building membranes and storing energy in plants. Among the more important lipids are phospholipids, which make up major components of the cell membrane. When a plant has excess energy available from photosynthesis, it sometimes stores that energy in the form of lipids known as triglycerides. When the plant is in need of more energy, the triglycerides can be broken down to produce it. Waxes are other important lipids stored in the smooth ER. They form protective coatings on the leaves of plants. Research indicates that smooth ER is also involved in the formation of cellulose for the cell wall.

Other Special ER Functions

Calcium is an essential nutrient for cellular function, growth, and development in plants. However, too much calcium can lead to cell death. To deal with high levels of calcium in the environment, many plants have developed a mechanism involving the ER to regulate bulk quantities of calcium through the formation of calcium oxalate crystals. Calcium oxalate crystals can account for more than 90 percent of the calcium found in a plant. Certain specialized ER cells, called crystal *idioblasts*, appear to participate in the formation of calcium oxalate and provide the storage locations for calcium in plants.

Plants have the capability to undergo rapid, large-scale movements when triggered by a wide variety of stimuli, such as changes in light intensity, temperature, and pressure. The ER is the plant sensor for pressure changes. For example, in Venus's flytrap and in the sensitive plant, the ER in cortex cells, referred to as *cortical ER*, provides the sense of touch. Inside the cytosol of these sensor cells, the ER aggregates at the top and the bottom of the cell. When the cells are compressed or squeezed, the cortical ER is strained and releases accumulated calcium, producing the sense of touch. The mechanism is very similar to muscle contraction in an animal. Because the cortical ER is interconnected through the plasmodesmata, which provide communication channels among cells and end at motor cells in specialized appendages such as *pulvini* (cushionlike swellings at the bases of leaves), flowers, or specialized leaves, a pressure stimulus at one cell can trigger a response throughout the whole plant.

Alvin K. Benson

See also: Cell-to-cell communication; Cytoplasm; Cytosol; Endomembrane system and Golgi complex; Growth habits; Plant cells: molecular level; Proteins and amino acids; Ribosomes.

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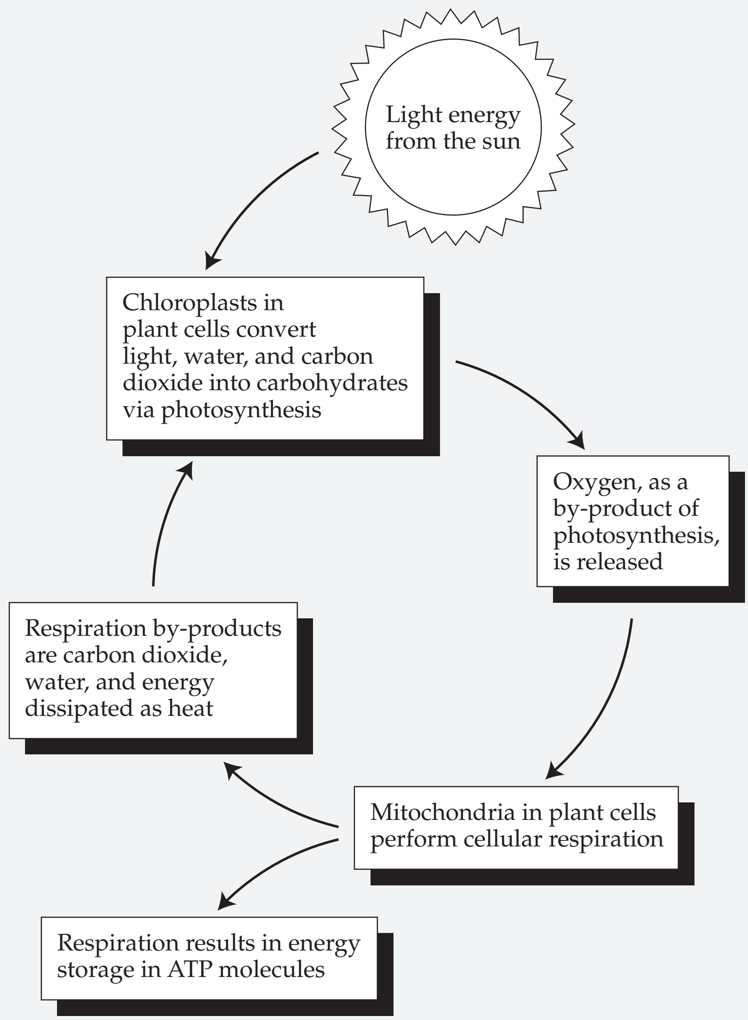
ENERGY FLOW IN PLANT CELLS

Categories: Cellular biology; photosynthesis and respiration; physiology

Life on earth is dependent on the flow of energy from the sun. A small portion of the solar energy, captured in the process of photosynthesis, drives many chemical reactions associated with living systems.

In living organisms, energy flows through chemical reactions. Each chemical reaction converts one set of substances, called the reactants, into another set, the products. All chemical reactions are essentially energy transformations, in which energy stored in chemical bonds is transferred to other, newly formed chemical bonds. *Exergonic* reactions release energy, whereas *endergonic* reactions

Transformation of Sunlight into Biochemical Energy



require an input of energy for a reaction to occur.

In plants, such reactions occur during the process whereby plant cells convert the energy of sunlight into chemical energy that fuels plant growth and other processes. During this process, called *photosynthesis*, carbon dioxide combines with simple sugars to form more complex carbohydrates in special structures called *chloroplasts*. These chloroplasts are membrane-bound organelles that occur in the cells of plants, algae, and some protists. The energy that drives the photosynthetic reaction is derived from the photons of sunlight; hence it is an endergonic reaction (it requires energy). Because plants, algae, and certain protists are the only living organisms that can produce their chemical energy using sunlight, they are called *producers*; all other life-forms are *consumers*. During seed germination, simple sugars, such as glucose, are broken down in a series of reactions called *respiration*. Energy is released to power the growth of embryo and young seedlings; hence, the reaction is exergonic. Within plant cells, both reactions occur.

In many reactions, electrons pass from one atom or molecule to another. These reactions, known as *oxidation-reduction* (or *redox*) reactions, are of great importance in living systems. The loss of an electron is known as *oxidation*, and the atom or molecule that loses the electron is said to be oxidized. Reduction involves the gain of an electron. Oxidation and reduction occur simultaneously; the electron lost by the oxidized atom or molecule is accepted by another atom or molecule, which is thus reduced.

Within plant cells, the energy-capturing reactions (photosynthesis) and the energy-releasing reactions (respiration) are redox reactions. Furthermore, all chemical reactions are orderly, linked and intertwined into sequences called *metabolic pathways*. All metabolic pathways in plant cells are finely tuned in three ways: the chemical reactions are regulated through the use of enzymes, exergonic reactions are always coupled with endergonic reactions, and energy-carrier molecules are synthesized and used for effective energy transfer.

Enzymes and Cofactors

Enzymes are biological catalysts, usually proteins, synthesized by plant cells. A number of characteristics make enzymes an essential component for energy flow in plant life. Enzymes dramatically speed up chemical reactions. Enzymes are normally very specific, catalyzing, in most cases, a single reaction that involves one or two specific molecules but leaves quite similar molecules untouched. In addition, enzyme activity is well regulated.

Many enzymes require a nonprotein component, or *cofactor*, for their optimal functions. Cofactors may be metal ions, part of or independent of the enzyme itself. Magnesium ions (Mg^{2+}), for example, are required in many important reactions in energy transfer, including photosynthesis and respiration. The two positive charges often hold the negatively charged phosphate group in position and help in moving it from one molecule to another. In other cases, ions may help enzymes maintain their proper three-dimensional conformation for optimal function. Some organic molecules can also be cofactors, including vitamins and their derivatives, and are usually called *coenzymes*. One example is the electron carrier nicotinamide adenine dinucleotide (NAD^+). NAD^+ is derived from nucleotide and vitamin-niacin. When NAD^+ accepts electrons, it is converted into NADH + H^+, which passes its electrons to another carrier; hence, NAD^+ is regenerated.

Plant cells regulate the amount and activity of their enzymes through various mechanisms. First, they control the synthesis of particular enzymes to meet their needs. They limit or stop the production of enzymes not needed by metabolic reactions and, hence, conserve energy. Second, plant cells may synthesize an enzyme in an inactive form and activate it only when needed. Third, plant cells can employ a feedback regulation mechanism by which an enzyme's activity is inhibited by an adequate amount of the enzyme's product. Furthermore, the activities of enzymes are affected by the environment, including temperature, pH (a measure of acidity versus alkalinity), and the presence of other chemicals. Different enzymes may require a slightly different physical environment for optimal function.

ATP: The Energy Carrier

During seed germination, stored glucose is broken down, making chemical energy available for movement, cellular repair, growth, and development. However, plant embryos cannot directly use the chemical energy derived from the breakdown of glucose. Within plant cells, most energy is transferred through a carrier—*adenosine triphosphate*, or ATP, known as the universal currency for energy transfer. Whether helping to convert light energy into chemical energy during photosynthesis or breaking down glucose in glycolysis and aerobic respiration, ATP acts as an agent to carry and transfer energy.

ATP is a nucleotide composed of the nitrogen-containing base adenine, the sugar ribose, and three phosphate groups. Energy released through glucose breakdown is used to drive the synthesis of ATP from adenosine diphosphate, or ADP, and inorganic phosphate (P_i):

$$\text{ADP} + P_i + \text{energy} \rightarrow \text{ATP}$$

The energy is largely stored in the bonds linking the phosphate groups. In reactions or processes where energy is needed, ATP releases energy through the hydrolysis and hence the removal of phosphate group:

$$\text{ATP} + H_20 \rightarrow \text{ADP} + P_i + \text{energy (7.3 kilocalories per mole)}$$

Sometimes the second phosphate group may also be removed via hydrolysis to generate the same amount of energy and adenosine monophosphate (AMP):

$$\text{ADP} + H_20 \rightarrow \text{AMP} + P_i + \text{energy (7.3 kilocalories per mole)}$$

The terminal phosphate group of ATP is not simply removed in most cases but is transferred to another molecule within a plant cell. This addition of a phosphate group to a molecule is defined as *phosphorylation*. The enzymes that catalyze such transfers are named *kinases*.

The following two examples of energy transfer involve ATP. The first is synthesis of sucrose by sugarcane:

$$\text{glucose} + \text{fructose} + 2\ \text{ATP} + 2\ H_20 \rightarrow \text{sucrose} + H_20 + 2\ \text{ADP} + 2\ P_i$$

The second example is the complete breakdown of glucose during cellular respiration:

$$\text{glucose} + 6\ O_2 + \text{36-38 ADP} + \text{36-38}\ P_i \rightarrow 6\ C0_2 + 6\ H_20 + \text{36-38 ATP}$$

Either ADP or ATP can be recycled through endergonic or exergonic reactions intertwined in the metabolic pathways. In the plant kingdom, energy flow begins with photosynthesis, through which ATP and then high-energy bonds are formed as sugar by the conversion of light energy from the sun. In respiration, these bonds are broken down to carbon dioxide and water, and energy is released. Some of this energy is used to power cellular processes, but some energy is lost in each energy-conversion step. The energy flow among all other organisms also starts from photosynthesis or plants, either directly or indirectly.

Yujia Weng

See also: Anaerobic photosynthesis; ATP and other energetic molecules; C_4 and CAM photosynthesis; Calvin cycle; Chloroplasts and other plastids; Exergonic and endergonic reactions; Glycolysis and fermentation; Krebs cycle; Mitochondria; Oxidative phosphorylation; Photorespiration; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Plant cells: molecular level; Respiration.

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ENVIRONMENTAL BIOTECHNOLOGY

Categories: Biotechnology; disciplines; ecology; economic botany and plant uses; environmental issues

Environmental biotechnology includes any process using biological systems (plants, microorganisms, and enzymes) to clean up and detoxify environmental contamination from hazardous and nonhazardous waste.

Bioengineering, *bioremediation*, and *biotechnological pollution control* are similar terms for the same idea: using naturally occurring plants, microorganisms, enzymes, and genetically engineered variants to clean up toxic wastes. Environmental biotechnology is becoming increasingly popular in waste treatment and remediation because it has several desirable characteristics. It is a "green" technology: It uses natural systems and naturally occurring organisms to detoxify environmental pollutants. It is not a particularly new, therefore uncertain, technology, so there are few unintended consequences of its use.

Bioremediation is inexpensive compared with other treatment technologies. If one can provide the proper environment and nutrients for the remediating organisms, there is relatively little other infrastructure involved. It can be done on-site without having to move hundreds of cubic yards of contaminated material. It can even be done in contaminated aquifers and soils that cannot be moved.

Plants and Microorganisms

Natural bioremediation of pollution is constantly occurring in the environment; without it, past pollution would still be present. Environmental biotechnology typically involves three types of organisms or biological systems: plants, microorganisms, and enzymes that may come from either group. Using plants to bioremediate an environment is referred to as *phytoremediation*. Phytoremediation is typically used when the environment is contaminated by heavy metals such as lead, mercury, or selenium. Certain plants (*Astragalus*, for example) are able to accumulate high concentrations of metals such as selenium in their tissues. The plants can be harvested, the tissue burned, and the metal-contaminated ash (now small in volume) can be stored in a hazardous waste facility.

Bioremediation most commonly refers to the use of soil microorganisms (bacteria and fungi) to degrade or immobilize pollutants. It can be used to treat a wide variety of wastes, including some nuclear wastes such as uranium. In one bioremediation process, the contaminated site is made favorable for microbial growth. Nutrients, such as nitrogen and phosphorus, are added. The area is kept moist and periodically stirred (if it is soil) to make sure it has sufficient air, or air is pumped into the system (if it is an aquifer). Microbes already present at the site start growing and use the waste as a food source.

Cometabolism and Seeding

Frequently, wastes cannot be used as a food source by microorganisms. These can still be biodegraded by a process called *cometabolism*. In cometabolism, wastes are biodegraded during the growth of microbes on some other compound. For example, trichloroethylene (TCE), one of the most common groundwater contaminants, is cometabolized during the growth of bacteria that use methane for their food source. Many other wastes, such as DDT, atrazine, and PCBs, are cometabolized by microbes in the environment.

Waiting for organisms to grow can take a long time, especially in winter. Often, environmental engineers speed the process using microorganisms grown in the laboratory on various pollutants. Therefore, when they are added to the environment in high numbers, they start bioremediating the pollutants immediately. This process is called *seeding*.

Enzymes

Sometimes a waste is so toxic or is present in such high concentration that neither plants nor microorganisms can survive in its presence. In this case, *enzymes* can be used to try to degrade the waste. Enzymes are proteins with *catalytic* activity; that is, they make chemical reactions occur faster than they normally would. Enzymes are not alive in a strict sense, but they come only from living organisms. They have an advantage over living organisms in that they can retain their catalytic activity in toxic environments. For example, horseradish peroxidase is a plant enzyme that has been used to treat chlorinated compounds. The peroxidase causes the compounds to bind together, becoming less soluble and thereby much less likely to enter the food chain of an ecosystem.

Use and Technology

Bioremediation has been used on a large scale mostly to treat oil spills. The best example of this was during the *Exxon Valdez* oil spill in Alaska in 1989. Rather than try to remove oil from beaches physically (by steam spraying or absorbing it into other materials), engineers sprayed several beaches with a nutrient solution that helped naturally occurring oil-degrading microbes in the environment to multiply and begin decomposing the pollutant. The experiment was successful, and the U.S. Environmental Protection Agency recommended that Exxon expand its bioremediation efforts to more of the affected beaches.

Environmental biotechnology is a growing industry, and numerous venture capital firms have started to supply remediation technology for various types of wastes. One application of this technology is "designer microbes" for sewage treatment facilities receiving industrial pollutants. Another involves creating unique microorganisms, using genetic engineering techniques, that have the ability to degrade new types of pollutants completely. The first living thing to be patented in the United States, a bacterium that was genetically engineered at the General Electric Company, was created specifically to degrade petroleum from oil spills.

Mark S. Coyne

See also: Biotechnology.

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EROSION AND EROSION CONTROL

Categories: Agriculture; environmental issues; soil

Erosion is the loss of topsoil through several types of action of wind or water.

Erosion control is vital because soil loss from agricultural land is a major contributor to *nonpoint-source pollution* and *desertification* and represents one of the most serious threats to world food security. In the United States alone, some 2 billion tons of soil erode from cropland on an annual basis. About 60 percent, or 1.2 billion tons, is lost through water erosion, while the remainder is lost through wind erosion. This is equivalent to losing 0.3 meter (1 foot) of topsoil from 2 million acres of cropland each year. Although soil is a renewable resource, soil formation occurs at rates of just a few inches per hundred years, much too slowly to keep up with erosive forces. The loss of soil fertility is incalculable, as are the secondary effects of polluting surrounding waters and increasing *sedimentation* in rivers and streams.

Leading No-Tillage States, 1994-1997

State	*Percent of Cropland Planted Using No-Till Practices*		
	1994	*1996*	*1997*
Kentucky	44	51	48
Maryland	41	46	45
Tennessee	42	44	43
West Virginia	37	39	39
Delaware	37	38	38
Ohio	35	37	36

Source: Data adapted from G. R. Haszler, "No Tillage Use for Crop Production in Kentucky Counties in 1997," *Soil Science News and Views* 19 (1998).

Erosion removes the topsoil, the most productive soil zone for crop production, and the plant nutrients it contains. The thinning of the soil profile, which decreases a plant's rooting zone in shallow soils, can disturb the topography of cropland sufficiently to impede farm equipment operation. Erosion carries nitrates, phosphates, herbicides, pesticides, and other agricultural chemicals into surrounding waters, where they contribute to cultural eutrophication. Erosion causes sedimentation in lakes, reservoirs, and streams, which eventually require dredging.

Water Erosion

There are several types of wind and water erosion. The common steps in water erosion are *detachment*, *transport*, and *deposition*. Detachment releases soil particles from soil aggregates, transport carries the soil particles away and, in the process, scours new soil particles from aggregates. Finally, the soil particles are deposited when water flow slows. In *splash erosion*, raindrops impacting the soil can detach soil particles and hurl them considerable distances. In *sheet erosion*, a thin layer of soil is removed by tiny streams of water moving down gentle slopes. This is one of the most insidious forms of erosion because the effects of soil loss are imperceptible in the short term. *Rill erosion* is much more obvious because small channels form on a slope. These small channels can be filled in by tillage. In contrast, *ephemeral gullies* are larger rills that cannot be filled by tillage. *Gully erosion* is the most dramatic type of water erosion. It leaves channels so deep that equipment operation is prevented. Gully erosion typically begins at the bottom of slopes, where the water flow is fastest, and works its way with time to the top of a slope as more erosion occurs.

Wind Erosion

Wind erosion generally accounts for less soil loss than water erosion, but in states such as Arizona, Colorado, Nevada, New Mexico, and Wyoming, it is actually the dominant type of erosion. Wind speeds 0.3 meter (1 foot) above the soil that exceed 16 to 21 kilometers (10 to 13 miles) per hour can detach soil particles. These particles, typically fine- to medium-sized sand fewer than 0.5 millimeter (0.02 inch) in diameter, begin rolling and then bouncing along the soil, progressively detaching more and more soil particles by impact. The process, called *saltation*, is responsible for 50 to 70 percent of all wind erosion. Larger soil particles are too big to become suspended and continue to roll along the soil. Their movement is called surface *creep*.

The most obvious display of wind erosion is called *suspension*, when very fine silt and clay particles detached by saltation are knocked into the air and carried for enormous distances. The Dust Bowl of the 1930's was caused by suspended silt and clay in the Great Plains of the United States. It is possible to see the effects of wind erosion on the sides of fences and similar objects. Wind passing over these obstacles deposits the soil particles it carries. Other effects of wind erosion are tattering of leaves, filling of road and drainage ditches, wearing of paint, and increasing incidence of respiratory ailments.

Soil Conservation Methods

The four most important factors affecting erosion are soil texture and structure, roughness of the soil surface, slope steepness and length, and soil cover. There are several passive and active methods of erosion control that involve these four factors. Wind erosion, for example, is controlled by creating windbreaks, rows of trees or shrubs that shorten a field and can reduce the wind velocity by about 50 percent. Tillage perpendicular to the wind direction is also a beneficial practice, as is keeping the soil covered by plant residue as much as possible.

Highly erosive, steeply sloped land in the United States can be protected by placing it in the government-sponsored Conservation Reserve Program. The program provides incentives and assistance to farmers and ranchers for establishing conservation practices that have a beneficial effect on resources both on and off the farm. It encourages farmers to plant grass and trees to cover land that is subject to wind and water erosion.

Additional ways to prevent water erosion include planting permanent grass waterways in areas of cropland that are prone to water flow. Likewise, grass filter strips can be planted between cropland

Image Not Available

and adjacent waterways to impede the velocity of surface runoff and cause suspended soil particles to sediment and infiltrate before they can become contaminants. In this way, vegetation can improve water quality or provide food and habitat for wildlife. Tillage practices are also beneficial in combating water erosion. Tillage can be done along the contour of slopes. Long slopes can be shortened by terracing, which reduces the slope steepness.

Conservation tillage practices, such as minimal tillage and no-tillage, are being widely adapted by farmers as a simple means of erosion control. As the names imply, these are tillage practices in which as little disruption of the soil as possible occurs and in which any crop residue remaining after harvest is left on the soil surface to protect the soil from the impact of rain and wind. The surface residue also effectively impedes water flow, which causes less suspension of soil particles. Because the soil is not disturbed, practices such as no-tillage promote rapid water infiltration, which also reduces surface runoff. No-tillage is rapidly becoming the predominant tillage practice in southeastern states such as Kentucky and Tennessee, where high rainfall and erodible soils are found.

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See also: Agriculture: modern problems; Desertification; Nutrients; Soil degradation; Soil salinization.

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ESTROGENS FROM PLANTS

Categories: Economic botany and plant uses; medicine and health

While the female hormones called estrogens are common in mammals, only a few plants contain estrogens. Others synthesize compounds which are chemically unrelated to estrogens but resemble them in their molecular size and shape. These compounds are called phytoestrogens (plant estrogens) and may, when ingested by animals or humans, have properties similar to those of mammalian estrogens.

The precursor of estrogens in plants and animals is the linear (straight-chain) triterpene known as squalene. Cyclization of squalene, via the intermediate cycloartenol in plants and via the intermediate lanosterol in animals, forms a group of very important compounds known as the *steroids*. Steroids include cholesterol, mammalian sex hormones (including the estrogens and androgens), corticosteroids, insects' molting hormones, and plant brassinosteroid hormones. All steroids have a tetracyclic (four-ringed) structure; the rings are named A, B, C, and D. Differences in the functional groups attached to the tetracyclic skeleton, differences in the side-chain attached to ring D, and differences in the overall shape of the molecule determine a steroid's biological activity.

Estrogens have an aromatic A ring (a ring of six carbon atoms joined by alternating single and double bonds). This constrains the junction between the A and B rings, resulting in a "flat," or planar, molecule. This shape is essential for the potent biological activity of estrogens, and chemical modifications that alter the planar nature of an estrogen molecule reduce its biological activity.

Estrogens in Plants Versus Animals

In animals, one of the most potent estrogens is *estradiol*. It triggers the production of gonadotropins leading to ovulation. It is metabolized to the less active estrogens, *estrone* and *estriol*. Estrone and estriol are produced by the placentas of pregnant mammals, and both compounds accumulate in the urine during pregnancy.

In plants, estrogens are *secondary metabolites*. Although many thousands of secondary metabolites occur in plants, the distribution of particular secondary metabolites is often limited to just a few genera. This appears to be the case for estrogens. Estrone has been isolated from the seeds of pomegranate and from the date palm, in which it is a component of the kernel oil. Estriol has been isolated from the pussy willow. It is not known what function these estrogens have in plants. It is possible that, like other secondary metabolites, they may function in plant defense.

Image Not Available

Isoflavonoids as Phytoestrogens

Isoflavonoids are a type of secondary metabolite and are found almost exclusively in the legume (pea) family of plants. They are known to function in plant defense. They have been shown to deter herbivores and also to facilitate a plant's defense response to pathogen attack. Interestingly, some isoflavonoids have chemical structures that, in overall size, shape, and polarity, resemble estrogens. The resemblance includes the flatness, or planarity, of the molecules and the positions and orientation of oxygen atoms. Isoflavonoids that have these molecular characteristics can mimic the biological activity of estrogens and are called *phytoestrogens*.

In terms of biosynthetic origins and chemical structure, phytoestrogens and estrogens are quite different. Phytoestrogens, being isoflavonoids, are phenolic compounds, formed from phenylalanine (an amino acid) by the shikimate pathway. In contrast, estrogens are triterpenoids, formed from acetyl coenzyme A by the isoprenoid pathway.

Isoflavonoids that are considered to be phytoestrogens exhibit only weak estrogenic activity in animals and humans. Examples of phytoestrogens are *coumestrol*, *daidzein*, and *genistein*. Coumestrol and daidzein are found in alfalfa (known as lucerne in Europe) and clover. Both of these plants belong to the legume family and are important forage crops for animals. If the content of phytoestrogens in alfalfa or clover is high, the reproductive cycles of grazing animals may be adversely affected. This can pose a problem for farmers wanting to breed livestock in the normal way. For this reason, the amount of grazing in fields of alfalfa or clover has to be restricted. Alternatively, varieties of alfalfa or clover that have been bred to contain lower levels of isoflavonoids can be grown. Unfortunately, plant varieties with lower isoflavonoid content are often more susceptible to both pathogen attack and attack by herbivorous pests.

Phytoestrogens in the Human Diet

One of the major sources of phytoestrogens in the human diet is the soybean. Genistein is the major phytoestrogen in soybeans. It is present in some soybean products such as tofu, although it is not present in soy sauce. Genistein, extracted from soybean plants, can also be obtained as a dietary supplement. Dietary supplements, which are often pills, powders, or tinctures containing plant-derived products, can be purchased over the counter. In the United States, the manufacture and sale of such products, classified as "dietary supplements," is far less closely regulated and standardized than the manufacture and sale of food and drugs.

Genistein has been promoted as a possible preventive treatment or therapy for several diseases and conditions. There are claims that it reduces hot flashes associated with menopause, that it can prevent or delay the onset of osteoporosis in postmenopausal women, and that it can lower blood cholesterol levels. In each instance the potential effectiveness of genistein would be attributable to its acting as an estrogen replacement in older women, in whom the level of estradiol is naturally low. Genistein may also be effective in the treatment of certain breast cancers that require estrogen in order to grow. In this case it is theorized that the genistein, with weak estrogen activity, acts to reduce cancer growth by competing with the more potent estradiol for the estrogen receptor.

Some of the evidence for the role of phytoestrogens in women's health is circumstantial. It is based, in part, on observations that women who live in countries such as Japan and China, where soy products are widely consumed, have a lower incidence of diseases such as osteoporosis and breast cancer. Clearly, other factors, genetic and environmental, may be contributory. Health claims attributed to phytoestrogens, including genistein, need further evaluation in well-designed clinical trials before such claims can be accepted by the scientific and medical communities or relied upon by those using dietary supplements.

Valerie M. Sponsel

See also: Medicinal plants; Metabolites: primary vs. secondary.

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ETHANOL

Category: Economic botany and plant uses

Ethanol, sometimes called grain alcohol, is an alcohol produced by fermentation of carbohydrates from a broad range of plant matter for many uses in the chemical industry. It has potentially significant use as a gasoline replacement and is also the primary alcohol component of alcoholic beverages.

Ethanol is produced by carbohydrate fermentation processes, hydration of ethylene, and, to a lesser extent, reduction of acetaldehyde obtained from acetylene. Also called ethyl alcohol, alcohol, and grain alcohol, ethanol is a colorless liquid with a mild and distinct aroma and taste. It has a boiling point of 78.3 degrees Celsius and a melting point of ¯114.5 degrees Celsius. Ethanol is completely soluble in water and most organic solvents. It has a flash point of 8 degrees Celsius and is thus highly flammable. Ethanol undergoes numerous commercially important reactions and is thus a vital industrial chemical. It has been used as a partial replacement for gasoline (the hybrid fuel is called "gasohol"). As the major component of alcoholic beverages, ethanol has been known and recognized for thousands of years.

Primary Uses

Alcohol obtained from fermentation processes is generally included with other fermentation products and extracts from the carbohydrate-rich grains, fruits, and so on that are the raw materials for the many alcoholic beverages produced and consumed. Alcohol produced by yeast fermentation is obtained at a maximum concentration of 14 percent; therefore, alcoholic beverages other than beer and nonfortified wines require the addition of concentrated alcohol, which is obtained by distilling dilute alcohol from the fermentation of molasses and other sugar sources. In the United States and other highly industrialized countries, the alcohol added to beverages is increasingly being produced by other methods.

Ethanol is also used in large quantities for chemical synthesis in the organic chemical industry. It is used for the preparation of numerous esters vital to many polymer industries and for the production of diethyl ether (also called ether or ethyl ether), a major solvent. Other synthetic procedures lead to the manufacture of acetaldehyde, acetic acid, ethyl halides, and acetonitrile, which are in turn employed for the preparation of drugs, explosives, adhesives, pesticides, detergents, synthetic fibers, and other substances. Ethanol itself is used in vast quantities as a solvent.

Ethanol is added to gasoline to reduce air pollution, and it is frequently considered to be a likely replacement for gasoline when petroleum resources decline or drastically increase in price. Gasohol, ethanol combined with varying amounts of gasoline, is being vigorously promoted and is already in use in Brazil and elsewhere. *Biomass conversion* (conversion of plant matter) to ethanol by cost-efficient methods will speed the entry of gasohol into large-scale use in the industrial world.

Production Processes

Until biomass conversion becomes more widely used, carbohydrate fermentation processes are destined to be a decreasingly important source of industrial ethanol. Beverage alcohol is produced from a great variety of sources, including grains, potatoes, and fruit, but fermentation-based industrial alcohol is almost entirely obtained by yeast fermentation of molasses. Molasses (50 percent sucrose residue from sugar processing) is diluted with water to approximately 15 percent and under slightly acidic conditions is fermented by yeast to give 14 percent ethanol. Fractional distillation of the solution yields the commercial product: 95 percent ethanol. Approximately two and one-half gallons of blackstrap molasses is needed to make a gallon of 190-proof ethanol. (Alcohol content is usually described in terms of its proof value, which is twice its ethanol percentage.)

Although ethylene hydration was known in the early part of the nineteenth century, it was not until 1929 that it became an industrial process. Today it is the dominant method of producing ethanol. Ethylene, obtained from the thermal cracking of petroleum fractions or from natural gas separation processes, is treated with complex phosphoric acid-based catalysts at temperatures above 300 degrees Celsius and steam at pressures of thousands of pounds per square inch. The ethanol can be fractionally distilled, and the residual ethylene can be recycled. Ethylene can also be passed into concentrated sulfuric acid, and after hydrolysis the ethanol can be distilled from the diluted sulfuric acid.

The 95 percent alcohol produced by any of these methods can be converted to nearly pure (absolute) alcohol by removal of the water by azeotropic distillation using benzene or trichloroethylene. Trace amounts of the hazardous benzene or trichloroethylene remaining make the absolute alcohol undesirable for beverage purposes but useful for industrial purposes in which the 5 percent water interferes with use requirements.

William J. Wasserman

See also: Glycolysis and fermentation; Grains; Sugars.

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EUDICOTS

Categories: Angiosperms; *Plantae*; taxonomic groups

The eudicots, class Eudicotyledones *(literally "true dicots"), are descended from a common ancestor and comprise three-quarters of all flowering plants. It is one of the two main classes of the angiosperms, the other being the monocots, or* Monocotyledones.

Eudicots, the common name used for class *Eudicotyledones*, are the most common group of flowering plants, comprising 75 percent of all angiosperms. The other 25 percent, monocots (*Monocotyledones*), are often characterized by pollen grains that have a single aperture (or line of weakness). Eudicots have pollen grains that typically possess three apertures, referred to as triaperturate pollen. Thus, there is no monocot-dicot division among the flowering plants. Whereas "monocot" remains a useful term, "dicot" does not represent a clade (a collection of organisms which have a single common ancestor) and should no longer be used. It is more useful to refer to eudicots, which represent a well-defined clade of angiosperms.

Previously, the angiosperms were divided into two major groups, traditionally recognized as classes: the dicots (short for dicotyledons, class *Magnoliopsida*) and the monocots (monocotyledons, class *Liliopsida*). Dicots have been distinguished from monocots by several morphological (external physical) and anatomical features, but all of these were subject to exception. For example, most dicots possess two seedling leaves, or *cotyledons*, and typically have net-veined leaves; monocots, in contrast, usually have one cotyledon and leaves with parallel venation.

The monocot-dicot division was recognized as early as the nineteenth century. However, later studies of *phylogeny* (the evolutionary history of a group of organisms) have demonstrated that this split does not reflect the evolutionary history of angiosperms. Phylogenetic trees (which are visual representations of the evolution of a group of organisms) showing historical relationships have been constructed based on deoxyribonucleic acid (DNA) sequences, as well as morphological, chemical, and other characteristics. These trees indicate that whereas the monocots form a *clade*, all dicots do not form a distinct group. The monocots appear among the groups of early-diverging (or early-evolving) lineages of angiosperms, all of which have traditionally been considered dicots. All early branches of the angiosperm phylogenetic tree, including the monocots, are best referred to informally as *basal angiosperms*.

Most angiosperms form a distinct clade, referred to by J. S. Doyle and C. L. Hotton as the eudicots, or true dicots. Whereas basal angiosperms are often characterized by pollen grains that have a single aperture (or line of weakness), eudicots have pollen grains that typically possess three apertures, referred to as triaperturate pollen. The eudicot clade receives strong support from analyses based on DNA sequence data. Importantly, the eudicots represent only a subset of the formerly recognized group dicots. Many basal angiosperms are traditional dicots but are not eudicots. Thus, there is no monocot-dicot split in the angiosperms. Whereas "monocot" remains a useful term, "dicot" does not represent a clade (a collection of organisms which have a single common ancestor) and should no longer be used. It is more useful to refer to eudicots, which represent a well-marked clade of flowering plants.

Eudicot (Dicot) Families Common in North America

Common Name	*Scientific Name*
Acanthus family	*Acanthaceae*
Borage family	*Boraginaceae*
Buckwheat family	*Polygonaceae*
Buttercup family	*Ranunculaceae*
Cactus family	*Cactaceae*
Daisy family	*Asteraceae*
Evening primrose family	*Onagraceae*
Gentian family	*Gentianaceae*
Ginseng family	*Araliaceae*
Madder family	*Rubiaceae*
Milkweed family	*Asclepiadaceae*
Mint family	*Lamiaceae*
Mustard family	*Brassicaceae*
Pea family	*Fabaceae*
Phlox family	*Polemoniaceae*
Pink family	*Caryophyllaceae*
Pokeweed family	*Phytolaccaceae*
Primrose family	*Primulaceae*
Purslane family	*Portulacaceae*
Rose family	*Rosaceae*
Saxifrage family	*Saxifragaceae*
Verbena family	*Verbenaceae*
Violet family	*Violaceae*
Waterleaf family	*Hydrophyllaceae*

Note: For a full list of angiosperm families, see the tables that accompany the essay "Angiosperms," in volume 1.

Source: U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Classification

The eudicots contain 75 percent of all angiosperms, or about 165,000 species distributed among roughly 300 families. The eudicots include all the familiar angiosperm trees and shrubs and many herbaceous groups. Some of the larger, better-known families of eudicots include *Rosaceae* (rose family), *Fabaceae* (bean family), *Brassicaceae* (mustard family), *Ranunculaceae* (buttercup family), *Apiaceae* (parsley family), *Asteraceae* (sunflower family), and *Lamiaceae* (mint family). The eudicots include many familiar trees, such as those of the *Fagaceae* (oak or beech family), *Betulaceae* (birch family), *Juglandaceae* (walnut or hickory family), *Aceraceae* (maple family), and *Platanaceae* (plane tree or sycamore family).

A good understanding of the major groups of eudicots has emerged from the use of DNA sequence data. The early-diverging eudicots consist of a number of ancient lineages, including *Ranunculales*, a group containing the *Ranunculaceae* and *Papaveraceae* (poppy family). Other early-diverging eudicots include *Buxaceae* (boxwood family) and *Proteales*; the latter includes the *Platanaceae* and *Proteaceae* (sycamore and protea families).

Following the early-diverging eudicots is a large clade, referred to as the core eudicots, that contains most eucidots. The core eudicots consist of three major clades (rosids, asterids, and *Caryophyllales*) and several smaller ones (*Santalales*, *Saxifragales*, and *Gunnerales*). The rosids and asterids are very large groups, each containing roughly one-third of all angiosperms. Traditional classifications, such as presented by botanist Arthur Cronquist in 1981, do not reflect modern views of phylogenetic relationships. For comparison, the rosid clade now recognized is made up of members of the traditional subclasses *Rosidae*, *Dilleniidae*, and *Asteridae* (in the sense of Cronquist, 1981); the asterid clade contains members of subclasses *Asteridae*, *Dilleniidae*, and *Rosidae*; and *Caryophyllales* contains taxa previously placed in *Caropyllidae* and *Dilleniidae*.

Relationships among the core eudicots are still unclear, despite intensive study using DNA sequence data. The difficulty in clearly describing relationships among these groups appears to stem from the fact that following the origin and initial diversification of the eudicots, a rapid radiation (evolution of many organisms in a short period of time) occurred, yielding the groups of core eudicots seen today.

Evolution

The eudicots can be easily identified in the fossil record by their three-grooved pollen; they appeared in the fossil record as early as 110 million years ago. Prominent early fossil eudicots include *Platanaceae*. Following the origin of the eudicots, the fossil record also suggests a rapid diversification; by 90 to 80 million years ago, many of today's prominent families were established and are clearly recognizable in the fossil record. Thus, the fossil evidence suggesting a rapid radiation of eudicots agrees with the phylogeny obtained using gene sequence data.

Horticulturally important eudicots include numerous representatives of Ranunculaceae, *such as columbine.*

Economic Uses

Outside the grasses, such as wheat, corn, and rice (all in the monocot family *Poaceae*), most plants of economic importance are eudicots. Examples of economically important eudicot families include members of the bean or legume family (*Fabaceae*), such as soybean, lentils, and green beans; and the sunflower family (*Asteracae*), which includes sunflowers, lettuce, and artichokes. The mustard family (*Brassicaceae*) contains numerous members of economic importance, including cabbage, kale, cauliflower, mustard, and horseradish. The rose family (*Rosaceae*) provides fruits such as strawberries, raspberries, apples, cherries, peaches, and plums as well as numerous ornamentals. The family *Solanaceae* is the source of tomatoes and potatoes.

Most familiar horticultural plants are also eudicots. They include a diverse array of trees, shrubs, and annual and perennial herbs. Horticulturally important eudicots include begonias (*Begoniaceae*), dogwoods (*Cornaceae*), rhododendrons and heaths (*Ericaceae*), numerous members of the *Asteraceae* including sunflower, asters, chrysanthemums, and marigolds; and numerous representatives of *Ranunculaceae* such as columbine, buttercups, and monkshood. Some other families that contain ornamental plants include the cactus family (*Cactacae*), the geranium family (*Geraniaceae*), and members of the mint family (*Lamiaceae*).

Because 75 percent of all flowering plants are eudicots, they are extremely diverse in ecology and morphology. The eudicots are also diverse in *habit* (pattern of growth) and include annual and perennial herbs, shrubs, and trees. In size, they range from the smallest terrestrial angiosperms, plants 1 centimeter in height (*Lepuropetalon*, *Parnassiaceae*), to eucalyptus trees well over 100 meters. Flowers are also highly diverse in structure, form, and size across the eudicots. The smallest eudicot flowers are those of *Lepuropetalon*, which are less than 1 millimeter in diameter; the largest eudicot flowers are more than 0.3 meter (1 foot) in length.

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See also: Angiosperm evolution; Angiosperms; Magnoliids; Monocots vs. dicots.

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EUGLENOIDS

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

Organisms called euglenoids, the algal phylum Euglenophyta *in the kingdom* Protista*, make up a large group of common microorganisms numbering between 750 and 900 known species.*

Euglenoids can be found in both fresh and stagnant water. Some genera of euglenoids can also be found in marine habitats. *Euglena* and *Phacus* are representative common genera. Euglenoids are unicellular, except for those of the colonial genus *Colacium*. Because euglenoids have flexible cell coverings, move about freely, and ingest their food through a structure called a gullet, many scientists have classified the euglenoids as animals. Some species of euglenoids, however, have chloroplasts and are able to supply at least some of their food needs through photosynthesis.

Structure

The cells of most euglenoids are spindle-shaped and do not have cell walls or other rigid structures covering the plasma membrane. However, one genus, *Trachelomonas*, has a covering called a lorica, which is similar to a cell wall and contains iron and magnesium minerals. Spiral strips of protein that originate in the cytoplasm support the plasma membrane, creating a structure called a *pellicle*. The pellicle may be either flexible or rigid. Euglenoids with a flexible pellicle are able to change their shape, which helps them move about in muddy habitats.

A euglenoid has two *flagella*. One, a functional flagellum, has numerous tiny hairs along one side and pulls the cell through the water. This flagellum originates in a structure called a reservoir found on the anterior end of the cell. Another, smaller flagellum is contained within the reservoir but does not protrude.

Other features of euglenoids include the presence of a *gullet*, or groove, in many species, through which food is ingested. About one-third of the euglenoids have disk-shaped *chloroplasts* and can supply at least part of their own food through photosynthesis. Even these photosynthetic euglenoids are capable of ingesting dissolved or particulate food through their gullet if necessary.

A reddish-colored structure called an *eyespot*, or *stigma*, is located in the cytoplasm near the base of the flagella. This eyespot acts as a light-sensing device. The eyespot appears to be connected to the flagellum by special strands of cytoplasm, which may serve to transmit signals from one organelle to the other.

Euglenoid cells also contain a *contractile vacuole*. The contractile vacuole functions as a pump that removes excess water from the interior of the euglenoid cell. The water is pumped out of the cell through the reservoir. A new contractile vacuole is formed after each discharge of water.

Pigments and Food Reserves

Some scientists believe that similarities between euglenoids and green algae indicate that the chloroplasts of euglenoids originated in endosymbiotic green algae. The chloroplasts of both euglenoids and green algae contain chlorophyll *a* and chlorophyll *b*. Euglenoids and green algae also have some carotenoid pigments in common, although euglenoids contain two pigments derived from carotenoids that are not found in either green algae or the higher plants.

While there are some similarities in pigmentation between euglenoids and green algae, the two groups have different food reserves. Green algae have food reserves of starch, while euglenoids have a carbohydrate food reserve called *paramylon*, which normally is present in the form of small, whitish bodies of varying shapes scattered throughout the cell.

Reproduction

Reproduction in euglenoids takes place by mitotic cell division. Even as the euglenoids are swimming about, the cell begins to divide, starting at the end of the cell, where the flagellum is located. Eventually the cell splits lengthwise, forming two complete cells. Unlike the nuclear membrane in most organisms, the membrane surrounding the euglenoid nucleus does not break down during mitosis.

Many scientists believe that euglenoids do not reproduce sexually; meiosis and gametogenesis have never been observed in euglenoids. Some scientists suspect sexual reproduction must occur, even though it has not been seen. Other scientists believe that even individuals of the same euglenoid species have different amounts of DNA in their nuclei, which would preclude meiosis. Still others believe that euglenoids branched off the main evolutionary lines of protoctists before sexual reproduction had evolved.

Some species of euglenoids have developed the capacity to make thick-walled resting cells. Inside these cells, the euglenoids can wait out unfavorable environmental conditions. When conditions are favorable, the organisms break out of their resting cells and resume their normal shapes and activities.

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See also: Algae; Green algae.

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EUKARYA

Categories: Cellular biology; evolution; taxonomic groups

The Eukarya *form one of the domains of life in the three-domain classification system.* Eukarya *consists of the advanced, complex organisms, formed by eukaryotic cells (cells with nuclei), including fungi, algae, plants, and animals. The other two domains of life,* Archaea *and* Bacteria*, consist of simpler organisms formed by prokaryotic (nucleus-free) cells.*

Two Types of Cell

The domain concept of biological organization is relatively new. As recently as the mid-twentieth century, two kingdoms—plant and animal—were widely accepted as describing the most significant split in the biological world. Every living thing was classified as either a plant or an animal. Subsequently, three additional kingdoms were recognized. Only in the late twentieth century did it become clear, based on molecular and other evidence, that distinctions at the level of the kingdom did not acknowledge the most fundamental differences among organisms. A higher category, the domain, was therefore posited. The general acceptance of the domain concept by the scientific community was an acknowledgment that, at least according to current knowledge, the differences between the prokaryotic organisms and the eukaryotic ones, and further, the split within the prokaryotic organisms, are the major dividing lines in the biological world.

Bacteria is the domain of prokaryotic organisms that are considered to be true bacteria, and *Archaea* is the domain of prokaryotic organisms able to live in extreme environments. *Eukarya* differs from the prokaryotic domains in basic characteristics of cellular organization, biochemistry, and molecular biology. Further, unlike the prokaryotic organisms, many of the *Eukarya* are truly multicellular. Eukaryotic cells, which are structurally more complex than prokaryotic ones, have many of their cellular functions segregated into semiautonomous, membrane-bound cell regions, called *organelles*. The principal organelle is the *nucleus*, which contains the genetic material, deoxyribonucleic acid (DNA). In prokaryotic organisms, in contrast, the DNA is not segregated from the rest of the cell.

Other distinguishing organelles in eukaryotic cells include the *mitochondria*. These are the sites of *respiration*, in which energy is generated by breaking down food, in the presence of oxygen, into water and carbon dioxide. The plants and the algae have additional organelles, the *plastids*. The most common plastid is the *chloroplast*, which contains chlorophyll, the key molecule that allows algae and plants to manufacture their own food from carbon dioxide and water, by photosynthesis. In contrast, in those bacteria that are photosynthetic, chlorophyll is not confined within an organelle.

Evolutionary Origin

Prokaryotic cells are much older than eukaryotic cells and had a long reign in the primordial seas before one of them, probably a member of the domain *Archaea*, gave rise to the first eukaryotic cell, between 2.5 billion and 1 billion years ago. This was at least a billion years after life had arisen. The first eukaryotic cell lacked mitochondria and chloroplasts. Subsequently, two kinds of prokaryotic organisms belonging to the domain *Bacteria* took up residence, as symbionts, inside early eukaryotic cells and eventually became so dependent on their hosts that they could no longer live on their own. These so-called *endosymbionts* developed into mitochondria and plastids.

Mitochondria, which were acquired before chloroplasts, arose from small bacteria that were heterotrophic: They obtained their food from other organisms rather than manufacturing it themselves. Chloroplasts arose from bacteria known as *cyanobacteria*, which were autotrophic, manufacturing their food themselves by photosynthesis. Thus, the evolution of the eukaryotic cell involved three prokaryotic cells—the original archaean host cell and two kinds of endosymbiotic bacteria. The early eukaryotic organisms were single-celled and are classified in a group called protists.

Early Diversification

From their beginning as single-celled protists, eukaryotic organisms evolved rapidly. The first multicellular eukaryotic organisms appeared about 800 million years ago, during the Precambrian era, and developed into three great lineages: the fungi, plants, and animals. Scientists have accorded each of these groups "kingdom" rank within the domain *Eukarya*, as the kingdoms *Plantae*, *Animalia*, and *Fungi*. In addition, the protists, which have living representatives today, are considered to constitute a fourth kingdom, the *Protista*, within the *Eukarya*. The *Protista* consist of the predominantly unicellular phyla and some of the multicellular lines associated with them. All four of the kingdoms within the *Eukarya* arose in the sea. Transition to the land occurred later.

The three multicellular kingdoms—plants, animals, and fungi—each probably descended from a separate ancestor from among the protists, and thus each of these lineages constitutes a relatively well-defined natural kingdom. The protists, however, are something of a "catch-all" kingdom. They consist of a variety of lineages, which include both photosynthetic organisms, the algae, and nonphotosynthetic ones. Because the algae are capable of photosynthesis, older classification schemes lumped them with the plants. Scientists think that many kingdoms will ultimately be recognized among the *Protista*.

The protist that gave rise to the plant lineage was probably a now-extinct member of the family *Charophyceae*, a group of specialized, aquatic, multicellular green algae (phylum *Chlorophyta*) that includes members living today. Like the algal protists, plants are autotrophic, but plants have more complex, structurally integrated bodies than do the algae.

In contrast to the algal protists and the plants, the nonphotosynthetic protists, as well as all the fungi and the animals, obtain their food heterotrophically, from other organisms. The fungi, although lacking chloroplasts and photosynthetic pigments, were once, like the algae, classified within the plant kingdom. This was partly because, like plants, fungi are sedentary. The fungi, however, have little in common, nutritionally or structurally, with plants and are now recognized as an independent evolutionary line within the *Eukarya*. Molecular evidence indicates that the fungi are actually more closely related to animals than to plants.

Colonization of the Land

Although all of the lineages that are now recognized as kingdoms within the *Eukarya* originated from aquatic organisms, the *Eukarya* eventually achieved great success on the land. Multicellularity helped these organisms make the transition to an environment of earth and air, which was more complex and demanding than the relatively uniform conditions of the sea. With their many cells, the *Eukarya* were able to develop specialized structures for coping with this new environment. The evolution of plants shows a trend toward structures specialized for anchorage, photosynthesis, and support. This trend eventually led to the development of complex plant bodies, with roots, leaves, and stems, allowing the plants as a kingdom to be fully terrestrial, not aquatic. Had it not been for plants' pioneering of the land, animals could not have become established there, because plants form the base of terrestrial animals' food chain.

Plants may have first invaded the land sometime in the Ordovician period of the Paleozoic era, 510 million to 439 million years ago. Forms resembling modern land plants arose in the Late Silurian period of the Paleozoic, more than 408 million years ago. By the close of the Paleozoic's Devonian period, about 360 million years ago, plants had diversified into a wide variety of shapes and sizes, from small creeping forms to tall forest trees.

In fossils of early plants, fungi are often found in close association with the roots. Some scientists think that plants were able to colonize the land only because they developed symbiotic relationships with such representatives of the fungal kingdom. Scientists also think that fungi, in turn, may have been able to make the transition to land only because of their close relationship with plants. According to this view, the fungi helped the plants gain a terrestrial foothold by absorbing water and mineral nutrients from the poorly developed soils of that time and passing them on to their plant partners. The plants provided the fungi with sugars that the plants had manufactured photosynthetically. This is much the way that relationships between plant roots and certain fungi work today. These symbiotic, so-called mycorrhizal relationships are characteristic of the vast majority of plants that dominate the modern world—the plants having vascular, or conducting, tissues. Of these plants, the most important by far are the angiosperms, or flowering plants (phylum *Anthophyta*).

Jane F. Hill

See also: *Archaea*; Bacteria; Chloroplasts and other plastids; Eukaryotic cells; Evolution of cells; Evolution of plants; Mitochondria; Molecular systematics; Mycorrhizae; *Plantae*; Prokaryotes.

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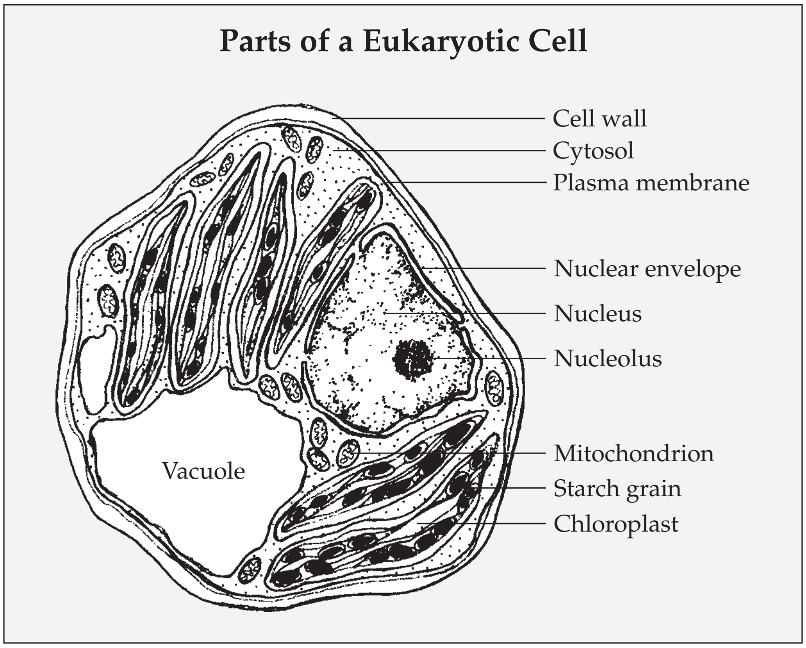
EUKARYOTIC CELLS

Category: Cellular biology

Eukaryotic cells (as opposed to prokaryotic cells) have internal, membrane-bound organelles and a distinct nucleus that physically separates the genetic material of the cell from the all of the other parts of the cell. All protists, fungi, plants, and animals are composed of eukaryotic cells.

The cells of all organisms can be divided into two broad categories: *prokaryotic* cells and *eukaryotic* cells. Prokaryotic cells are cells with a relatively simple structure, having no internal, membrane-



Kimberly L. Dawson Kurnizki

Eukaryotic cells constitute all but the simplest life-forms: protists, fungi, plants, and animals. Based on an electron microscope image of a leaf cell from a corn plant, this depiction shows the basic parts of the cell. Eukaryotic cells are distinguished from more primitive prokaryotic (mainly bacterial) cells by the presence of a nucleus that contains the genetic materials as well as membrane-bound organelles such as mitochondria and, in algae and plants, plastids such as chloroplasts.

bound organelles. The most striking feature of prokaryotic cells is that they lack a distinct *nucleus*, hence the name *prokaryotic*, literally translated from its Greek roots as "before nucleus." The prokaryotic organisms comprise two domains of the three domains of life: the ancient bacteria, *Archaea*; and the modern bacteria, *Bacteria* or *Eubacteria*. The *Archaea* are single-celled organisms that often inhabit extreme environments, such as hot springs. The remainder of bacteria are classified as *Eubacteria*.

All other organisms, including fungi, plants, and animals, are composed of eukaryotic cells and belong to the domain *Eukarya*. Eukaryotic cells are more structurally complex than prokaryotic cells, having internal, membrane-bound *organelles* and a distinct nucleus that physically separates the genetic material of the cell from the all of the other parts of the cell. Based on genetic analysis, the *Archaea* and *Eukarya* are more closely related to each other than they are to the *Bacteria*, suggesting that eukaryotic cells may have arisen from a single ancestral archaean cell.

Eukarya includes the traditional kingdoms *Plantae*, *Animalia*, *Fungi*, and *Protista*. Protists include a diverse assemblage of single-celled eukaryotic organisms including algae, amoebas, and paramecia. Because algae are photosynthetic, they have often been included in the study of plants, although they are not members of the plant kingdom.

Fungi include such organisms as smuts, rusts, molds, and mushrooms. Fungal cells have external cell walls and because of this have often been included in the study of plants. However, fungal cell walls have a completely different structure and composition from those of plant cell walls, and fungi lack plastids and photosynthetic pigments. Fungi represent a unique evolutionary line. They too, however, tend to be studied in botany courses, even though they are not plants.

Cell Parts

Eukaryotic cells are surrounded by a *cell membrane*, or *plasma membrane*, that is composed of a lipid structure in which other molecules, such as proteins and carbohydrates, are embedded. The cell membrane serves as a semipermeable, or selective, barrier between the cell and its environment. Some small, uncharged molecules can freely cross the cell membrane; others must be transported across the membrane before they can enter the cell. The cell membrane serves to protect the cell and to receive signals from the environment and other cells that help to direct cell activities.

In addition to the cell membrane, plant cells also have external *cell walls*. The presence of the external cell wall is one of the major characteristics that distinguishes plant cells from animal cells. The cell wall limits the size of the internal *protoplast* (the internal cytoplasm and nucleus) and prevents the plasma membrane from breaking when the protoplast enlarges following the uptake of water by the cell. Cell walls are not merely static support structures, however. They contain enzymes that are important in bringing essential molecules into the cell and in secreting molecules. They may also play important roles in the defense of the plant against bacterial and fungal pathogens.

Eukaryotic cells also have a prominent, membrane-bound organelle called the *nucleus*. The nucleus contains the genetic information of the cell that directs the cellular activity. A double membrane called the *nuclear envelope* surrounds the nucleus. Inside the nucleus, *deoxyribonucleic acid* (DNA) is transcribed to make molecules of *ribonucleic acid* (RNA), copies of the genetic information that can be delivered to the cytoplasm, where the RNA molecules serve to direct the manufacture of proteins. DNA in the eukaryotic nucleus exists as linear molecules that are associated with many proteins, and the DNA is packaged into a highly organized chromosomal structure by proteins called *histones*.

In addition to the nucleus, eukaryotic cells contain a number of internal membrane-bound organelles that help the cell carry out the functions necessary for life. The types of organelles found inside a eukaryotic cell reflect the function of that cell and the processes that it must carry out. Some of these organelles, such as *mitochondria* and *chloroplasts*, are important in capturing and releasing energy for cell function. Some, like the *Golgi complex* and the *endoplasmic reticulum* (ER), are involved in the manufacture, processing, and transport of proteins and other molecules within the cell. Others, such as *peroxisomes*, are involved in detoxifying chemicals and breaking down molecules.

The cell *cytoskeleton* is a highly dynamic structure that provides support and motility to cells as well as providing some of the apparatus that is used in the transduction of signals from the cell membrane to the nucleus. In plant cells, cytoskeletal elements form tracks for the movement of internal cellular organelles, such as the *cytoplasmic streaming* of chloroplasts, which can be observed by light microscopy. Work of the cytoskeleton is also necessary for the opening and closing of the stomata in plant leaves. The cytoskeleton consists of a variety of filamentlike proteins as well as proteins that serve as anchor points for filaments.

Origins of Mitochondria and Chloroplasts

The nucleus of the eukaryotic cell is not the only organelle that contains DNA and is enclosed by two membranes: The mitochondria of all cells and the chloroplasts of plant cells contain DNA and are surrounded by two membranes. The DNA of these organelles directs the synthesis of certain proteins that are necessary for the function of the organelles. This DNA is similar to DNA found in bacteria. Mitochondria and chloroplasts are thought to have evolved by a process known as *endosymbiosis*, in which bacteria were engulfed in the primitive eukaryotic cell, where they manufactured adenosine triphosphate (ATP), the nucleotide responsible for most of the chemical energy needed for metabolism, or captured energy from sunlight for the eukaryotic cell, establishing a mutually beneficial, or *symbiotic*, relationship with the eukaryotic cell.

Several lines of evidence support the endosymbiotic theory for the origin of mitochondria and chloroplasts. First, these organelles have areas of specialized cytoplasm called *nucleoids* that contain the DNA, much as bacteria do. The DNA molecules of the chloroplasts and mitochondria are circular and are associated with few proteins, like bacterial DNA, rather than linear and associated with histone proteins like most eukaryotic DNA. Chloroplasts and mitochondria also have ribosomes, structures that translate the genetic material into proteins, that are more similar to bacterial ribosomes than they are to eukaryotic ribosomes. These ribosomes are even sensitive to some of the same antibiotics, such as chloramphenicol and streptomycin, that inhibit the function of bacterial ribosomes.

Endomembrane System

The internal membranes of eukaryotic cells are dynamic, constantly changing structures. The concept of the *endomembrane system* describes all internal cytoplasmic membranes, with the exception of mitochondrial and plant plastid membranes, as a single continuum. In this model, the ER, generally the largest membrane system of eukaryotic cells, is the initial source of most other membranes. The ER is a network of interconnected, closed, membrane-bound *vesicles* that is contiguous with the nuclear envelope.

Vesicles from the ER carry proteins from the ER to the Golgi complex, fusing with its membranes. The Golgi complex can be described as a series of flattened membrane sacs, like a stack of hollow pancakes. The side closest to the nucleus receives vesicles from the ER, and the proteins inside these vesicles are processed and modified as they pass through the Golgi complex. Eventually, membrane vesicles containing the modified proteins will bud from the opposite surfaces of the Golgi complex and fuse with the cell membrane or the membranes of other organelles.

Michele Arduengo

See also: Cell theory; Cell-to-cell communication; Cell wall; Chloroplasts and other plastids; Chromatin; Cytoplasm; Cytoskeleton; Cytosol; DNA in plants; Endomembrane system and Golgi complex; Endoplasmic reticulum; *Eukarya*; Membrane structure; Microbodies; Mitochondria; Nuclear envelope; Nucleolus; Nucleoplasm; Nucleus; Oil bodies; Peroxisomes; Plasma membranes; Proteins and amino acids; Ribosomes; RNA; Vacuoles.

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EUROPEAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

European agricultural practices are affected by the policies of the European Union, in addition to global conditions which influence farming everywhere.

Agriculture in Europe goes back to classical times. The development first of the Greek city-states, then of the Roman Empire, created urban centers that required substantial amounts of food to be imported from as far away as Egypt. In the year 2000 European agriculture was dominated by two major groups: the European Union (EU), with fifteen member states, and those European states outside the EU. The EU, which began with the Common Market created by the Treaty of Rome, signed in 1957, initially comprised France, West Germany, Italy, Belgium, the Netherlands, and Luxembourg. By the year 2000 it had expanded to include Great Britain, Ireland, Denmark, Greece, Spain, Portugal, Finland, Sweden, and Austria.

Land and Workers

Only 11 percent of the land in the world (slightly more than 5 million square miles) is suitable for agriculture. Among the continents, Europe has the highest percentage of land suitable for farming: 36 percent. (In North America, the comparable figure is 22 percent.) Overall, 80 percent of the land in Europe is usable in some way, either as agricultural land or as forestland.

Smaller farms are more extensive in the southern countries of the EU than in the northern countries. Some 60 percent of all farms in the EU are less than 5 hectares (12.5 acres) in size. Many of these small farms are either part-time or subsistence farms. Farms that are more than 50 hectares in size (125 acres, a small farm by U.S. standards) constitute only 6 percent of all farms but produce most of the crops.

The percentage of the labor force employed in agriculture is small where the farms are large—in Great Britain, it is a mere 2 percent. In the rest of the EU, except for some of the more recent members, such as Greece, Spain, and Portugal, the percentages are all in the single digits. Where the farms are

Selected Agricultural Products of Europe

small, or in non-EU countries, without the EU's agricultural policy to push production up with high prices, the percentage of the labor force employed in agriculture is much higher. In Poland, 27 percent of the labor force is employed in agriculture; in Romania, 21 percent; and in the Ukraine, 19 percent.

Crops

Europe produces about 19 percent of the world's grains eaten by humans or livestock and almost 24 percent of the world's coarse grains (barley, rye, oats). Most of all these grains are grown in Russia. Half the world's potatoes are grown in Europe; the Russian Federation grows the largest share. Europe also grows half of the world's peas, with 40 percent produced in the Russian Federation. Three-quarters of the world's sugar beets are grown in Europe, Ukraine being the largest European producer. Rapeseed production has been increasing; Germany is its largest producer in Europe, followed closely by France. European production is a bit more than 17 percent of world production.

Europe grows 20 percent of the world's tomatoes, although the tomato is not a native European plant. Spain and Italy are the leading producers of tomatoes in Europe. Overall, Europe grows 16 percent of the world's vegetables, with Italy being the largest European producer, closely followed by the Russian Federation and Spain.

More than half of the world's grapes are grown in Europe. These grapes feed Europe's great wineries, which produce 70 percent of the world's wine, a substantial proportion of which is drunk in Europe, although it remains an important export item. Europe also produces nearly three-quarters of the world's hops, which go into the much-prized European beers. Europe grows more than half the world's olives, almost all of them in Italy, Spain, and Greece. These countries also produce about 60 percent of the world's olive oil.

Agricultural Revolution

Beginning in the 1970's, Europe underwent what has been called a new agricultural "revolution." Ownerships were consolidated, especially in Britain but also in France and Germany. As a result, owners of the larger holdings were able to invest in modern agricultural machinery. Now, 44 percent of the world's tractors are owned in Europe, mostly in France, Italy, and Poland. This has helped make European agriculture so productive that, according to the U.S. Department of Agriculture, Europe's best farms are as efficient as the best in the United States.

European farmers vastly increased their yields in the second half of the twentieth century. Britain's wheat output is up 60 percent from what it was immediately after World War II; the growth in output

Leading Agricultural Crops of European Countries with More than 20 Percent Arable Land

Country	*Products*	*Percent Arable Land*
Albania	Temperate-zone crops	21
Belarus	Grain, potatoes, vegetables	29
Belgium	Sugar beets, fresh vegetables, fruits, grain, tobacco	24
Bulgaria	Grain, oilseed, vegetables, fruits, tobacco	37
Denmark	Grain, potatoes, rapeseed, sugar beets	60
France	Wheat, cereals, sugar beets, potatoes, wine grapes	33
Germany	Potatoes, wheat, rye, barley, sugar beets, fruit, cabbage	—
Hungary	Wheat, corn, sunflower seed, potatoes, sugar beets	51
Italy	Fruits, vegetables, grapes, potatoes, sugar beets, soybeans, grain, olives	31
Liechtenstein	Wheat, barley, maize, potatoes	25
Luxembourg	Barley, oats, potatoes, wheat, fruit, wine grapes	24
Malta	Potatoes, cauliflower, grapes, wheat, barley, tomatoes, citrus, cut flowers, green peppers	38
Moldova	Vegetables, fruits, wine, grain, sugar beets, sunflower seed, tobacco	53
The Netherlands	Grains, potatoes, sugar beets, fruits, vegetables	27
Portugal	Grain, potatoes, olives, grapes	26
Romania	Corn, wheat, sugar beets, sunflower seed, potatoes, grapes	41
Russia	Grain, sugar beets, sunflower seed, vegetables, fruits	—
Spain	Grain, vegetables, olives, wine grapes, sugar beets, citrus	30
United Kingdom	Cereals, oilseed, potatoes, vegetables	25

Source: Data are from *The Time Almanac 2000*. Boston: Infoplease, 1999.

is nearly as great in France. In general, European agricultural productivity grew 5 percent a year between 1960 and 1999. Productivity grew much less in Eastern Europe than in Western Europe. This is partly because rainfall there varies so widely from year to year.

In 1979 the EU moved from being an importer of cereal grains to an exporter, as it did in 1975 for sugar and in 1976 for wine. Since 1960, the number of workers employed in agriculture has dropped by 50 percent, although the agricultural output remains the same or even higher. Authorities in Britain have estimated that farms there are at their most efficient when they employ no more than two or three people—a far cry from the hundreds of people who worked Europe's farms for subsistence wages in earlier centuries.

Irrigation and Drainage

Despite the generally favorable climate, Europe has 10 percent of the world's irrigated acreage. Most of that is in the Russian Federation, but Italy, Spain, and Romania also have significant amounts. A striking feature of European agriculture is the extent to which agricultural lands—some of them former wetlands—have been drained, to ensure uniform moisture for the crops being grown. In Finland, 91 percent of the agricultural land has been drained. Hungary has seen 70 percent of its land drained; the Netherlands, 65 percent; Britain, 60 percent; and Germany, 50 percent.

Environment

One factor that is assuming increasing influence over European agriculture is environmental concerns. The heavy use of fertilizers, pesticides, and herbicides has created damaging environmental conditions in some countries. The amount of cow manure generated in the Netherlands by its super-efficient dairy industry is more than the land of the entire country could absorb. The Dutch government subsidizes a company that composts some of this manure and sells it abroad as fertilizer for flowers. Sweden compensates farmers who reduce the runoff from their farms, a growing problem as the nitrogen content in water rises from fertilizer runoff. The EU has introduced a program to compensate those who set land aside for environmental protection, but more needs to be done to bring the EU's production levels closer to domestic demand, as well as to reduce the cost to consumers and taxpayers of the subsidies paid to farmers.

Organic Farming and Bioengineering

Several European countries, including the Czech Republic, France, and the United Kingdom, have introduced programs to encourage organic farming. At the beginning of the twenty-first century, however, a mere 2 percent of European crops were raised organically. Some scientists believe that environmental improvement could be generated if crops were developed that could ward off the insects that attack them, or that provide their own nitrogen, as the leguminous plants (peas and beans) do. Nevertheless, the European environmental movement has strongly opposed genetically modified foods, in part citing risks to health and the environment.

Nancy M. Gordon

See also: Biomes: types; European flora; Fruit crops; Vegetable crops; Wheat.

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EUROPEAN FLORA

Category: World regions

Flowering plants in Europe vary from those growing in mediterranean to alpine to Arctic regions.

Many of Europe's flowering plants are similar to those in North America, belonging to many of the same genera but to different species. Some of the most common North American flowering plants have cousins in Europe, but their location varies according to their latitude and altitude.

Climate and Soil

The most important factor determining the location of plants is climate. The continent of Europe ranges from the coastal areas on the northern shores of the Mediterranean Sea and Black Sea to the Arctic Ocean north of the Scandinavian peninsula. Although most of Europe is in the temperate climate zone, the areas that border the Mediterranean Sea are nearly all frost-free. By contrast, those parts of Europe that form the Scandinavian peninsula and northern Russia have frost-free periods each year of as little as two months. As a result, there is a south-to-north gradation of the flowering plants.

Moreover, mountains separate land that is also separated by latitude. The division is perhaps more marked than on other continents because the Alps run west to east, the highest peaks being without vegetation, whereas the mountains in North America run north to south. Since climate is strongly a function of latitude, there is, in effect, a double line separating the vegetation of the part of Europe along the Mediterranean from the part that is north of the Alps, instead of the gradual gradation that is more characteristic of North America.

Another factor in determining where flowering plants will be found is soil. The soil in the south of Europe tends to be sandy; the low annual rainfall at the Mediterranean shoreline means that what little rain there is flows rapidly through the soil, leaving relatively little for plants. In the north, much of the soil is permanently frozen, so only plants that can grow in a short period of time in the summer and survive many months of frozen life will be found there. In between these areas, European soils vary between those that make ideal growing conditions for flowering plants, the black earth soils of central Europe, and those that are thin layers over underlying rock or that trap water in the soil layers just below the surface, creating marshy conditions.

An east-to-west factor also influences which flowering plants are found where in Europe. The Atlantic coastline is warmed year-round by the Gulf Stream, so that normal temperatures in the parts of the continent touched by this current (including much of the western Baltic Sea) have warmer temperatures in winter than their latitudes would indicate. Southern Norway, for instance, is on the same latitude as Greenland, most of which is covered with ice and snow throughout the year; but many plants, including agricultural crops, grow in southern Norway because of the Gulf Stream. Because rainfall is high, these parts of Europe tend to be wetter and cooler in summer than other parts of the world at the same latitudes. Europe has been occupied by humans for such a long period of time that there are almost no parts of Europe where the vegetation has been unaffected by humans. There are virtually no "virgin forests" in Europe.

Forests

Most of Europe's trees are similar to those in North America, but these are related by genus and are not members of the same species. This is true of oaks, maples, ashes, elms, birches, beeches, chestnuts, walnuts, apples, and hornbeams as well as conifers. Some of the native tree species of Europe have been brought to North America and have become a part of the American forest. The sycamore, for example, is the same species in North America as in Europe. The sycamore is a long-lived tree; some sycamores that were planted in North America during the colonial era are still alive. The mountain ash, with its bright orange berries, is another tree from Europe (where it is known as the rowan) that has emigrated to North America. The horse chestnut is yet another tree native to Europe that has long been settled in North America.

Among the evergreens, the Norway spruce has been widely planted and now seeds itself in North America. The Scots pine has been widely planted in North America; many Christmas trees sold every year in the United States are Scots pine. The European larch has become popular with the U.S. forest industry because it is suited to *reforestation* after *clear-cutting*.

Some North American species have made the opposite journey: Much of Scotland has been reforested with the Sitka spruce, a native of the Pacific

PhotoDisc

The raspberry bush found throughout eastern North America is a European native.

Northwest. Another native American evergreen that has made the trip to Europe is the white pine, known in Europe as the Weymouth pine. Plantations of white pine have been set up all over Europe, because Europe did not have a soft pine, and the wood of the white pine is easily worked.

Apple Trees

One important European tree that has had a large impact on the United States is the apple. The apple tree that produces the familiar fruit appears to have originated in southern Russia and made its way throughout Europe. Many apple varieties were cultivated by the Romans. The English and other European settlers of North America, finding only crab apples (North America's only native apple) when they arrived, imported familiar apple varieties from Europe. Orchards were among the first things the English settlers of New England planted in Massachusetts Bay.

Shrubs

Many European shrubs have become immigrants too. The box and holly are much prized for foundation planting, and the privet makes a neat hedge. The buckthorn bush has also made the journey, although it is less widely sold at nurseries. The juniper in Europe is the same as the juniper in North America, but the raspberry is not. Currants and gooseberries are European shrubs that have been widely transplanted, although one of the European currant varieties harbors a disease that affects the North American white pine. By contrast, the cranberry is a North American shrub that has lately been transplanted to Europe. North American blueberries are quite different from the related species in Europe.

The raspberry bush found throughout eastern North America is a European native. Because birds are frequent consumers of its fruit, it has spread well beyond the beds where it was originally planted. The heather that covers many of the hills of northern Europe, where it is a native, has become popular with American florists as a filler for bouquets. One of the most common landscape shrubs in the United States, the lilac, is of European origin, but it was among the earliest to make the trip to North America. Today the foundations of old colonial homesteads can often be located because, although the house is gone, the lilacs that once surrounded it survive.

Herbs

Herbs or wildflowers have spread across the continents much as shrubs have. Many of the most common North American wildflowers, such as the dandelion, are immigrants. So is the wild strawberry as well as the plantain that infests lawns. Many wildflowers are both European and American in origin, although in most cases the species differ. Among them are the violets, some of the cinquefoils, many buttercup varieties, and the marsh marigold. The clovers that are so familiar to Americans are all imports—the white clover, the red clover, and the alsike clover—are all natives of Europe.

Several genera of grasses are found on both continents: Kentucky bluegrass is really the European smooth meadow grass. Annual rye grass, often used to green up new lawns quickly, is a European import, as is red fescue, common in hayfields. Timothy hay, cultivated in the United States as feed hay, is also an import from Europe.

The marshes and swamps of Europe are populated mostly by indigenous plants. Large numbers of sedges that are native to Europe are grouped together in the *Carex* genus and can be found in Europe's wetlands. Wetlands may have more "virgin" plant communities than anywhere else in Europe, because they were unsuitable for cultivation. Europeans have drained many of the continent's wetlands to convert the land to farmland; the most notable case is the Netherlands, where land has been reclaimed from the sea so that crops can be grown on it. Among the shrubs, Europe's wetlands, like those in North America, harbor alders, but Europe's are different species from those found in North America. The same can be said for willows, which grow well where ample moisture is available.

Commercial Plants

Ever since the first agricultural revolution, ten thousand years ago, humans have adapted plants to their needs. This is especially true for the grains, most of which originated in the Middle East. Wheat, oats, barley, rye, and others that could become food for humans were altered from their original form by careful plant breeding. This is also true for the flowers that are the staple of the florists' trade—roses, chrysanthemums, begonias, and carnations are all adaptations of wild plants.

Tulips are widely known flowers that originated in Eurasia from Austria and Italy eastward to Japan, with two-thirds of them native to the eastern Mediterranean and the southeastern parts of Russia. The Dutch cultivated tulips beginning in the 1500's and made them into a staple export. The grape hyacinth is a European native, as is the full-size hyacinth. Crocuses are natives of the Mediterranean basin.

Olive Trees

One native flowering plant of Europe deserves special mention: the olive tree. Having originated along the shores of the Mediterranean Sea, it has been cultivated and modified to increase the size of its fruit since ancient times. It remains an important agricultural resource for Mediterranean nations, especially Greece, Italy, France, and Spain. The Spanish conquerors of Central America carried the olive to the new world, and it was successfully introduced into California.

The Maquis

Uncultivated olive trees form part of the vegetation of the maquis, an area in France and Spain where the native olive grows with the carob, a small native tree like the olive, and the holm oak. Most of these trees are so stunted by the impoverished soil, heavily eroded over the centuries, that they are little more than bushes. There are also a variety of shrubs characteristics of the maquis, such as a clematis vine, the Mediterranean buckthorn, and the common myrtle. A local variety of grass covers the ground between the trees and shurbs. Similar communities can also be found in Greece, where they provide grazing for goats.

Vines

The grapevine has been of commercial importance for centuries. The Greeks and Romans raised grapes and made wine from them. The wine grape appears to have originated in the Mediterranean basin, but many varieties of grape have developed. European varieties have been transplanted to North America, and the process has also worked in reverse. In the late nineteenth century, when a devastating disease known as *phylloxera* ravaged French vineyards, American grapevine rootstock was imported into France, and the French vines grafted onto it, because the American rootstock had shown itself less subject to the disease.

Another vine is the ivy. There are ivies native to almost every continent, but European ivy, sometimes called English ivy, has spread far beyond its native ground. It is popular as a wall covering and is frequently seen in gardens.

Nancy M. Gordon

See also: Arctic tundra; European agriculture; Forests; Mediterranean scrub.

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EUTROPHICATION

Categories: Algae; diseases and conditions; environmental issues; microorganisms; poisonous, toxic, and invasive plants; pollution; water-related life

The overenrichment of water by nutrients, eutrophication causes excessive plant growth and stagnation, which leads to the death of fish and other aquatic life.

The word "eutrophic" comes from the Greek *eu*, which means "good" or "well," and *trophikos*, which means " food" or "nutrition." Eutrophic waters are well-nourished and rich in nutrients; they support abundant life. Eutrophication refers to a condition in aquatic systems (ponds, lakes, and streams) in which nutrients are so abundant that plants and algae grow uncontrollably and become a problem. The plants die and decompose, and the water becomes stagnant. This ultimately causes the death of other aquatic animals, particularly fish, that cannot tolerate such conditions. Eutrophication is a major problem in watersheds and waterways such as the Great Lakes and Chesapeake Bay that are surrounded by urban populations.

The stagnation that occurs during eutrophication is attributable to the activity of microorganisms growing on the dead and dying plant material in water. As they decompose the plant material, microbes consume oxygen faster than it can be resupplied by the atmosphere. Fish, which need oxygen in the water to breathe, become starved for oxygen and suffocate. In addition, noxious gases such as hydrogen sulfide (H_2S) can be released during the decay of the plant material. The hallmark of a eutrophic environment is one that is plant-filled, littered with dead aquatic life, and smelly.

Eutrophication is actually a natural process that occurs as lakes age and fill with sediment, as deltas form, and as rivers seek new channels. The main concern with eutrophication in natural resource conservation is that human activity can accelerate the process and can cause it to occur in previously clean but nutrient-poor water. This is sometimes referred to as *cultural eutrophication*. For example, there is great concern with eutrophication in Lake Tahoe. Much of Lake Tahoe's appeal is its crystal-clear water. Unfortunately, development around Lake Tahoe is causing excess nutrients to flow into the lake and damaging the very thing that attracts people to the lake.

Roles of Nitrogen and Phosphorus

Nitrogen and phosphorus are the key nutrients involved in eutrophication, although silicon, calcium, iron, potassium, and manganese can be important. Nitrogen and phosphorus are essential in plant and animal growth. Nitrogen compounds are used in the synthesis of amino acids and proteins, whereas phosphate is found in nucleic acids and phospholipids. Nitrogen and phosphorus are usually in limited supply in lakes and rivers. Plants and animals get these nutrients through natural recycling in the water column and sediments and during seasonal variations, as algae and animals decompose, fall to the lower depths, and release their nutrients to be reused by other organisms in the ecosystem. A limited supply of nutrients—as well as variations in optimal temperature and light conditions—prevents any one species of plants or animals from dominating a water ecosystem.

Effects of Excess Nutrients

Although nutrient enrichment can have detrimental effects on a water system, an increased supply of nitrogen and phosphorus can have an initial positive effect on water productivity. Much like adding fertilizer to a lawn, increases in nutrients in a lake, river, or ocean cause it to be more productive by stimulating plant and animal growth in the entire food chain. *Phytoplankton*—microscopic algae that grow on the surface of sunlit waters—take up nutrients directly and are able to proliferate. Through photosynthesis, these primary producers synthesize organic molecules that are used by other members of the ecosystem. Increased algal growth thus stimulates the growth of zooplankton—microscopic animals that feed on algae and bacteria—as well as macroinvertebrates, fish, and other animals and plants in the food web. Indeed, many fisheries have benefited from lakes and oceans that are productive.

When enough nutrients are added to a lake or river to disrupt the natural balance of nutrient cycling, however, the excess nutrients effectively become *pollutants*. The major problem is that excess nutrients encourage profuse growth of algae and rooted aquatic weeds, species that can quickly take advantage of favorable growth conditions at the expense of slower-growing species. Algae convert carbon dioxide and water into organic molecules during photosynthesis, a process that produces oxygen. When large blooms of algae and other surface plants die, however, they sink to the bottom of the water to decompose, a process that consumes large amounts of oxygen. The net effect of increased algae production, therefore, is depletion of dissolved oxygen in the water, especially during midsummer.

Reduced oxygen levels (called *hypoxia*) can have dire consequences for lakes and rivers that support fish and bottom-dwelling animals. Oxygen depletion is greatest in the deep bottom layers of water, because gases from the oxygen-rich surface cannot readily mix with the lower layers. During summer and winter, oxygen depletion in eutrophic waters can cause massive fish kills. In extreme cases of eutrophication, the complete depletion of oxygen (*anoxia*) occurs, leading to ecosystem crashes and irreversible damage to plant and animal life. Oxygen depletion also favors the growth of anaerobic bacteria, which produce hydrogen sulfide and methane gases, leading to poor water quality and taste.

Excessive algal and plant growth has other negative effects on a water system. Algae and plants at the surface block out sunlight to plants and animals at the lower depths. Loss of aquatic plants can affect fish-spawning areas and encourage soil erosion from shores and banks.

Eutrophication often leads to loss of diversity in a water system, as high nutrient conditions favor plants and animals that are opportunistic and short-lived. Native sea grasses and delicate sea plants often are replaced by hardier weeds and rooted plants. Carp, catfish, and bluegill fish species replace more valuable coldwater species such as trout.

Thick algal growth also increases water turbidity and gives lakes and ponds an unpleasant pea-soup appearance. As algae die and decay, they wash up on shores in stinking, foamy mats.

Algal blooms of unfavorable species can produce toxins that are harmful to fish, animals, and humans. These toxins can accumulate in shellfish and have been known to cause death if eaten by humans. So-called red tides and brown tides are caused by the proliferation of unusual forms of algae, which give water a reddish or tealike appearance and in some cases produce harmful chemicals or neurotoxins.

Assessing Eutrophication

While eutrophication effects are generally caused by nutrient enrichment of a water system, not all cases of nutrient accumulation lead to increased productivity. Overall productivity is based on other factors in the water system, such as grazing pressure on phytoplankton, the presence of other chemicals or pollutants, and the physical features of a body of water. Eutrophication occurs mainly in enclosed areas such as estuaries, bays, lakes, and ponds, where water exchange and mixing are limited. Rivers and coastal areas with abundant flushing generally show less phytoplankton growth from nutrient enrichment because their waters run faster and mix more frequently. On the other hand, activities that stir up nutrient-rich sediments from the bottom, such as development along coastal waters, recreational activities, dredging, and storms, can worsen eutrophication processes.

The nutrient status of a lake or water system is often used as a measure of the extent of eutrophication. For example, lakes are often classified as *oligotrophic* (nutrient-poor), *eutrophic* (nutrient-rich), or *mesotrophic* (moderate in nutrients) based on the concentrations of nutrients and the physical appearance of the lake. Oligotrophic lakes are deep, clear, and unproductive, with little phytoplankton growth, few aquatic rooted plants, and high amounts of dissolved oxygen. In contrast, eutrophic lakes are usually shallow and highly productive, with extensive aquatic plants and sedimentation. These lakes have high nutrient levels, low amounts of dissolved oxygen, and high sediment accumulation on the lake bottom. They often show sudden blooms of green or blue-green algae (or blue-green bacteria, cyanobacteria) and support only warm-water fish species.

Mesotrophic lakes show characteristics in between those of unproductive oligotrophic waters and highly productive eutrophic waters. Mesotrophic lakes have moderate nutrient levels and phytoplankton growth and some sediment accumulation; they support primarily warm-water fish species. As a lake naturally ages over hundreds of years, it usually (but not always) gets progressively more eutrophic, as sediments fill in and eventually convert it to marsh or dryland. Nutrient enrichment from human sources can speed this process greatly.

Limiting Damage

The negative effects of eutrophication can be reduced by limiting the amount of nutrients—in most cases nitrogen and phosphorus—from entering a water system. Nutrients can enter water bodies through streams, rivers, groundwater flow, direct precipitation, and dumping and as particulate fallout from the atmosphere. While natural processes of eutrophication are virtually impossible to control, eutrophication from human activity can be reduced or reversed.

Phosphorus enrichment into water systems occurs primarily as the result of wastewater drainage into a lake, river, or ocean. Phosphate is common in industrial and domestic detergents and cleaning agents. Mining along water systems is also a major source of phosphorus. When phosphorus enters a water system, it generally accumulates in the sediments. Storms and upwelling can stir up sediments, releasing phosphorus. Treatment of wastewater to remove phosphates and the reduction of phosphates in detergents have helped to reduce phosphorus enrichment of water systems.

Nitrogen enrichment is harder to control; it is present in many forms, as ammonium, nitrates, nitrites, and nitrogen gas. The major sources of nitrogen eutrophication are synthetic fertilizers, animal wastes, and agricultural runoff. Some algae species can also fix atmospheric nitrogen directly, converting it to biologically usable forms of nitrogen. Since the atmosphere contains about 78 percent nitrogen, this can be a major source of nitrogen enrichment in waters that already have significant algal populations.

Efforts to control nitrogen and phosphorus levels have examined both point and nonpoint sources of nutrient loading. Point sources are concentrated, identifiable sites of nutrients that include municipal sewage-treatment plants, feed lots, food-processing plants, pulp mills, laundry detergents, and domestic cleaning agents. Nonpoint, or diffuse, sources of nutrients include surface runoff from rainwater, fertilizer from agricultural land and lawns, eroded soil, and roadways.

Linda Hart and Mark S. Coyne

See also: Algae; Dinoflagellates; Environmental biotechnology; Phytoplankton.

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EVOLUTION: CONVERGENT AND DIVERGENT

Categories: Ecosystems; evolution; paleobotany

Some of the most dramatic examples of natural selection are the result of adaptation in response to stressful climatic conditions. Such selection may cause unrelated species to resemble one another in appearance and function, a phenomenon known as convergence. In other situations, subpopulations of a single species may split into separate species as the result of natural selection. Such divergence is best seen on isolated islands.

Convergent Evolution

Convergent evolution occurs when organisms from different evolutionary lineages evolve similar adaptations to similar environmental conditions. This can happen even when the organisms are widely separated geographically. A classic example of convergent evolution occurred with *Cactaceae*, the cactus family, of the Americas and with the euphorbs, or *Euphorbiaceae*, the spurge family of South Africa, both of which have evolved *succulent* (water-storing) stems in response to desert conditions.

The most primitive cacti are vinelike, tropical plants of the genus *Pereskia*. These cacti, which grow on the islands of the West Indies and in tropical Central and South America, have somewhat woody stems and broad, flat leaves. As deserts developed in North and South America, members of the cactus family began to undergo selection for features that were adaptive to hotter, dryer conditions.

The stems became greatly enlarged and succulent as extensive water-storage tissues formed in the pith or cortex. The leaves became much reduced. In some cactus species, such as the common prickly pear (*Opuntia*), the leaves are small, cylindrical pegs that shrivel and fall off after a month or so of growth. In most cacti, only the leaf base forms and remains as a small hump of tissue associated with an axillary bud. In some cacti this hump is enlarged and is known as a tubercle. Axillary buds in cacti are highly specialized and are known as areoles. The "leaves" of an areole are reduced to one or more spines. Particularly in columnar cacti, the areoles are arranged in longitudinal rows along a multiple-ridged stem.

With the possible exception of the genus *Rhipsalis*, which has one species reported to occur naturally in Africa, all cacti are native to the Americas. As deserts formed in Africa, Eurasia, and Australia, different plant families evolved adaptations similar to those in cacti. The most notable examples are the candelabra euphorbs of South Africa. Desert-dwelling members of the *Euphorbiaceae* frequently have succulent, ridged, cylindrical stems resembling those of cacti. The leaves are typically reduced in size and are present only during the rainy season. They are arranged in rows along each of several ridges of the stem. Associated with each leaf are one or two spines. As a result, when the leaves shrivel and fall off during the dry season, a spiny, cactuslike stem remains.

The succulent euphorbs of Africa take on all of the forms characteristic of American cacti, from pincushions and barrels to branched and unbranched columns. Other plant families that show convergence with the cacti, in having succulent stems or leaves, are the stem succulents of the milkweed family, *Asclepiadaceae*; sunflower family, *Asteridaceae*; stonecrop family, *Crassulaceae*; purslane family, *Portulacaceae*; grape family, *Vitaceae*; leaf succulents of the ice plant family, *Aizoaceae*; daffodil family, *Amaryllidaceae*; pineapple family, *Bromeliaceae*; geranium family, *Geraniaceae*; and lily family, *Liliaceae*.

Divergent Evolution

Some of the most famous examples of divergent evolution have occurred in the Galápagos Islands. The Galápagos comprise fourteen volcanic islands located about 600 miles west of South America. A total of 543 species of vascular plants are found on the islands, 231 of which are endemic, found nowhere else on earth. Seeds of various species arrived on the islands by floating in the air or on the water or being carried by birds or humans.

With few competitors and many different open habitats, variant forms of each species could adapt to specific conditions, a process known as *adaptive radiation*. Those forms of a species best suited to each particular habitat were continually selected for and produced progeny in that habitat. Over time, this natural selection resulted in multiple new species sharing the same ancestor. The best examples of divergent evolution in the Galápagos have occurred in the *Cactaceae* and *Euphorbiaceae*. Eighteen species and variety of cacti are found on the islands, and all are endemic. Of the twenty-seven species and varieties of euphorbs, twenty are endemic.

Image Not Available

An interesting example of the outcome of divergent evolution can be seen in the artificial selection of different cultivars (cultivated varieties) in the genus *Brassica*. The scrubby Eurasian weed colewort (*Brassica oleracea*) is the ancestor of broccoli, brussels sprouts, cabbage, cauliflower, kale, and kohlrabi (rutabaga). All of these vegetables are considered to belong to the same species, but since the origin of agriculture, each has been selected for a specific form that is now recognized as a distinct crop.

Marshall D. Sundberg

See also: Adaptations; Adaptive radiation; Cacti and succulents; Coevolution; Deserts; Plant domestication and breeding; Selection.

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EVOLUTION: GRADUALISM VS. PUNCTUATED EQUILIBRIUM

Categories: Evolution; paleobotany

The gradualism model of evolution proposes that a progenitor species gradually gave rise to many new species, with no special mechanisms accounting for the origins of new genera or groups of higher classifications—only the accumulation of many small changes in the frequencies of alleles in gene pools. The punctuated equilibrium model of evolutionary change supposes long periods of little or no change interspersed with short intervals of rapid change.

Charles Darwin, author of *On the Origin of Species by Means of Natural Selection* (1859), believed that morphological change was inevitable and proceeded slowly, encompassing slight, successive, and gradual changes within lineages. Speciation, therefore, was the result of the gradual accumulation of changes within ancestral populations over time, ultimately leading to the formation of recognizably new and different species. According to Darwin, sudden, large-scale changes were improbable or impossible—an idea epitomized by the phrase *Natura non facit saltum*, or "Nature never makes leaps." Darwin's concept of the slow and gradual transformation of a species' entire ancestral population into distinct descendant species over time has been termed "phyletic gradualism," or *anagenesis*.

If true, the expectation of anagenic transformation leads to the supposition that the fossil record for any lineage should contain an "inconceivably great" number of intermediate forms. Darwin, however, realized that the fossil record is, in fact, not littered with an "interminable" and "enormous" number of intermediate forms. Darwin's solution to this problem with his theory was presented in a chapter of his book *On the Origin of Species by Means of Natural Selection* titled "On the Imperfection of the Geological Record." Here Darwin persuasively argued that the paleontological record of the past is extremely imperfect because of degradation of fossiliferous deposits and differential rates of deposition and fossilization among lineages. He also noted that, on geologic time scales, persistent, long-lived and widespread species are more likely to appear in the fossil record than short-lived species or species confined to narrow geographic ranges.

The "Modern Synthesis," Microevolution, and Species Formation

In the 1930's and 1940's Darwin's theory of natural selection was melded with then-current knowledge of genetics, heritability, and mathematics to produce the *modern synthesis theory of evolution*. Under this paradigm, evolution came to be defined as a change in gene frequency over time. The microevolutionary processes of mutation, migration, random genetic drift, and natural selection were recognized as the primary mechanisms that alter gene frequencies.

At this time other authorities began to carefully consider the mechanism(s) by which species arise. One particular mode of species formation, and one supported by considerable empirical evidence, is termed the *allopatric model of speciation*. Allopatric species are formed as subpopulations of a more widespread ancestral species become geographically isolated and, in time, reproductively isolated from one another.

Paleospecies and Punctuated Equilibria

These ideas, particularly those of gradual, inevitable change by microevolutionary processes and the imperfection of the fossil record, and were accepted by paleontologists for more than a century. However, in 1972 Niles Eldredge and Stephen J. Gould published a paper in which paleontologists were challenged to examine fossil sequences (and gaps) more objectively. Eldredge and Gould drew three important conclusions about the fossil record. First, some gaps in the fossil record are real and cannot be attributed to other factors; gradual series of transitional forms do occur, but they are extremely rare. Second, paleospecies often persist for millions of years without substantial morphological change. Third, they recognized that paleospecies found in older strata are sometimes rapidly replaced by morphologically different taxa in younger deposits.

Thus, a literal interpretation of the fossil record requires the acknowledgment of short, rapid bursts of evolution. That is, within the paleontological history of a lineage, morphological stasis is occasionally interrupted by near-instantaneous (in geological time) formation of morphologically different species. If these gaps are real, how are they to be explained? How is one species suddenly (in geologic time) replaced by a morphologically modified form in the fossil record?

To answer these questions, Eldredge and Gould developed the theory of *punctuated equilibria* that, in essence, fused a literal interpretation of the fossil record with the mode of speciation most often observed in extant populations (such as the allopatric model of speciation).

Eldredge and Gould's theory of punctuated equilibria is based on the following postulates or observations. First, speciation typically occurs via allopatric speciation. Second, the origin of descendant species is, in geological time, rapid and occurs in a limited geographic area. Third, most adaptive change occurs at the time of speciation. Fourth, speciation is typically followed by long periods of morphological stasis, particularly within large, widespread species. Fifth, the abrupt appearance of a new species within the range of the ancestral species is a result of ecological succession, immigration, or competition. Finally, apparent adaptive trends (such as macroevolutionary trends) observed in the fossil record are the result of species selection within lineages over time.

The authors reasoned that as long as a species is capable of successfully exploiting its habitat, adaptations that originated at the time of speciation are unlikely to be altered, and morphological stasis is the result. Thus, in terms of the geologic time scale, most species seem to persist unchanged over long periods of time. The origin of a new species, its growth in numbers, and the extension of its geographic range are, therefore, determined by reproductive and ecological characteristics. In short, under the punctuated equilibrium model new species can be successful if they are sufficiently distinct in their habitat requirements and if they are able to compete with or outcompete close relatives should they come into contact with one another. This theory of speciation and diffential reproduction and survival of species produces well-documented, large-scale evolutionary patterns or "macroevolutionary" trends.

Punctuated Equlibria and Plants

The theory of punctuated equilibria was constructed based on studies of animal fossils; unfortunately, no mention is made of plants. The theory has therefore received less attention from paleobotanists. It is true that in extant plants rapid changes in physiological or morphological characteristics associated with speciation are not uncommon. However, such phenomena are rarely documented in the fossil record.

For example, interspecific hybridization or polyploidization may (almost instantaneously) form new, reproductively isolated species whose niches may differ from those of their immediate progenitors. Thus, in plants, rapid species formation is empirically known. Stasis is also known from the fossil records of some plant lineages. For example, in terms of floral structure, extant members of the *Loraceae*, *Chloranthaceae*, *Nymphaceae*, and the magnoliids scarcely differ from their early- to mid-Cretaceous ancestors. Morphological stasis is also observed in gingkos, *Metasequoia*, cycads, lycopods, sphenopsids, and ferns as well as the genus *Pinus*, which arose in the Jurassic. Rapid radiations are also documented in the plant fossil record, as occurred after the rise of angiosperms during the early Cretaceous. Thus, the plant fossil record provides clear evidence for stasis in some lineages and rapid diversification in others. Despite these observations, paleobotanical examples of lineages whose evolution fits the predictions of the punctuated equilibrium model are few.

J. Craig Bailey

See also: Adaptive radiation; Cladistics; Competition; Evolution: convergent and divergent; Evolution of plants; Fossil plants; Genetics: post-Mendelian; Paleobotany; Population genetics; Species and speciation; Succession.

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EVOLUTION: HISTORICAL PERSPECTIVE

Categories: Classification and systematics; evolution; history of plant science; paleobotany

Evolution is the theory that biological species undergo sufficient change with time to give rise to new species.

The concept of evolution has ancient roots. Anaximander suggested in the sixth century B.C.E. that life had originated in the seas and that humans had evolved from fish. Empedocles (c. 450 B.C.E.) and Lucretius (c. 96-55 B.C.E.), in a sense, grasped the concepts of adaptation and natural selection. They taught that bodies had originally formed from the random combination of parts, but that only harmoniously functioning combinations could survive and reproduce. Lucretius even said that the mythical centaur, half horse and half human, could never have existed because the human teeth and stomach would be incapable of chewing and digesting the kind of grassy food needed to nourish the horse's body.

Early Biological Theory

For two thousand years, however, evolution was considered an impossibility. The theory of forms (also called his *theory of ideas*) proposed by Plato (c. 428-348 B.C.E.) gave rise to the notion that each species had an unchanging "essence" incapable of evolutionary change. As a result, most scientists from Aristotle (384-322 B.C.E.) to Carolus Linnaeus (1707-1778) insisted upon the *immutability of species*.

Many of these scientists tried to arrange all species in a single linear sequence known as the *scale of being* (also called the great chain of being or *scala naturae*), a concept supported well into the nineteenth century by many philosophers and theologians as well. The sequence in this scale of being was usually interpreted as a static "ladder of perfection" in God's creation, arranged from higher to lower forms. The scale had to be continuous, for any gap would detract from the perfection of God's creation. Much exploration was devoted to searching for *missing links* in the chain, but it was generally agreed that the entire system was static and incapable of evolutionary change. Pierre-Louis Moreau de Maupertuis and Jean-Baptiste Lamarck (1744-1829) were among the scientists who tried to reinterpret the scale of being as an evolutionary sequence, but this single-sequence idea was later replaced by the concept of branching evolution proposed by Charles Darwin (1809-1882). Georges Cuvier (1769-1832) finally showed that the major groups of animals had such strikingly different anatomical structures that no possible scale of being could connect them all; the idea of a scale of being lost most of its scientific support as a result.

The theory that new biological species could arise from changes in existing species was not readily accepted at first. Linnaeus and other classical biologists emphasized the immutability of species under the Platonic-Aristotelian concept of *essentialism*. Those who believed in the concept of evolution realized that no such idea could gain acceptance until a suitable mechanism of evolution could be found. Many possible mechanisms were therefore proposed. Étienne Geoffroy Saint-Hilaire (1805-1861) proposed that the environment directly induced physiological changes, which he thought would be inherited, a theory now known as *Geoffroyism*. Lamarck proposed that there was an overall linear ascent of the scale of being but that organisms could also adapt to local environments by voluntary exercise, which would strengthen the organs used; unused organs would deteriorate. He thought that the characteristics acquired by use and disuse would be passed on to later generations, but the inheritance of acquired characteristics was later disproved. Central to both these explanations was the concept of adaptation, or the possession by organisms of characteristics that suit them to their environments or to their ways of life. In eighteenth century England, the Reverend William Paley (1743-1805) and his numerous scientific supporters believed that such adaptations could be explained only by the action of an omnipotent, benevolent God. In criticizing Lamarck, the supporters of Paley pointed out that birds migrated toward warmer climates before winter set in and that the heart of the human fetus had features that anticipated the changes of function that take place at birth. No amount of use and disuse could explain these cases of anticipation, they claimed; only an omniscient God who could foretell future events could have designed things with their future utility in mind.

Darwin's Theory

The nineteenth century witnessed a number of books asserting that living species had evolved from earlier ones. Before 1859, these works were often more geological than biological in content. Most successful among them was the anonymously published *Vestiges of the Natural History of Creation* (1844), written by Robert Chambers (1802-1871). Books of this genre sold well but contained many flaws. They proposed no mechanism to account for evolutionary change. They supported the outmoded concept of a scale of being, often as a single sequence of evolutionary "progress." In geology, they supported the outmoded theory of *catastrophism*, an idea that the history of the earth had been characterized by great cataclysmic upheavals. From 1830 on, however, that theory was being replaced by the modern theory of *uniformitarianism*, championed by Charles Lyell (1797-1875). Charles Darwin read these books and knew their faults, especially their lack of a mechanism that was compatible with Lyell's geology. In his own work, Darwin carefully tried to avoid the shortcomings of these books.

Darwin brought about the greatest revolution in biological thought by proposing both a theory of branching evolution and a mechanism of natural selection to explain how it occurred. Much of Darwin's evidence was gathered during his voyage around the world aboard HMS *Beagle* between 1831 and 1836. Darwin's stop in the Galápagos Islands and his study of tortoises and finchlike birds on these islands is usually credited with convincing him that evolution was a branching process and that *adaptation* to local environments was an essential part of the evolutionary process. Adaptation, he later concluded, came about through *natural selection*, a process that killed the maladapted variations and allowed only the well-adapted ones to survive and pass on their hereditary traits. After returning to England from his voyage, Darwin raised pigeons, consulted with various animal breeders about changes in domestic breeds, and investigated other phenomena that later enabled him to demonstrate natural selection and its power to produce evolutionary change.

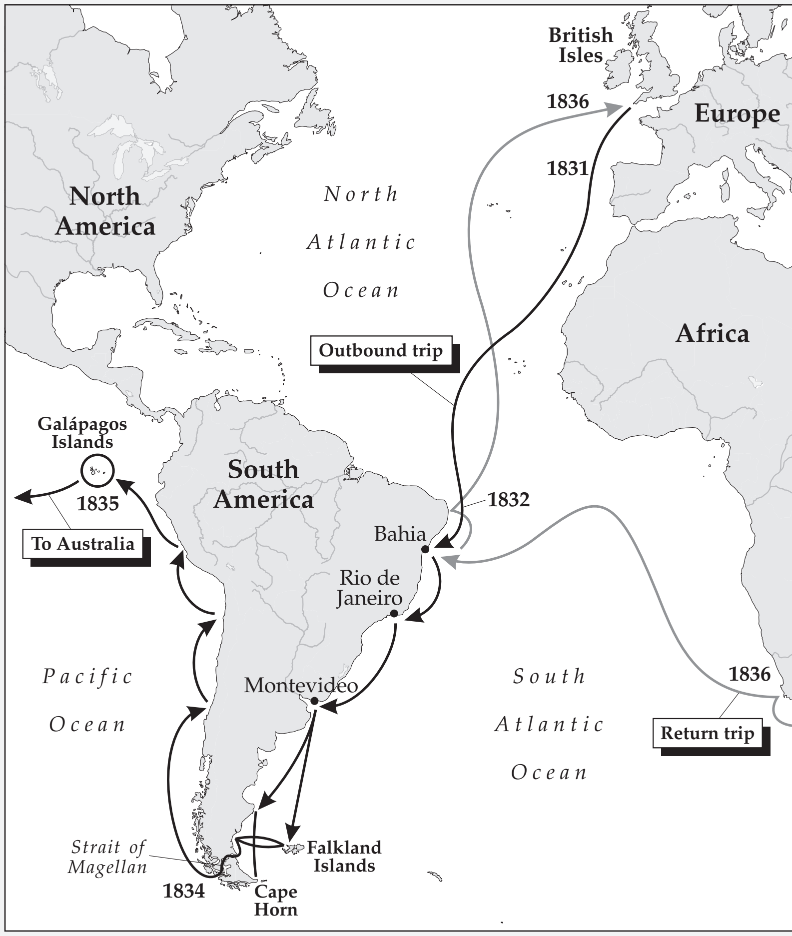
Darwin delayed the publication of his book for seventeen years after he wrote his first manuscript version. He might have waited even longer, except that his hand was forced. From the East Indies, another British scientist, Alfred Russel Wallace (1823-1913), had written a description of an identical the-

Charles Darwin and the *Beagle*

In 1831, a twenty-two-year-old Charles Darwin, who had been studying for the ministry at Cambridge, by luck was offered a position as naturalist on the ship HMS *Beagle*, which was about to embark on a round-the-world voyage of exploration. His domineering father was against the trip at first, but he finally relented. The expedition would turn the young man into a scientist. Over the next five years, Darwin recorded hundreds of details about plants and animals and began to notice some consistent patterns. His work led him to develop new ideas about what causes variations in different plant and animal species:

> [The] preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest. . . . slight modifications, which in any way favoured the individuals of any species, by better adapting them to their altered conditions, would tend to be preserved. . . .
> —*On the Origin of Species by Means of Natural Selection*, 1859

Until Darwin and such colleagues as Alfred Russel Wallace, the "fixity" or unchangingness of species had been accepted as fact, and the appearance over time of new species remained a mystery. Darwin's lucky trip laid the foundation for today's understanding of life and its diversity.



ory and submitted it to Darwin for his comments. Darwin showed Wallace's letter to Lyell, who urged that both Darwin's and Wallace's contributions be published, along with documented evidence showing that both had arrived at the same ideas independently. Darwin's great book, *On the Origin of Species by Means of Natural Selection*, was published in 1859, and it quickly won most of the scientific community to a support of the concept of branching evolution. In his later years, Darwin also published *The Descent of Man and Selection in Relation to Sex* (1871), in which he outlined his theory of *sexual selection*. According to this theory, the agent that determines the composition of the next generation may often be the opposite sex. An organism may be well adapted to live, but unless it can mate and leave offspring, it will not contribute to the next or to future generations.

After Darwin

In the early 1900's, the rise of Mendelian genetics (named for botanist Gregor Mendel, 1822-1884) initially resulted in challenges to Darwinism. Hugo de Vries (1848-1935) proposed that evolution occurred by *random mutations*, which were not necessarily adaptive. This idea was subsequently rejected, and

Mendelian genetics was reconciled with Darwinism during the period from 1930 to 1942. According to this modern synthetic theory of evolution, mutations initially occur at random, but natural selection eliminates most of them and alters the proportions among those that survive. Over many generations, the accumulation of heritable traits produces the kind of adaptive change that Darwin and others had described. The process of branching evolution through *speciation* is also an important part of the modern synthesis.

The branching of the evolutionary tree has resulted in the proliferation of species from the common ancestor of each group, a process called *adaptive radiation*. Ultimately, all species are believed to have descended from a single common ancestor. Because of the branching nature of the evolutionary process, no one evolutionary sequence can be singled out as representing any overall trend; rather, there have been different trends in different groups. Evolution is also an opportunistic process, in the sense that it follows the path of least resistance in each case. Instead of moving in straight lines toward a predetermined goal, evolving lineages often trace meandering or circuitous paths in which each change represents a momentary increase in adaptation. Species that cannot adapt to changing conditions die out and become extinct.

Evolutionary biology is itself the context into which all the other biological sciences fit. Other biologists, including physiologists and molecular biologists, study how certain processes work, but it is evolutionists who study the reasons why these processes came to work in one way and not another. Organisms and their cells are built one way and not another because their structures have evolved in a particular direction and can only be explained as the result of an evolutionary process. Not only does each biological system need to function properly, but it also must have been able to achieve its present method of functioning as the result of a long, historical, evolutionary process in which a previous method of functioning changed into the present one. If there were two or more ways of accomplishing the same result, a particular species used one of them because its ancestors were more easily capable of evolving this one method than another.

Eli C. Minkoff

See also: Genetics: Mendelian.

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EVOLUTION OF CELLS

Categories: Cellular biology; evolution; paleobotany

The earliest cells evolved sometime early in the Precambrian era, which includes the first four billion years of Earth's history. Attempts to understand life's origins are difficult, as there are very few clues left in the fossil record from those early times. The hypotheses and models of the origin of life that have been developed are based on contemporary understanding of how life works at the molecular and cellular levels and on assumptions about the conditions on Earth three billion to four billion years ago.

One assumption made about the origins of life involves the composition of the atmosphere shortly after the earth was formed. According to this assumption, the earth's atmosphere at this time contained very little free oxygen. It was an atmosphere perhaps made primarily of methane, ammonia, carbon dioxide, nitrogen, carbon monoxide, and water vapor. The first organisms are believed to have been anaerobic and did not require oxygen for *respiration*. This early atmosphere lacked a protective shield of ozone, which is derived from oxygen and which absorbs ultraviolet radiation from the sun. Intense ultraviolet radiation is lethal, and early forms of life may have evolved in water deep enough to avoid it. In some later stages of chemical evolution, however, ultraviolet radiation may actually have driven molecular interactions, producing more complex structures that were forerunners to living organisms.

Building Blocks of Life

The basic elements found in organic compounds are carbon, oxygen, hydrogen, nitrogen, phosphorus, and sulfur. These elements are also the main components of living cells and are the most plentiful elements in the solar system. The basic materials for the development of life were present on the early earth. Scientists have discovered that some of these building blocks, especially molecules of hydrogen sulfide, hydrogen cyanide, methanol, acetic acid, methyl formate, and a simple sugar called glycol aldehyde, exist in space and may have been brought to Earth by comets passing close by the plant. These compounds were, in fact, given off as Comet Hale-Bopp passed through the earth's solar system during 1995-1997. Perhaps comets "seeded" the earth with inorganic and organic compounds that triggered the chemical evolution that led to life itself.

Proteins and Amino Acids

One of the components of life is *proteins*. Proteins are made of even more basic organic molecules called *amino acids*. Proteins act as building materials for an organism's body and function in chemical reactions within an organism.

Amino acids may have been formed naturally in early earth history. In a process called photochemical dissociation, ultraviolet radiation is capable of separating the atoms in compounds such as water, ammonia, and hydrocarbons such as methane, allowing these atoms to recombine. Some of those atoms would have formed amino acids. A second form of energy that could trigger recombination of atoms is electrical discharge, occurring naturally as lightning. Lightning and ultraviolet radiation, acting separately or together, could have triggered the formation of amino acids in the atmosphere or in the oceans.

Other Building Blocks

Another of life's basic components is *nucleic acids*, such as deoxyribonucleic acid (DNA) and ribonucleic acid (RNA), which transmit genetic information from generation to generation. The building blocks of nucleic acids are nucleotides, which also participate, as nucleotide phosphates like adenosine triphosphate (ATP), in biochemical energy transactions.

Even with the first three components present on the early earth, living organisms could not develop unless those components were in close proximity to one another so they could interact. Some sort of structure was needed to contain all the components. Cell membranes would have provided just such a structure and so must be considered an essential fourth component of the first living organisms.

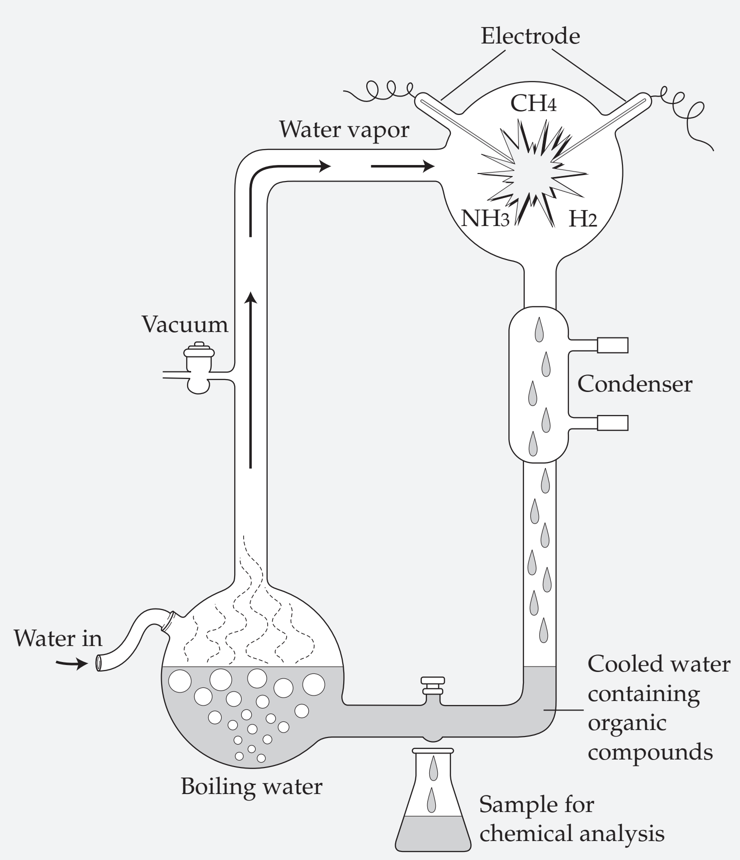
Wöhler's Experiment

Before 1828, many scientists believed that all organic molecules were products of living organisms. However, in 1828 the German chemist Friedrich Wöhler produced crystals of urea quite by accident after heating an inorganic compound called ammonium cyanate. Urea, a component of urine, is an organic compound. Over the next several decades, other chemists were able to duplicate Wöhler's experiment and, by using other simple inorganic compounds, succeeded in producing several other simple organic substances. This led many scientists to believe that life on Earth could have developed from inorganic materials. Between 1828 and the 1960's, however, scientists were able to produce only simple organic molecules from inorganic substances. It was only during the 1960's that scientists could create and detect complex protein molecules.

Miller-Urey Experiments

It was not until 1953 that scientists produced amino acids and similar molecules using simulated conditions like those assumed to have been present in the early earth's atmosphere. Stanley Miller, a graduate student working for Dr. Harold Urey, cre-

The Miller-Urey Experiment



It has been shown many times that organic compounds, the beginnings of life, including amino acids, are produced readily within water in sealed flasks containing reducing gases such as carbon dioxide energized by electrical discharges, ultraviolet light, or even shock waves. The most famous of these experiments, depicted here, was conducted by Stanley L. Miller and Harold C. Urey in 1953. Since then, however, scientists have come to believe that hydrothermal vents, openings along mid-ocean ridges where heated water is vigorously expelled into the sea, act as flow reactors capable of stripping oxygen from carbon dioxide to produce organic matter.

ated an atmosphere of methane, ammonia, hydrogen, and water vapor in a bottle, thinking that this mixture would have been similar to the atmosphere of the very early earth. As the mixture was circulated through the apparatus, sparks of electricity, to simulate lightning, were discharged into the mixture. At the end of eight days, the condensed water in the apparatus had become cloudy and deep red. Analysis of the material showed that it contained a number of amino acids along with a few other, more complicated organic compounds.

Other scientists carried out similar experiments, with much the same results, leading many scientists to believe that organic compounds could be produced from a mixture of gases, including a mix of carbon dioxide, nitrogen, and water vapor, also found in Earth's early atmosphere. What was necessary for the success of these experiments was the lack of free oxygen. The experimenters felt it almost inevitable that amino acids would have developed in the earth's pre-life environment. Amino acids are relatively stable and probably became abundant in the early oceans, over time, joining together into more complex molecules.

Amino Acids to Proteinoids

In order to form proteins, amino acid molecules must lose some water from their molecular structures, which happens when amino acids are heated to temperatures of 140 degrees Celsius. Volcanic activity would have been capable of providing such temperatures. A biochemist named S. W. Fox and his coworkers were able to produce proteinlike chains from a mixture of eighteen common amino acids. Fox termed these structures *proteinoids* and thought that billions of years ago proteinoids were the transitional structures leading to true proteins. Fox actually found proteinoids similar to those he created in the laboratory in lava and cinders spewed out by Hawaiian volcanoes. Amino acids formed in the vapors emitted by the volcanoes and were combined into proteinoids by the heat of escaping gases.

Proteinoids to Microspheres

When solutions of proteinoids in hot water are cooled, they form tiny spheres with many characteristics of living cells. These *microspheres* have a filmlike outer wall, somewhat like a cell membrane; are capable of osmotic swelling and shrinking; exhibit budding, as do yeast cells; and can be observed to divide into "daughter" microspheres. Sometimes these microspheres join together to form lines, or filaments, as some bacteria do, and it is possible to observe movement of internal particles within microspheres, similar to cytoplasmic streaming in living cells.

Nucleic Acids in the Laboratory

Complete long-chain nucleic acids have not yet been experimentally produced under pre-life conditions. However, short stretches of nucleic acid components were produced in 1976 by Har Gobind Khorana and his associates at the Massachusetts Institute of Technology. In yet another experiment, parts of a nucleic acid called peptide nucleic acid, or PNA, were produced by discharging electricity through a blend of methane, ammonia, nitrogen, and water. PNA is more stable than RNA and may have existed during the earth's very early days. However, the big questions remain: How did replication of these nucleic acids begin? How did the first organisms manage to pass along their genetic information to the next generation?

Life Begins in the Sea

The earliest organisms apparently originated in the sea, which contains many of the organic compounds, minerals, and other nutrients needed by living organisms. This reflects the viewpoint of many scientists, including Charles Darwin, who said in 1871 that life started in a "warm little pond," and Aleksandr I. Oparin, who proposed in the 1930's that many chemical substances would have washed out of the atmosphere and been carried into the oceans by rain, creating a "primordial soup" of nutrients for the first organisms. These organic molecules, kept in constant motion by the ocean currents, may have bumped together, recombining into larger molecules and increasing in complexity. Exactly how, or exactly when, the transition from not-quite-living to living took place is not known, but scientists assume that it could not happen under present-day conditions. Oxygen and microbial predators would destroy similar structures today.

Heterotrophs

The first living organisms were microscopic in size and unicellular. These earliest forms of life were not able to make their own food but instead assimilated small pieces of organic molecules present in the surrounding waters. They no doubt ate one another as well. Organisms with this type of nutritional mechanism are called *heterotrophs*. The food of these ancient organisms was digested externally by excreted enzymes before being ingested and metabolized by fermentation, a process that does not require free oxygen.

Autotrophs and Photoautotrophs

When nearby food resources became exhausted, the resulting food shortages might have caused selective pressures for evolutionary change. Some organisms evolved the ability to synthesize their food from simple inorganic substances. These became organisms called *autotrophs*. The autotrophs began to evolve in many different directions, using different substances, such as carbon dioxide, ammonia, and hydrogen sulfide, as food.

Another group evolved into the *photoautotrophs*, capable of carrying out *photosynthesis*, which uses solar energy to incorporate carbon dioxide into organic molecules and releases oxygen as a byproduct. Carbon combined with other elements to promote cellular growth, and the oxygen escaped into the atmosphere, which prepared the environment for the next important step in the evolution of primitive organisms.

As the photoautotrophs multiplied, photosynthesis began to gradually change Earth's original oxygen-poor atmosphere to a more oxygen-rich one. A rapid buildup of oxygen in the atmosphere was delayed, as iron in rocks exposed at the earth's surface was oxidized before oxygen could accumulate in the atmosphere. This allowed many microorganisms to evolve oxygen-mediating enzymes that permitted them to cope with the new atmosphere.

Once atmospheric oxygen concentrations reached about 10 percent, solar radiation converted part of the oxygen to ozone, forming a shield against ultraviolet radiation. Life, still primitive and vulnerable, was now protected and could expand into environments that formerly had not been able to harbor life, setting the stage for the appearance of aerobic organisms.

Aerobic Metabolism

Aerobic organisms use oxygen to convert their food into energy. Aerobic metabolism provides far more energy in relation to food consumed than does the fermentation carried out by anaerobic organisms. Aerobic metabolism provided a surplus of energy, which was an important factor in the evolution of more complex forms of life. With more energy available, organisms could move about more, colonize new niches, and engage in sexual reproduction, allowing new and innovative genetic recombinations to emerge, and may have increased the rate of evolution, which led to the evolution of complex multicellular organisms called metazoans.

Prokaryotes and Eukaryotes

The first organisms were unicellular organisms called *prokaryotes*, which today are classified in two of the three domains of life as either *Archaea* or *Bacteria*, the latter including the cyanobacteria, which are photosynthetic. Both of these domains comprise unicellular life-forms consisting of prokaryotes. Prokaryotic cells lack internal organelles and a membrane-bound nucleus. Their genetic material resides in the cytoplasm of the cell. Modern prokaryotes do have cell walls and most are able to move about. Prokaryotes are asexual, reproducing by binary fission, which limits the possibilities for variation.

Evolution proceeded from the prokaryotes to organisms with a definite nuclear wall, well-defined chromosomes, and the capacity to reproduce sexually. These more advanced life-forms are termed *eukaryotes*. Eukaryotic cells contain organelles such as mitochondria, which metabolize carbohydrates and fatty acids to carbon dioxide and water, releasing energy-rich phosphate compounds in the process. Some eukaryotes have organelles called chloroplasts, the structures in which sunlight is converted into energy in the process of photosynthesis.

The forms of life made of eukaryotic cells are now classified in the third great domain of life, *Eukarya*, which comprises most of the life-forms familiar as plants and animals—from fungi and plants to human beings—classified in several kingdoms, phyla, classes, genera, and millions of species. Biologists believe that the organelles in eukaryotic cells were once independent microorganisms that entered other cells and then established symbiotic relationships with the primary cell. This process is called the endosymbiont theory.

Ancestral Algae

The various divisions of algae make up an important group of photosynthetic eukaryotes. One group of algae, the *Chlorophyta*, or green algae, are the probable ancestors of terrestrial plants. Common characteristics of green algae and terrestrial plants include the chlorophyll pigments *a* and *b* in the chloroplasts of both green algae and land plants, a number of carotenoid pigment derivatives, starch as the carbohydrate food reserve, and cell walls made up of cellulose.

From Sea to Land

If, as scientists believe, life originated in the sea, how did it get onto the land? Did the ongoing push to find new sources of food drive organisms from the depths of the oceans to coastal areas, where environmental conditions were harsher? To cope with the intense wave action along shorelines, multicellular organisms with diversified parts, some designed to hold onto rocks, evolved. To prevent desiccation in coastal environments and to provide support against the pounding waves, these organisms also evolved rigid cell walls, which allowed them to increase in size. As plants increased in size, they had adapt to do two things: First, they needed to be able to move water and mineral nutrients from the substrate to other parts of the plant not tied directly to the ground. A second problem involved how to move the products of photosynthesis from the site of manufacture to those parts of the plant where photosynthesis could not take place.

The solution to these problems became more critical as plants began to colonize habitats farther from permanent supplies of water. Roots evolved to anchor plants in the ground and to supply the rest of the plant with water and mineral nutrients from the ground. Stems evolved to provide support for the leaves, the main organs of photosynthesis; in some cases, the stems themselves evolved the capability of photosynthesis. All of the aboveground portions of plants developed a waxy cuticle that slows down water loss and prevents desiccation. Internally, plants evolved specialized tissues, called the vascular tissues. One type of vascular tissue, the *xylem*, conducts water and mineral nutrients from the soil through the roots and stems to the leaves. The other type of vascular tissue, the *phloem*, transports the sugars manufactured in the leaves during photosynthesis to other parts of the plant body.

Many plants also evolved chemical attractants and defenses in the form of *secondary metabolites*: metabolic products, such as alkaloids, glycosides, or saponins, to deter plant-eating animals. With the appearance of flowering plants (angiosperms), plants began to evolve odors, colors, flowers, and fruits that attracted pollinators and herbivores, ensuring seed dispersal and the survival and propagation of flowering species. It was these specializations that allowed plants to move from the sea and colonize the land between 500 million and 450 million years ago.

Carol S. Radford

See also: Anaerobes and heterotrophs; *Archaea*; Bacteria; Chloroplasts and other plastids; *Eukarya*; Evolution of plants; Green algae; Prokaryotes.

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EVOLUTION OF PLANTS

Categories: Evolution; paleobotany; *Plantae*

As a result of prehistoric events such as the Permian-Triassic extinction event and the Cretaceous-Tertiary mass extinction event, many plant families and some ancestors of extant plant were extinct before the beginning of recorded history.

The general trend of earth's plant diversification involves four major plant groups that rose to dominance from about the Middle Silurian period to present time. The first major group providing land vegetation comprised the seedless vascular plants, represented by the phyla *Rhyniophyta*, *Zosterophyllophyta*, and *Trimerophytophyta*. The second major group appearing in the late Devonian period was made up of the ferns (*Pterophyta*). The third group, the seed plants (sometimes called the Coal Age plants), appeared at least 380 million years ago (mya). This third group includes the gymnosperms (*Gymnospermophyta*), which dominated land flora for most of the Mesozoic era until 100 mya. The last group, the flowering angiosperms (*Anthophyta*), appeared in the fossil record 130 mya. The fossil record also shows that this group of plants was abundant in most parts of the world within 30 million to 40 million years. Thus, the angiosperms have dominated land vegetation for close to 100 million years.

The Paleozoic Era

The Proterozoic and Archean eons have restricted fossil records and predate the appearance of land plants. Seedless, vascular land plants appeared in the middle of the Silurian period (437-407 mya) and are represented by the rhyniophytes or rhyniophytoids and possibly the *Lycophyta* (lycophytes or club mosses). From the primitive rhyniophytes and lycophytes, land vegetation rapidly diversified during the Devonian period (407-360 mya). Pre-fern ancestors and maybe true ferns (*Pterophyta*) were developed by the mid-Devonian. By the Late Devonian the horsetails (*Sphenophyta*) and gymnosperms (*Gymnospermophyta*) were present. By the end of the period, all major divisions of vascular plants had appeared except the angiosperms.

Development of vascular plant structures during the Devonian allowed for greater geographical diversity of plants. One such structure was flattened, planated leaves, which increased photosynthetic efficiency. Another was the development of secondary wood, allowing plants to increase significantly in structure and size, thus resulting in trees and probably forests. A gradual process was the reproductive development of the seed; the earliest structures are found in Upper Devonian deposits.

Ancestors of the conifers and cycads appeared in the Carboniferous period (360-287 mya), but their documentation is poor in the fossil record. During the early Carboniferous in the high and middle latitudes, vegetation shows a dominance of club mosses and progymnosperms (*Progymnospermophyta*). In the lower latitudes of North America and Europe, a greater diversity of club mosses and progymnosperms are found, along with a greater diversity of vegetation. Seed ferns (lagenostomaleans, calamopityaleans) are present, along with true ferns and horsetails (*Archaeocalamites*).

Late Carboniferous vegetation in the high latitudes was greatly affected by the start of the Permo-Carboniferous Ice Age. In the northern middle latitudes, the fossil record reveals a dominance of horsetails and primitive seed ferns (pteridosperms) but few other plants.

In northern low latitudes, landmasses of North America, Europe, and China were covered by shallow seas or swamps and, because they were close to the equator, experienced tropical to subtropical climatic conditions. The first tropical rain forests appeared there, known as the Coal Measure Forests or the Age of Coal. Vast amounts of peat were laid down as a result of favorable conditions of year-round growth and the giant club mosses' adaptation to the wetland tropical environments. In drier areas surrounding the lowlands, forests of horsetails (calamites, sphenophylls), seed ferns (medullosans, callistophytes, lagenostomaleans), cordaites, and diverse ferns (including marattialean tree ferns) existed in great abundance.

The Permian period (287-250 mya) marks a major transition of the conifers, cycads, glossopterids, gigantopterids, and the peltasperms from a poor fossil record in the Carboniferous to significantly abundant land vegetation. The two most prevalent plant assemblages of the Permian were the horsetails, peltasperms, cycadophytes, and conifers. The second most prevalent were the gigantopterids, peltasperms, and conifers. These two plant assemblages are considered the typical paleo-equatorial lowland vegetation of the Permian. Other plants, such as the tree ferns and giant club mosses, were present in the Permian but not abundant. As a result of the Permian-Triassic extinction event, tropical swamp forests disappeared, with the extinction of the club mosses; the cordaites and glossopterids disappeared from higher latitudes; and 96 percent of all plant and animal species became extinct.

The Mesozoic Era

At the beginning of the Triassic period (248-208 mya), a meager fossil record reveals diminished land vegetation (that is, no coal formed). By the middle to late Triassic, the modern family of ferns, conifers, and a now-extinct group of plants, the bennettites (cycadeoids), inhabited most land surfaces. After the mass extinction, the bennettites moved into vacant lowland niches. They may be significant because of the similarity of their reproductive organs to the reproductive organs of the angiosperms.

Image Not Available

Late Triassic flora in the equatorial latitudes are represented by a wide range of ferns, horsetails, pteriosperms, cycads, bennettites, leptostrobaleans, ginkgos, and conifers. The plant assemblages in the middle latitudes are similar but not as species-rich. This lack of plant variation in low and middle latitudes reflects a global frost-free climate.

In the Jurassic period (208-144 mya), land vegetation similar to modern vegetation began to appear, and the ferns of this age can be assigned to modern families: *Dipteridaceae*, *Matoniaceae*, *Gleicheniaceae*, and *Cyatheaceae*. Conifers of this age can also be assigned to modern families: *Podocarpaceae*, *Araucariaceae* (Norfolk pines), *Pinaceae* (pines), and *Taxaceae* (yews). These conifers created substantial coal deposits in the Mesozoic.

During the Early to Middle Jurassic, diverse vegetation grew in the equatorial latitudes of western North America, Europe, Central Asia, and the Far East and comprised the horsetails, pteridosperms, cycads, bennettites, leptostrobaleans, ginkgos, ferns, and conifers. Warm, moist conditions also existed in the northern middle latitudes (Siberia and northwest Canada), supporting Ginkgoalean forests and leptostrobaleans. Desert conditions

Evolution of Plants

Origin	*Geologic Period*	*Plant Life*
420 mya	Silurian	Seedless vascular plants (earliest land plants)
400 mya	Devonian	Ferns
380 mya	Devonian	Progymnosperms
365 mya	Carboniferous	Seed plants: gymnosperms, conifers
245 mya	Permian	Cycads (earliest fossils, but may have preceded gymnosperms)
130 mya	Cretaceous	Angiosperms (flowering plants)

Notes: Dates are approximate and are often debated, but the paleobotanists generally agree on the sequence; mya = millions of years ago.

existed in central and eastern North America and North Africa, and the presence of bennettites, cycads, peltasperms and cheirolepidiacean conifers there are plant indicators of drier conditions. The southern latitudes had similar vegetation to the equatorial latitudes, but owing to drier conditions, cheirolepidiacean conifers were abundant, ginkgos scarce. This southern vegetation spread into very high latitudes, including Antarctica, because of the lack of polar ice.

In the Cretaceous period (144-66.4 mya), arid, subdesert conditions existed in South America, Central and North Africa, and central Asia. Thus, the land vegetation was dominated by cheirolepidiacean conifers and matoniacean ferns. The northern middle latitudes of Europe and North America had a more diverse vegetation comprising bennettites, cycads, ferns, peltasperms, and cheirolepidiacean conifers, with the southern middle latitudes dominated by bennettites and cheirolepidiaceans.

A major change in land vegetation took place in the late Cretaceous with the appearance and proliferation of flowering seed plants, the angiosperms. The presence of the angiosperms marked the end of the typical gymnosperm-dominated Mesozoic flora and a definite decline in the leptostrobaleans, bennettites, ginkgos, and cycads.

During the late Cretaceous in South America, central Africa, and India, arid conditions prevailed, resulting in tropical vegetation dominated by palms. The southern middle latitudes were also affected by desert conditions, and the plants that fringed these desert areas were horsetails, ferns, conifers (araucarias, podocarps), and angiosperms, specifically *Nothofagus* (southern beech). The high-latitude areas were devoid of polar ice; owing to the warmer conditions, angiosperms were able to thrive. The most diverse flora was found in North America, with the presence of evergreens, angiosperms, and conifers, especially the redwood, *Sequoia*.

The Cretaceous-Tertiary (K/T) mass extinction event occurred at about 66.4 mya. This event has been hypothesized to be a meteoritic impact; whatever the cause, at this time an event took place that suddenly induced global climatic change and initiated the extinction of many species, notably the dinosaurs. The K/T had a greater effect on plants with many families than it did on plants with very few families. Those that did become extinct, such as the bennettites and caytonias, had been in decline. The greatest shock to land vegetation occurred in the middle latitudes of North America. The pollen and spore record just above the K/T boundary in the fossil record shows a dominance of ferns and evergreens. Subsequent plant colonization in North America shows a dominance of deciduous plants.

The Cenozoic Era

Increased rainfall at the beginning of the Paleogene-Neogene period (66.4-1.8 mya) supported the widespread development of rain forests in southerly areas. Rain forests are documented by larger leaf size and drip tips at leaf edge, typical characteristics of modern rain-forest floras.

Notable in this period was the polar Arcto-Tertiary forest flora found in northwest Canada at paleolatitudes of 75-80 degrees, north. Mild, moist summers alternated with continuous winter darkness, with temperatures ranging from 0 to 25 degrees Celsius. These climatic conditions supported deciduous vegetation that included *Platanaceae* (sycamore), *Judlandaceae* (walnut), *Betulaceae* (birch), *Menispermaceae*, *Cercidophyllaceae*, *Ulmaceae* (elm), *Fagaceae* (beech), *Magnoliaceae*; and gymnosperms such as *Taxodiaceae* (redwood), *Cypressaceae* (cypress), *Pinaceae* (pine), and *Ginkgoaceae* (gingko). This flora spread across North America to Europe via a land bridge between the continents.

About eleven million years ago, during the Miocene epoch, a marked change in vegetation occurred, with the appearance of grasses and their subsequent spread to grassy plains and prairies. The appearance of this widespread flora supported the development and evolution of herbivorous mammals.

The Quaternary period (1.8 mya to present) began with continental glaciation in northwest Europe, Siberia, and North America. This glaciation affected land vegetation, with plants migrating north and south in response to glacial and interglacial fluctuations. Pollen grains and spores document the presence of *Aceraceae* (maple), hazel, and *Fraxinus* (ash) during interglacial periods.

Final migrations of plant species at the close of the last ice age (about eleven thousand years ago), formed the modern geographical distribution of land plants. Some areas, such as mountain slopes or islands, have unusual distribution of plant species as a result of their isolation from the global plant migrations.

Mariana Louise Rhoades

See also: Angiosperm evolution; Angiosperms; Cycads and palms; Endangered species; Evolution of plants; Ferns; Fossil plants; Ginkgos; Gymnosperms; Horsetails; Lycophytes; Mosses; Paleobotany; *Rhyniophyta*; Seedless vascular plants; Stromatolites; *Trimerophytophyta*; *Zosterophyllophyta*.

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EXERGONIC AND ENDERGONIC REACTIONS

Category: Cellular biology

Exergonic reactions are spontaneous chemical reactions in which the products are at a lower energy level than the reactants; these reactions release energy. Endergonic reactions are nonspontaneous chemical reactions in which the products are at a higher energy level than the reactants; these reactions consume energy.

The primary source of energy for life on the earth is the sun, which is the energy source for photosynthesis: the biological process that transforms radiant energy into chemical energy. Chemical energy is stored in biological molecules, which can then be used as the fuel to provide an organism's energy needs. Such biological molecules include sugars (or carbohydrates), proteins, and lipids (or fats). In the reactions of metabolism, many types of molecules are synthesized (*anabolism*), and many are broken down (*catabolism*). Changes in energy content occur in all these reactions. *Bioenergetics* is the science that studies the description of the basic mechanisms that govern the transformation and use of energy by organisms. A basic tenet of bioenergetics is that no chemical reaction can be 100 percent energy-efficient. In other words, in all reactions there is some transfer of energy, but some of it is always lost in the form of heat.

The energy (often measured in *calories*) contained in the molecular structure of a compound is called *Gibbs free energy* (after Josiah Willard Gibbs, 1839-1903, who founded the discipline of physical science) and is the energy available to perform work. The difference between the free energy of the products and the *free energy* of the reactants in a chemical reaction is called the *change in free energy* and is fundamental in determining if a reaction can occur spontaneously. If the change in free energy is negative, energy is released, and the free energy content is less in the products than in the reactants. Such reactions are considered exergonic. On the other hand, if the change in free energy is positive, the reaction is considered endergonic and is nonspontaneous (that is, endergonic reactions require a source of energy to enable them to occur).

Energy Coupling

Many cellular reactions are endergonic and cannot occur spontaneously. Nevertheless, cells can facilitate endergonic reactions using the energy released from other exergonic reactions, a process called *energy coupling*. As an example, consider a common endergonic reaction in plants in which glucose and fructose are joined together to make sucrose. To enable this reaction to take place, it is coupled with a series of other exergonic reactions as follows:

glucose + adenosine triphosphate (ATP) →
glucose-p + ADP

fructose + ATP →
fructose-p + adenosine diphosphate (ADP)

glucose-p + fructose-p →
sucrose + 2 P_i (inorganic phosphate)

Therefore, although producing sucrose from glucose and fructose is an endergonic reaction, all three of the foregoing reactions are exergonic. This is representative of the way cells facilitate endergonic reactions.

Role of ATP

The principal molecule involved in providing the energy for endergonic cellular reactions to take place is adenosine triphosphate, or ATP, the same molecule used in the example above. ATP is typically produced by joining an inorganic phosphate to adenosine diphosphate (ADP), which is an endergonic reaction. This, too, represents a characteristic of chemical reactions: If a reaction is exergonic in one direction, it will be endergonic in the opposite direction. Thus, the breakdown of ATP is exergonic, while the production of ATP is endergonic. The energy for production of most of the ATP in plant cells comes from the *light reactions* of photosynthesis and the *electron transport system* in the mitochondria.

The enigma is why ATP, and not any other molecule, is used. Although no complete justification is available, there are several points that support its significance. First, there is the high stability of the ATP molecule at the physiological pH (around 7.4) toward hydrolysis and decomposition in the absence of an enzyme catalyst. This stability allows ATP to be stored in the cell until needed. Second, ATP is one of the molecules (a nucleotide) that is used in synthesis of DNA. Finally, the magnitude of the change in free energy involved in the ATP-ADP transformation is of an amount useful for driving many of the endergonic reactions in the cell. As a result, it can play the role of an intermediate quite easily.

Paris Svoronos, updated by Bryan Ness

See also: Anaerobic photosynthesis; ATP and other energetic molecules; C_4 and CAM photosynthesis; Calvin cycle; Chloroplasts and other plastids; Energy flow in plant cells; Glycolysis and fermentation; Krebs cycle; Mitochondria; Oxidative phosphorylation; Photorespiration; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Plant cells: molecular level; Respiration.

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EXTRANUCLEAR INHERITANCE

Categories: Cellular biology; genetics; reproduction and life cycles

Extranuclear inheritance is a non-Mendelian form of heredity that involves genetic information located in cytoplasmic organelles, such as mitochondria and chloroplasts, rather than on the chromosomes found in the cell nucleus.

Extranuclear genes, also known as *cytoplasmic genes*, are located in mitochondria and chloroplasts of a cell rather than in the cell's nucleus on the chromosomes. Both egg and sperm contribute equally to the inheritance of nuclear genes, but extranuclear genes are more likely to be transmitted through the maternal line because the egg is rich in the cytoplasmic organelles where these genes are located, whereas the sperm contributes only its nucleus to the fertilized egg. Therefore, extranuclear genes do not follow genetic pioneer Gregor Mendel's statistical laws of *segregation* and *recombination*. Cytoplasmic genes are of interest in understanding evolution, genetic diseases, and the relationship between genetics and embryology.

History

Since the discovery of Mendel's principles, research in genetics has been guided by the belief that the fundamental units of inheritance are located on chromosomes in the cell nucleus. T. H. Morgan, one of the founders of modern genetics, declared that the cytoplasm could be ignored genetically. However, some biologists resisted the concept of a "nuclear monopoly" over inheritance. Embryologists, in particular, argued that nuclear genes, identical in every cell, could not explain how cells *differentiated* from one another in the course of development. They argued that differences among cells in the developing embryo must have a basis in the *cytoplasm*, the part of the cell outside the nucleus. Trying to formulate a compromise, some biologists suggested that Mendelian genes play a role in determining individual characteristics, while cytoplasmic determinants are responsible for more fundamental aspects of plants and animals. The discovery of a wide variety of cytoplasmic entities seemed to support the concept that cytoplasmic factors played a role in development and heredity.

In the 1940's, Boris Ephrussi's work on "petite" mutants in yeast suggested that inheritance of this trait depended on some factor in the cytoplasm rather than the nucleus. Yeast cells with the *petite mutation* produce abnormally small colonies when grown on a solid medium, with glucose as the energy source. Petite mutants grow slowly because they lack important membrane-bound enzymes of the respiratory system.

Similar studies have been made of slow-growing mutants of the bread mold *Neurospora*. Inheritance of the trait known as "poky" shows a non-Mendelian pattern. Microinjection of purified mitochondria from poky strains into normal strains has been used to demonstrate the cytoplasmic inheritance of this trait.

Chloroplasts

As early as 1909, geneticists were reporting examples of non-Mendelian inheritance in higher plants, usually green and white variegated patterns on leaves and stems. These patterns seemed to be related to the behavior of the *chloroplasts*, photosynthetic organelles in green plants. Because of the relatively large size of chloroplasts, scientists have been able to study their behavior in dividing cells with the light microscope since the 1880's. Like mitochondria, chloroplasts contain their own deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). Although *chloroplast DNA* (cpDNA) contains many of the genes needed for chloroplast function, chloroplasts do not seem to be totally autonomous; nuclear genes are required for some chloroplast functions. Another interesting case of extranuclear inheritance in plants is that of *cytoplasmic pollen sterility*. Many species of plants seem to produce strains with cytoplasmically inherited pollen sterility.

Advances in experimental methods made in the 1960's allowed scientists to demonstrate that organelles located in the cytoplasm contain DNA. This finding came as a great surprise to most biologists. In 1966 the first vertebrate *mitochondrial DNA* (mtDNA) was isolated and characterized. Like bacterial DNA, mtDNA generally consists of a single double helix of "naked," circular DNA. The mitochondrial genome is usually smaller than that of even the simplest bacterium. Most of the proteins in the mitochondrion are encoded by nuclear genes, but mtDNA contains genes for mitochondrial ribosomal RNAs, transfer RNAs, and some of the proteins of the electron transport system of the inner membrane of the mitochondrion.

Extranuclear DNA

The DNA found in chloroplasts and mitochondria is chemically distinct from the DNA in the nucleus. Moreover, the extranuclear genetic systems behave differently from those within the nucleus. Even more surprising is the finding that mitochondria have their own, slightly different version of the genetic code, which was previously thought to be common to all organisms, from viruses to humans. In general, because of its greatly smaller size, the DNA found in cytoplasmic organelles has a limited coding capacity. Thus, by identifying the functions under the control of mitochondrial or chloroplast genes, all other functions carried on by the organelle can be assigned to the nuclear genome. Coordinating the contributions of the organelle and the nuclear genomes is undoubtedly a complex process.

In addition to the genes found in mitochondria and chloroplasts, extranuclear factors are found in various kinds of *endosymbionts* (symbiotic organisms that live within the cells of other organisms) and *bacterial plasmids*. Some biologists think that all organelles may have evolved from ancient symbiotic relationships. Endosymbionts may be bacteria, algae, fungi, protists, or viruses. Unlike the mitochondria and chloroplasts, some endosymbionts seem to have retained independent genetic systems. The "killer" particles in paramecia, discovered by T. M. Sonneborn in the 1930's, provide a historically significant example. After many years of controversy, the killer particles were identified as bacterial symbionts. These cytoplasmic entities are not vital to the host cell, as the paramecia are capable of living and reproducing without them. Certain peculiar non-Mendelian conditions found in fruit flies also appear to be caused by endosymbionts.

Although bacteria lack nuclei, their circular DNA is usually referred to as bacterial chromosomes. Some bacteria also contain separate DNA circles smaller than the bacterial chromosome. In the 1950's Joshua Lederberg proposed the name "plasmid" for such extrachromosomal hereditary determinants. Some of the most interesting examples of these entities are the F (fertility) factor, the R (resistance transfer) factors, and the Col (colicin) factors. *Resistance transfer factors* can transmit resistance to antibiotics between bacteria of different species and genera. *Col factors*, toxic proteins produced by bacteria that kill other bacteria, were studied as toxins for many years before their genetic basis was discovered. Because of their simplicity, the bacterial systems are better understood and can serve as models for the kinds of studies that should be performed for extranuclear genes in higher organisms as techniques improve.

Evolutionary Advantages and Uses

The recognition of extranuclear genetic systems raises important questions about their possible evolutionary advantage. In contrast to the remarkable universality of the nuclear genetic system, extranuclear genetic systems are quite diverse in function and mechanisms of transmission. Although extranuclear genes control only a small fraction of the total hereditary material of the cell, in eukaryotic organisms the genes found in mitochondria and chloroplasts are clearly essential for maintaining life.

Although organelle DNAs clearly play an important part in cell organization, it has been difficult to pinpoint the essential roles of organelle DNA and protein-synthesizing systems. Many technical difficulties, and the traditionally low priority of this field, meant that adequate techniques for studying organelle genomes emerged slowly. Studies of cytoplasmic genetics will doubtless have significant applications in medical science and agriculture as well as an impact on understanding of the evolution of genetic control mechanisms.

For example, M. M. Rhoades's work on corn in the 1940's forced American geneticists to take note of research on cytoplasmic genes, while plant breeders began to use cytoplasmically inherited pollen sterility in the production of hybrid seed. Cytoplasmic pollen sterility is a useful trait to incorporate into commercial inbred lines because it ensures cross-pollination and thus simplifies seed production. Unfortunately, a toxin-producing fungus to which the major corn cytoplasmic gene for pollen sterility was susceptible destroyed more than 50 percent of the corn crop in certain areas of the United States in 1970. This disaster prompted a return to hand-detasseling.

Lois N. Magner

See also: Chloroplast DNA; Chloroplasts and other plastids; DNA in plants; Genetics: Mendelian; Genetics: Post-Mendelian; Mitochondria; Mitochondrial DNA; RNA.

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FARMLAND

Categories: Agriculture; economic botany and plant uses; soil

Land used as farmland typically has good agricultural soil and is able to produce food and fiber in an efficient way.

Land suitable for agriculture is not evenly distributed throughout the world; it tends to be concentrated in limited areas. In order to be considered good farmland, land must be located at the proper elevation and slope. Because the soil supplies the mineral nutrients required for plant growth, it must also have the appropriate fertility, texture, and pH. Approximately 64 percent of the world's land has the proper topography, and about 46 percent has satisfactory soil fertility to grow crops.

Plants require large amounts of water for photosynthesis and access to soil nutrients; therefore, farmland must receive an adequate supply of moisture, either from rainfall or from irrigation water. About 46 percent of the world's land has adequate and reliable rainfall. Because plant growth is dramatically affected by temperature, farmland must be located in areas with growing seasons long enough to sustain the crop from planting to harvest.

Approximately 83 percent of the world's land has favorable temperatures. Plants also require sufficient sunlight and atmospheric carbon dioxide levels to support the photosynthetic process necessary for growth and development. Virtually all the world's land has adequate sunlight and sufficient carbon dioxide to support plant growth. Crop production requires the right combination of all these factors, and only about 7 percent of the world's land currently has the proper combination of these factors to make the production of crops feasible without additional technological advances.

Farmland in the United States

With its temperate climate, the United States devotes considerably more of its land area to agriculture than do many other parts of the world. About 45 percent of the land in the United States is used for various forms of agriculture; however, only about 20 percent of the land is actual cropland. Of the rest, approximately 4 percent is devoted to *woodlands*, and the other 21 percent is used for other purposes, such as pastures and *grasslands*. Of the farmland devoted to crop production, only 14 percent is used at any given time to produce harvestable crops. Approximately 21 percent of this harvested cropland is used to produce food grains for human consumption. Feed grains for livestock are grown on 31 percent, and the remaining 48 percent of harvested cropland is devoted to the production of other crops.

There are seven major agricultural regions in the United States. The dairy region is located in the North Atlantic states and extends westward past the Great Lakes and along the Pacific Coast. The wheat belt is centered in the central and northern Great Plains and in the Columbia Basin of the Northwest. The general and self-sufficing regions primarily made up of small, family-owned farms are found mostly in the eastern highlands region, which includes the Appalachian Mountains, a few hundred miles inland from the Atlantic Coast, and the Ozark-Ouachita mountains west of the Mississippi River. The corn and livestock belt is found throughout the Midwestern states. The range-livestock region of the western United States stretches in a band from 500 to 1,000 miles wide and extends from the Canadian border to Mexico. The western specialty-crops area is primarily composed of irrigated land in seventeen western states and produces the vast majority of the nation's vegetable crops. The cotton belt, located in the southern states (most notably Georgia, Alabama, and Mississippi), contains more farmers than any other region. While this area has been known historically for its cotton production, many other crops, including tobacco, peanuts, truck crops, and livestock are also produced in the South.

In addition to these major regions, smaller farming areas are located throughout the country. To-

PhotoDisc

Two properties of productive farmland are receipt of an adequate supply of moisture, either from rainfall or from irrigation, and location in an area with a growing season long enough to sustain crops from planting to harvest.

bacco is produced throughout Kentucky, Virginia, Tennessee, and North and South Carolina. Apples and other fruits are grown in a variety of places, including the Middle Atlantic seaboard, around the Great Lakes, and the Pacific Northwest. Potatoes are produced in Maine, Minnesota, Idaho, North Dakota, and California. Citrus is grown in southern Texas, Florida, and California. Sugarcane is cultivated in southern Louisiana and Florida.

Loss of Farmland

In the United States, both the quantity of land devoted to farming and the number of farmers have been decreasing since 1965. Likewise, there has been a decrease in the amount of good farmland worldwide. Most of this decrease is attributed to a combination of *urbanization* and poor agricultural methods that have led to loss of *topsoil* through water and wind *erosion*. Historically, large tracts of farmland have been located near metropolitan areas. In recent times, these urban centers have grown outward into large suburban areas, and this sprawl has consumed many acres of farmland. Erosion destroys thousands of acres of farmland every year, and *desertification*—the conversion of productive rangeland, rain-fed cropland, or irrigated cropland into desertlike land with a resulting drop in agricultural productivity—has reduced productivity on 2 billion acres over the past fifty years. In many cases, the desertified land is no longer useful as farmland. Steps must be taken to preserve this valuable resource, or it is quite possible that the world will suffer mass food shortages in the future.

D. R. Gossett

See also: Agriculture: history and overview; Biomes: types; Fertilizers; Erosion and erosion control; Green Revolution; North American agriculture; North American flora; Rangeland; Soil management; Strip farming.

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FERNS

Categories: Paleobotany; *Plantae*; seedless vascular plants; taxonomic groups

Ferns are among the most recognizable members of the phylum Pterophyta*, which are primitive, nonflowering, vascular plants that primarily reproduce by spores and occur in many variations, complicating classification.*

Approximately twelve thousand extant species of fern are classified in the phylum *Pterophyta*. These seedless plants display a diversity of physical and reproductive characteristics that separate them taxonomically. They have leaves containing branching veins known as megaphylls. Fossils from the Devonian period, about 395 million years ago, include some structures resembling *Pterophyta*. These plants are believed to have been the source for gymnosperms. Most early fernlike plants that evolved in a variety of forms during the next period, the Carboniferous (approximately 345 million to 280 million years ago), which is often referred to as the age of the ferns, became extinct afterward. Evaluating the many fossils from this period containing fernlike structures, paleobotanists have identified *Archaeopteris*, which they call the primitive fern, and *Protopteridium*, labeled the first fern, which they hypothesize are the ancestors of modern ferns. Botanists have linked two existing fern genera as possible descendants of Carboniferous ferns.

Some fossilized leaves thought to be ferns had characteristics indicating that they had seeds and were not ferns. Seed ferns, or *pteridosperms*, were trees and vines with fronds but were not directly related to true ferns. Before the seed ferns became extinct in the Cretaceous period, about 136 million years ago, they were the predecessors to angiosperms. Based on anatomical comparisons, modern ferns and seed ferns may have descended from the same ancestors. Eleven modern fern families are present in fossils from the Mesozoic era, approximately 245 million years ago.

Although many modern ferns are morphologically similar to one another, they deviate in expression of specific traits. Theories differ about the evolutionary origins and development of ferns, specifically their stems and leaves. Many botanists designate the family *Schizeaceae*, or the curly grass, in phylum *Pterophyta* as the evolutionary origin of ferns. Types of curly grass also belong to family *Thelypteridaceae*. Tropical ferns are classified in family *Dicksoniaceae*. Other familiar families in phylum *Pterophyta* include *Adiantaceae*, which represents the maidenhair ferns; *Hymenophyllaceae*, which are the filmy ferns; *Blechnaceae*, the deer ferns, with reddish leaves; and *Cyathaceae*, the arborescent tree ferns. Spleenworts are in family *Aspleniaceae*. Brackens in family *Dennstaeditaceae* are further classified into the tribes *Dennstaediteae*, *Lindsaeeae*, and *Mona-*

Classification of Ferns

Class *Filicopsida*
- Order *Hydropteridales*
  - Families:
    - *Azollaceae* (azollas)
    - *Marsileaceae* (water clovers)
    - *Salviniaceae* (floating ferns)
- Order *Marattiales*
  - Family:
    - *Marattiaceae* (vessel ferns)
- Order *Ophioglossales*
  - Family:
    - *Ophioglossaceae* (adder's-tongues)
- Order *Polypodiales*
  - Families:
    - *Anemiaceae* (flowering ferns)
    - *Aspleniaceae* (spleenworts)
    - *Blechnaceae* (chain ferns)
    - *Cyatheaceae* (tree ferns)
    - *Dennstaedtiaceae* (bracken ferns)
    - *Dicksoniaceae* (tree ferns)
    - *Dryopteridaceae* (wood ferns)
    - *Gleicheniaceae* (forking ferns)
    - *Grammitidaceae* (kihi ferns)
    - *Hymenophyllaceae* (filmy ferns)
    - *Lophosoriaceae* (diamond leaf ferns)
    - *Lygodiaceae* (climbing ferns)
    - *Osmundaceae* (royal ferns)
    - *Parkeriaceae* (water ferns)
    - *Polypodiaceae* (polypodys)
    - *Pteridaceae* (maidenhair ferns)
    - *Schizaeaceae* (curly grasss)
    - *Thelypteridaceae* (marsh ferns)
    - *Vittariaceae* (shoestring ferns)

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

chosorae. The family *Dryopteridaceae* is divided into six tribes.

Floating *Pterophyta* plants belong to the families *Salviniaceae* and *Azollaceae*, the latter of which is considered to display the plant world's most complex reproductive system. *Marsileaceae* is the water-clover family. Variants of *Pterophyta* that grow on forest floors belong to the family *Marattiaceae*. The royal ferns (family *Osmundaceae*) exhibit some primitive characteristics such as stipular leaf bases. Family *Ophioglossaceae*, which includes adder's-tongue, are not closely related to extant ferns and express primitive traits such as high-spore-yielding sporangia, indicating an origin among the progymnosperms. The epiphytic family *Polypodiaceae*, divided by tribes, also is isolated from most *Pterophyta* ferns and is considered most closely related to the family *Gleicheniaceae*.

Pteridium, the bracken, is the most familiar fern worldwide and is among the earth's six most common and oldest plants. Classification of ferns fluctuates according to different authorities. Many known groups of ferns have not been fully examined, while other species are being discovered in previously uncharted places. Some researchers consider such plants as whiskferns (*Psilotophyta*), horsetails (*Sphenophyta*), and club mosses (*Lycophyta*) to be closely related to ferns, but most botanists stress that ferns differ morphologically from those plants, although their life cycles are alike.

Reproduction

Pterophytes such as ferns exist as two alternating forms during their sexual reproductive cycle. Initially, in the gametophyte phase, ferns are a stem known as the rhizome, from which roots and leaves, called fronds, grow as the fern matures into an adult sporophyte. The sporophyte exists separately from the gametophyte, which usually dies as soon as the sporophyte's root sinks into soil. Growing on or near the soil surface, rhizomes, the most common stem form, can be as thin as threads or as thick as ropes and sometimes have hollows that house ants that scientists believe to be living in symbiosis with the fern, protecting it from insect predators. The roots also have differing characteristics of quantity, width, length, and texture that aid in classification.

Ferns do not flower or create seeds; instead, they produce brown sacs, or sporangia, on the bottom surfaces of their fronds which contain single-cell spores. These spores vary in size and have tetrahedral or oval shapes. Spore arrangement aids fern classification. Spores are distributed by wind to germinate and form a small, heart-shaped *prothallus* which has sexual organs. The prothallus is tiny, averaging 8 millimeters (0.3 inch), and often is not visible before it dies. Water is necessary for fertilization to occur, opening the sex organs by swelling. Sperm from the antheridium fertilizes eggs, located in the archegonium on either the same or a different prothallus, which protects the resulting embryos until they mature. Embryos renew the cycle by maturing as rhizomes, which form fronds and roots to spread ferns to different areas. While spores are haploid (with one set of chromosomes), fern cells have two sets of chromosomes, one set acquired from the egg and one from sperm. Ferns create genetically identical clones in colonies.

Most fern reproduction is vegetative (asexual, without gametophytes) and occurs during the sporophytic stage, in which rhizomes produce fern clones or fragments are distributed by wind, water, or insects. The walking ferns, members of the species *Camptosorus rhizophyllus* and *Camptosorus sibiricus*, grow from sprouts emerging where parent leaves touch soil. As a result, large groups of identical ferns can be formed.

Sexual reproduction's role is to introduce ferns to new habitats and geographical areas. Genetic changes that occur because of meiotic cell division before the production of spores result in subtle variations.

Structure and Distribution

Most *Pterophyta* tissues, specifically those in ferns, are created near the top of the fronds, with the most mature cells being located at the base. Some fern genera have deviations in leaf structure. Fern leaves, known as the pteridophyll, have a fiddlehead, called the crosier, from which they unroll, instead of unfolding, as do other plants' leaves. Ferns are vascular, and most have pinnate leaves with leaflets extending from a central rib. Other types of leaves include palmate ferns, in which the leaflets emerge from one place, and staghorn ferns, with dichotomous leaves.

Leaves can be simple or compound, depending on whether they are segmented. Such appearances help identify species, especially when they are closely related. Leaves and their bases protect the stems, which have a surface consisting of one layer of flat epidermal cells with wide outer walls. Sometimes stems are covered with leaf armor, which is

NOAA/National Estuarine Research Reserve Collection

Bracken ferns by a roadside in Georgia.

formed by the hardened remains of leaf bases. This armor thickens stems and can store food in addition to shielding ferns from harm. Scales and hairs are also often present on stems, guarding them and providing identifiable traits for classification. Internally, stems have vascular tissues called steles.

Fronds are of varying shapes and sizes, ranging from 1 millimeter to 30 meters (0.04 inch to 100 feet). Some leaves appear feathery, while others look solid. They exhibit different shades of green and textures, such as glossy or leathery. Fern height also ranges broadly, from a few millimeters (0.1 inch) to as tall as 10 to 25 meters (30 to 80 feet) for some tropical tree ferns.

Habitats

Pterophyta habitats are numerous. The greatest number of species live in tropical rain forests. Most ferns are terrestrial, while some ferns are vines; others are epiphytes, wrapping around trees; and some float on bodies of water. Ferns prefer damp, warm environments but can also grow in arid and cold settings. Because less moisture and lower temperature occur at higher latitudes than in tropical and subtropical zones, fewer native ferns are found at the higher latitudes, although some species can live in the polar regions of the Arctic and Antarctic. Epipteric ferns grow in rocky landscapes, with different species preferring acidic or alkaline stones and others thriving in marshes, bogs, forests, and fields. Several ferns grow at high elevations, living on volcanoes and mountains. Ferns adapt to arid, sunny, and salty conditions by developing harder tissues, waxy surfaces, hair or scale coverings, and altered life cycles.

Species are occasionally introduced into areas where they are not indigenous and then thrive to become common. Hybrids also occur between species within genera, adding to classification confusion. Rarely, hybridization between genera happens. Because they are primarily sterile, hybrids reproduce with vegetative propagation or apogamy, whereby spores with the same number of chromosomes as parent cells generate gametophytes that bud a sporophyte without undergoing fertilization.

Some ferns, including the bracken, are regarded as weeds because they cover fields and bodies of water, blocking light and oxygen necessary for other organisms to survive.

Uses

Economically, *Pterophyta* are not as significant as other plants. Nevertheless, some ferns species are edible, with crosiers being considered delicacies. Other ferns are used medicinally.

By contrast, *Osmunda* and *Pteridium* ferns are considered to be carcinogenic. The aquatic mosquito fern (*Azolla*) hosts *Anabaena azollae*, which converts nitrogen for use by plants such as rice, enhancing production in rice paddies and other fields. Animals often root for fern rhizomes, which store starches. The braken fern *Pteris vittata* absorbs arsenic, a carcinogenic heavy metal, from soil. By removing this toxin, ferns can restore contaminated areas into viable agricultural, industrial, and recreational sites.

The most important economic use of *Pterophyta* is as ornamental garden plants and houseplants. Fern fronds are used in cut-flower arrangments as ornamental greenery. Botanical collectors have identified rare ferns, for which they pay high prices; there is even an underground economy of smuggling ferns illegally from protected areas. Masses of fern roots are used to cultivate such epiphytic greenhouse plants as orchids. In the Middle Ages, some people believed that at midnight on June 24, St. John's Day, ferns would produce blossoms which contained magical seeds.

Elizabeth D. Schafer

See also: Bryophytes; Evolution of plants; Psilotophytes; Seedless vascular plants.

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FERTILIZERS

Categories: Agriculture; economic botany and plant uses; nutrients and nutrition; soil

Fertilizers are materials used to modify the chemical composition of soil in order to enhance plant growth. They represent an important use of natural resources because agricultural systems depend upon an ability to retain soil fertility.

Soil is a dynamic, chemically reactive medium, and agricultural soils must provide structural support for plants, contain a sufficient supply of plant nutrients, and exhibit an adequate capacity to hold and exchange minerals.

Topsoil, the 6-inch layer of soil covering the earth's landmasses, is the *root zone* for the majority of the world's food and fiber crops. As plants grow and develop, they remove the essential mineral nutrients from the soil. Because crop production normally requires the removal of plants or plant parts, nutrients are continuously being removed from the soil. Therefore, the long-term agricultural use of any soil requires periodic fertilization to replace these lost nutrients. Fertilizers are associated with every aspect of this nutrient replacement process. The application of fertilizer is based on a knowledge of plant growth and development, soil chemistry, and plant-soil interactions.

Soil Nutrients

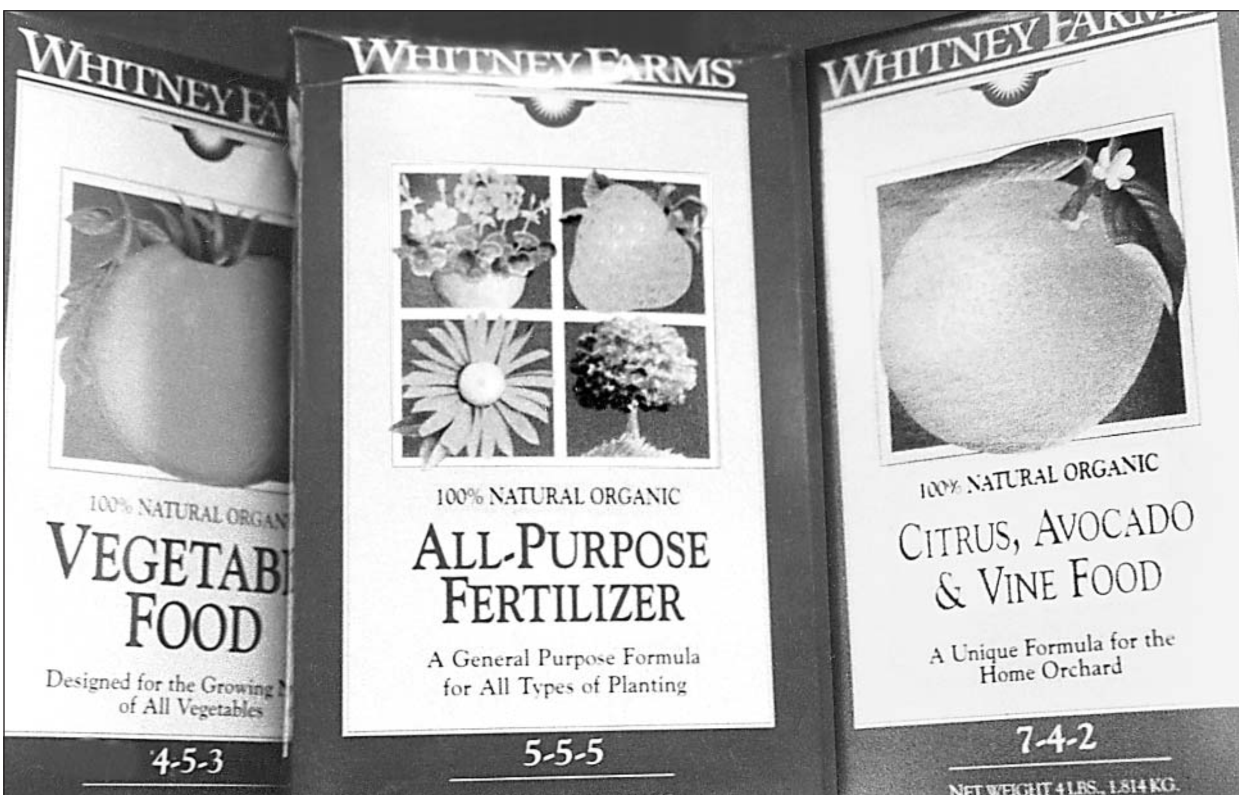
Plants require an adequate supply of both macronutrients (calcium, magnesium, sulfur, nitrogen, potassium, and phosphorus) and micronutrients (iron, copper, zinc, boron, manganese, chloride, and molybdenum) from the soil. If any one of these nutrients is not present in sufficient amounts, plant growth and, ultimately, yields will be reduced. Because micronutrients are required in small quantities, and deficiencies in these minerals occur infrequently, the majority of agricultural fertilizers contain only macronutrients. Although magnesium and calcium are utilized in large quantities, most agricultural soils contain an abundance of these two elements, either derived from parent material or added as lime. Most soils also contain sufficient amounts of sulfur from the weathering of sulfur-containing minerals, the presence of sulfur in other fertilizers, and atmospheric pollutants.

The remaining three macronutrients (nitrogen, potassium, and phosphorus) are readily depleted and are referred to as fertilizer elements. Hence, these elements must be added to most soils on a regular basis. Fertilizers containing two or more nutrients are called mixed fertilizers. A fertilizer labeled 10-10-10, for example, means that the product contains 10 percent nitrogen, 10 percent phosphorus, and 10 percent potassium. These elements can be supplied in a number of different forms, some of which may not be immediately useful to plants. In the United States, where fertilizer labeling is regulated for sales, most states require that the label reflect the percentage of nutrients available for plant use. Fertilizers are produced in a wide variety of single and mixed formulations, and the percentage of available nutrients generally ranges from a low of 5 percent to a high of 33 percent. Mixed fertilizers may also contain varying amounts of different micronutrients.

Sources and Production

Nitrogen fertilizers can be classified as either chemical or *natural organic*. Natural organic sources are derived from plant and animal residues and include such materials as animal manure, cottonseed meal, and soybean meal. Because natural organic fertilizers contain relatively small amounts of nitrogen, commercial operations rely on chemical fertilizers derived from sources other than plants and animals. Major chemical sources of nitrogen include ammonium compounds and nitrates. The chemical fixation of atmospheric nitrogen by the Claude-Haber ammonification process is the cornerstone of the modern nitrogen fertilizer manufacturing process. Once the ammonia is produced, it can be applied directly to the soil as anhydrous ammonia, or it can be mixed with water and supplied as a solution of aqueous ammonia and used in chemical reactions to produce other ammonium fertilizers, urea, or nitrates for nitrate fertilizers.

Some organic fertilizers contain small amounts of phosphorus, and organically derived phosphates from guano or acid-treated bone meal were used in the past. However, the supply of these materials is scarce. Almost all commercially produced agricultural phosphates are applied as either phosphoric acid or superphosphate derived from rock phosphate. The major phosphate component in commercially important deposits of rock phosphate is apatite. The apatite is mined, processed to separate the



Yasmine Cordoba

Commercial fertilizers containing two or more nutrients are called mixed fertilizers. The numbers on the packaging refer to nitrogen, phosphorus, and potassium content. For example, the fertilizer above labeled 5-5-5 contains 5 percent nitrogen, 5 percent phosphorus, and 5 percent potassium, respectively.

phosphorus-containing fraction from inert materials, and then treated with sulfuric acid to break the apatite bond. The superphosphate precipitates out of the solution and sets up as a hard block, which can be mechanically granulated to produce a fertilizer containing calcium, sulfur, and phosphorus.

Potassium fertilizers, commonly called "potash," are also obtained from mineral deposits below the earth's surface. The major commercially available potassium fertilizers are potassium chloride extracted from sylvanite ore, potassium sulfate produced by various methods (including extraction from langbeinite or burkeite ores or chemical reactions with potassium chloride), and potassium nitrate, which can be manufactured by several different chemical processes. Although limited, there are sources of organic potassium fertilizers, such as tobacco stalks and dried kelp.

While the individual nitrogen, phosphorus, and potassium fertilizers can be applied directly to the soil, they are also commonly used to manufacture mixed fertilizers. Between two and ten different materials with widely different properties are mixed together in the manufacturing process. The three most common processes used in mixed fertilizer production are the ammonification of phosphorus materials and the subsequent addition of other materials, bulk blending of solid ingredients, and liquid mixing. Fillers and make-weight materials are often added to make up the difference between the weight of fertilizer materials required to furnish the stated amount of nutrient and the desired bulk of mixed products. Mixed fertilizers have the obvious advantage of supplying all the required nutrients in one application.

Application and Environment

The application of fertilizer to agricultural soil is by no means new. Farmers have been applying *manures* to improve plant growth for more than four thousand years. For the most part, this practice had little environmental impact. Since the development of chemical fertilizers in the late nineteenth century, however, fertilizer use has increased tremendously. During the second half of the twentieth century, the amount of fertilizer applied to the soil increased more than 450 percent. While this increase has more than doubled the worldwide crop production, it has also generated some environmental problems.

The production of fertilizer requires the use of a variety of natural resources, and some people have argued that the increased production of fertilizers has required the use of energy and mineral reserves that could have been used elsewhere. For every crop, there is a point at which the yield may continue to increase with the application of additional nutrients, but the increase will not offset the additional cost of the fertilizer. The economically feasible practice, therefore, is to apply the appropriate amount of fertilizer that produces maximum profit rather than maximum yield. Unfortunately, many farmers still tend to *overfertilize*, which wastes money and contributes to environmental degradation. Excessive fertilization can result in adverse soil reactions that damage plant roots or produce undesired growth patterns. Overfertilization can actually decrease yields. If supplied in excessive amounts, some micronutrients are toxic to plants and will dramatically reduce plant growth.

The most serious environmental problem associated with fertilizers, however, is their contribution to *water pollution*. Excess fertilizer elements, particularly nitrogen and phosphorus, are carried from farm fields and cattle feedlots by water runoff and are eventually deposited in rivers and lakes, where they contribute to the pollution of aquatic ecosystems. High levels of plant nutrients in streams and lakes can result in increased growth of phytoplankton, a condition known as *eutrophication*. During the summer months, eutrophication can deplete oxygen levels in lower layers of ponds and lakes. Excess nutrients can also be leached through the soil and contaminate underground water supplies. In areas where intense farming occurs, nitrate concentrations are often above recommended safe levels. Water that contains excessive amounts of plant nutrients poses health problems if consumed by humans and livestock, and it can be fatal if ingested by newborns.

Importance to Food Production

Without a doubt, the modern use of fertilizer has dramatically increased crop yields. If food and fiber production is to keep pace with the world's growing population, increased reliance on fertilizers will be required in the future. With increasing attention to the environment, future research will be aimed at finding fertilizer materials that will remain in the field to which they are applied and at improving application and cultivation techniques to contain materials within the designated application area. The use of technology developed from discoveries in the field of molecular biology to develop more efficient plants holds considerable promise for the future.

D. R. Gossett

See also: Agronomy; Biofertilizers; Composting; Eutrophication; Hormones; Nutrient cycling; Nutrients; Nutrition in agriculture; Soil.

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FLAGELLA AND CILIA

Categories: Anatomy; bacteria; cellular biology; microorganisms

Flagella and cilia are hairlike structures, made primarily of protein, found on the surfaces of cells and used for movement by microorganisms and some specialized cells, such as the gametes of certain plants with motile sperm. Because flagella and cilia are so similar, many scientists use the term "undulipodia" for both in reference to eukaryotic organisms.

Although the term "flagellum" is used in reference to both prokaryotes (archaea and bacteria) and eukaryotes (fungi, protists, plants, and animals), the structure and mechanism of action of this structure in prokaryotes are quite different from the structure and mechanism of action in eukaryotes. Eukaryotic flagella and cilia, however, are structurally and functionally identical. The differences between them are in their number, length, and position. Flagella are less numerous, longer, and usually polar, while cilia are more numerous and shorter, covering much of the cell's surface. Because the dividing line between eukaryotic flagella and cilia is not precise, many scientists use the term *undulipodia* as a collective word for both eukaryotic flagella and cilia. In some algae, other protists, and the gametes of certain plants with motile sperm, flagella and cilia can occur.

Bacterial Flagella

Bacterial flagella are composed of a single protein called *flagellin*. Molecules of this globular protein are stacked to form a thin filament approximately 0.01-0.015 micrometer in diameter. The filament protrudes through the cell wall at the tip of the bacterium (polar flagella) or over the entire surface of the bacterium (peritrichous flagella). *Spirochetes* are unusual in this regard because the flagella do not pierce the cell wall but are located in the space between it and the plasma membrane. The base of each flagellum connects to a rotary motor anchored in the plasma membrane. The cell provides energy to the motor, which then rotates the flagellum to allow cell movement. Rotational movement may be counter-clockwise, which leads to generally straight-line motion, or clockwise, which leads to a more random tumbling motion.

Eukaryotic Flagella and Cilia

Eukaryotic flagella and cilia, or undulipodia, are more complex and larger (approximately 0.25 micrometer in diameter) than their prokaryotic counterparts. The main component of these eukaryotic structures is the *microtubule*; a long, cylindrical structure composed of *tubulin* proteins. In eukaryotic flagella and cilia, two central microtubules are surrounded by a circular arrangement of nine microtubule pairs. Eukaryotic flagella and cilia also contain more than five hundred other proteins, including dynein and kinesin, motor proteins that use cell energy to slide the microtubules past each other, causing an undulating motion (hence the name undulipodium). Unlike bacterial flagella, eukaryotic flagella and cilia are considered to be intracellular structures because they are covered by a continuation of the plasma membrane.

Although absent from fungi, undulipodia are found in many protists and in some plants. Unicellular algae (such as *Chlamydomonas* and *Euglena*) and colonial algae (*Volvox*) use undulipodia for locomotion. Multicellular algae (*Phaeophyta*, *Rhodophyta*) produce flagellated sperm. Among the true plants, bryophytes (*Hepatophyta*, *Anthocerotophyta*, and *Bryophyta*), ferns and their allies (*Psilotophyta*, *Lycophyta*, *Sphenophyta*, and *Pterophyta*), and some gymnosperms (*Cycadophyta* and *Ginkgophyta*) also produce flagellated sperm. Other gymnosperms (*Coniferophyta*) and angiosperms (*Anthophyta*) do not produce cells with flagella or cilia.

Richard W. Cheney, Jr.

See also: Algae; Bacteria; Chemotaxis; Cryptomonads; Cytoskeleton; Diatoms; Dinoflagellates; Euglenoids; Evolution of plants; Haptophytes; Heterokonts; Oomycetes; Phytoplankton; Prokaryotes; *Protista*; Reproduction in plants; *Ulvophyceae*.

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FLOWER STRUCTURE

Categories: Anatomy; angiosperms

Flowers are the modified shoots bearing modified leaves that serve as the sexual reproductive organs of angiosperms. This strategy for reproduction has been so successful that angiosperms now dominate the plant world, and accordingly there are many variations on the basic structure of a flower.

Flowers are organs of sexual reproduction produced by the angiosperms (phylum *Anthophyta*), the largest phylum of photosynthetic organisms, with roughly 250,000 species. This large number represents a great diversity of flower types, but all flowers have some common structural elements.

Flower Parts

Flowers are modified shoots bearing modified leaves. In the typical flower, the modified leaves can be grouped into four sets based on appearance and function: sepals, petals, stamens, and pistils. The *sepals* and *petals* are lowermost on the shoot toward the sides of the flower. The *stamens* and *pistils* are at the tip of the shoot at the inside. While sepals and petals are easy to see, stamens and pistils are often visible only when the flower is closely examined. Two other important parts are the *pedicel*, a stalk on which flowers are frequently borne, and the top of the pedicel, called the *receptacle*, to which the other flower parts are typically attached.

Of the four main parts, the sepals are generally the most leaflike and generally are attached to the bottom of the receptacle. Sepals protect the immature flower during the bud stage. Flowers typically have three to eight sepals, depending on the species. Collectively, the sepals in a flower are called the *calyx*. Above the sepals are the *petals*. Although flattened like the sepal, each petal is usually soft and colored—white, yellow, pink, blue, purple, orange, maroon, or even brown. Petals attract insects, hummingbirds, bats, or other animals, aiding the reproductive process. Usually, the number of petals in a flower will be the same as the number of sepals. Collectively, the petals in a flower are called the *corolla*.

The *stamens*, located inside the petals, are composed of a small *anther* (ball-shaped, egg-shaped, or tubular) and a threadlike *filament* connecting the anther to the rest of the flower. The anther, in turn, is composed of two or four tiny chambers, within which powdery *pollen* grains are produced and stored. Each grain of pollen contains the immature sperm of the plant. Thus, the stamens function as the male part of the flower in sexual plant reproduction, and they may number from one to dozens. The term *androecium* refers collectively to all the stamens within a flower.

The *pistils* form the final set of parts. Each pistil is often shaped like a vase, although the shape varies. The *ovary*, the base of the pistil, is swollen and hollow. The wall of the ovary, called the *pericarp*, is typically green, and the hollow space in the ovary is called the *locule*. Within the locule are one or more tiny globular *ovules*, each containing an egg nucleus and thus functioning as the female structure in sexual reproduction. In addition to the ovary, the pistil is typically composed of two or more parts: the *style*, a slender necklike structure above the ovary, and the *stigma*, a swollen area at the top of the style that traps pollen grains with minute hairs covered by a sticky, sugary film. While most flowers have only one pistil, many have several pistils, attached to the receptacle. The pistils within a flower are collectively called the *gynoecium*.

Functions of Flower Parts

Flowers and their parts function to achieve sexual reproduction, including pollination and seed formation. After pollination is finished, the flower begins the process of seed and finally fruit formation. During *pollination*, pollen grains are released from the anther and carried to the stigma, either by animals (such as insects, birds, and bats) or by wind. Animals, attracted by the flower's colors or aromas, visit flowers to obtain food—either the pollen itself or the *nectar*, a sugary liquid produced by small glands called nectaries at the base of the flower. The animal brushes up against the anthers, which deposit pollen on the animal's body. The animal transfers the pollen to the stigma of either the same flower (self-pollination) or a second flower (cross-pollination). During wind pollination, the anthers release their pollen, which is then borne by air currents. Some of the grains are deposited on a stigma of the same or another flower.

Each pollen grain germinates and produces a slender thread of protoplasm that grows downward through the style and into the ovary. This thread, the *pollen tube*, contains the sperm and grows toward an ovule, where it deposits its sperm. The sperm then fuses with the egg, achieving fertilization as the first cell of the new generation is produced. The ovule matures to form a seed. At the same time, the surrounding ovary enlarges greatly, becoming a fruit as other parts of the flower recede and die off.

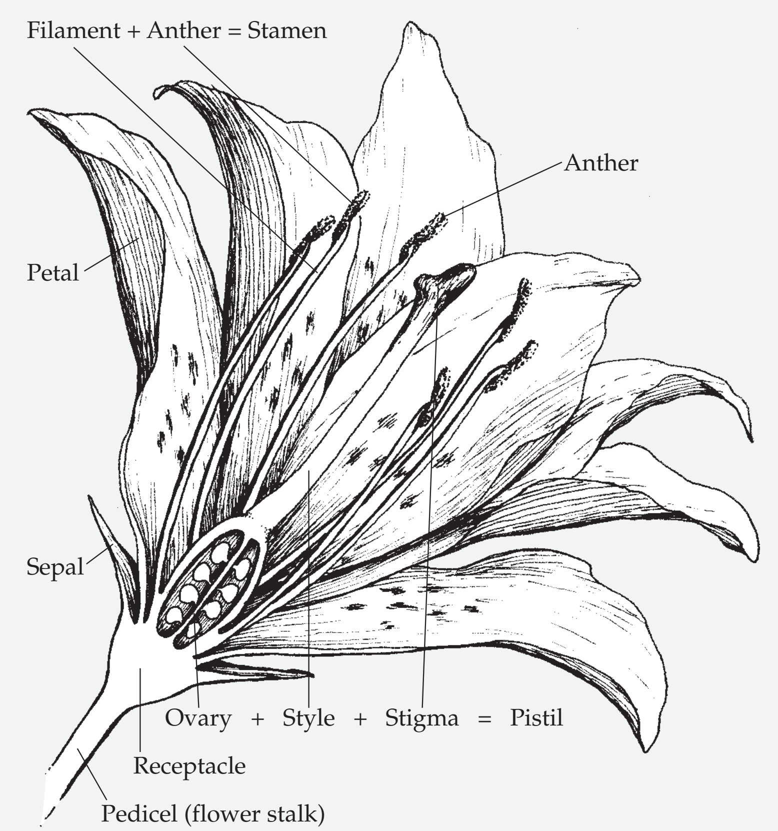
Because the stamens and pistils are intimately involved in reproduction, botanists refer to these as *essential parts*. The sepals and petals are termed *nonessential parts*, though in fact they remain important. The sepals and petals are sometimes called the *perianth* because they are found on the periphery of the anthers. A *complete flower* is one that has all four sets of parts. A *perfect flower* is one that has both androecium and gynoecium and is thus bisexual.

Structural Variations

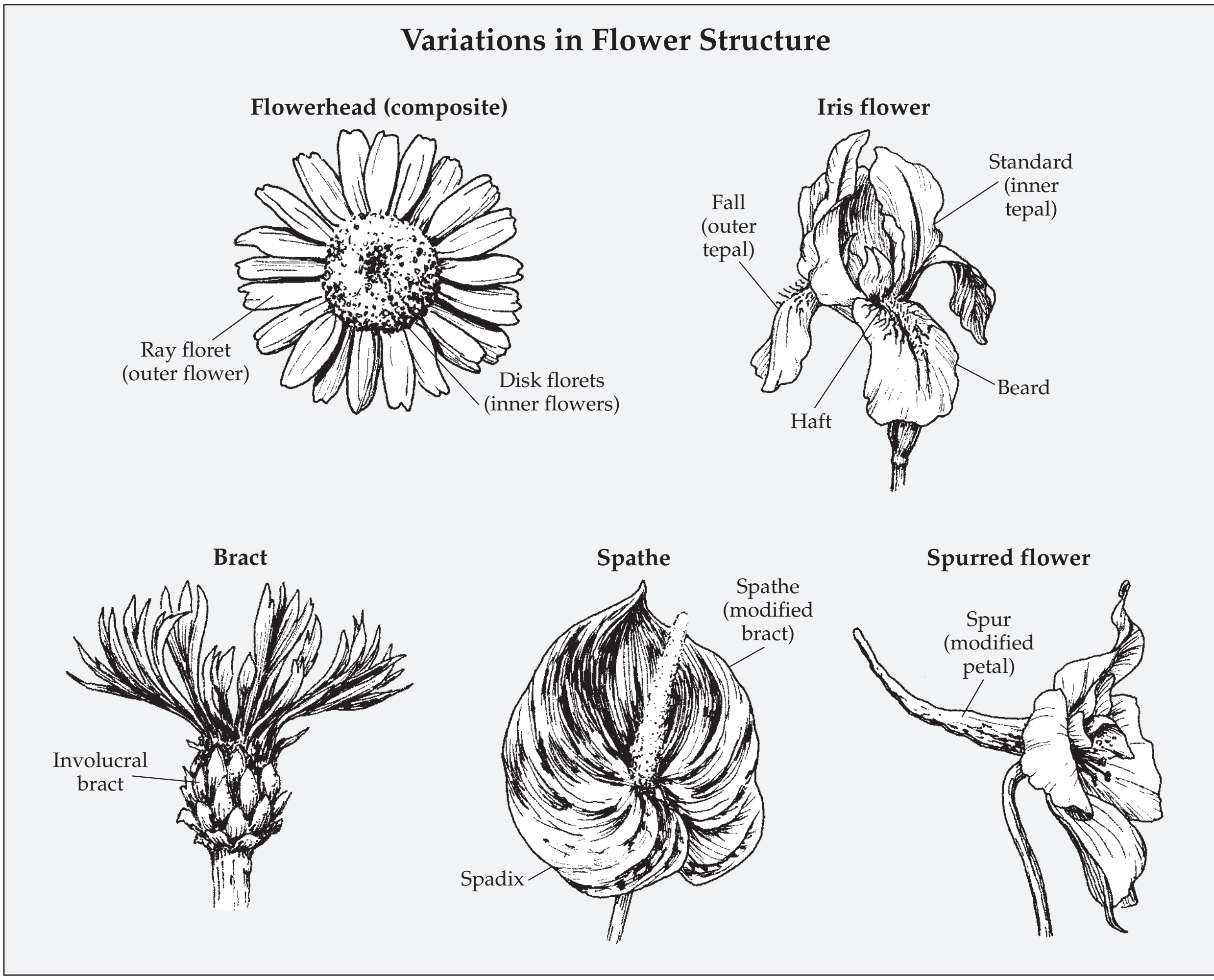
Many plant species produce flowers that deviate from the idealized format. Certain lilies, for example, do not have sepals and petals that are clearly distinguishable from each other. In magnolias and some water lilies, each flower produces perianth parts that intergrade from a sepal-like form toward the outside to a petal-like form toward the inside.

Many flowers have evolved to become simpler and are called *incomplete flowers*; they may lack one or more sets of parts. *Apetalous flowers* have only sepals, although some, such as those of the liverleaf and anemone, may be petal-like. Elms, mulberries, oaks, plantains, pigweeds, and goosefeet have sepals that remain green and are usually tiny. *Naked flowers*, including those of birches and willows, develop neither sepals nor petals. Grass flowers are associated with tiny green parts called *bracts*, which are neither sepals nor petals. The nature of the perianth is related to the way a plant undergoes

Parts of a Flower



In the idealized flower, the parts are free down to the receptacle. Many flowers, however, exhibit connation, in which similar parts are fused above the receptacle: for example, the petals of the morning glory, fused to form a corolla, or the sepals of carnations, which form a calyx tube. Many plants have pistils composed of individual fused segments, called carpels, while others, such as the mallow, have connate stamens, forming a stamen tube.



Kimberly L. Dawson Kurnizki

Flowers take on many different forms, which have evolved to facilitate pollination by animals, wind, or water. Smaller, less showy flowers tend to be pollinated by wind (which can easily lift and carry their pollen), whereas animal-pollinated flowers have evolved colors, odors, and even structures that mimic insects or store nectar—all designed to attract the pollinators.

pollination. Flowers with a well-developed corolla or a calyx made up of petal-like sepals are attractive to animals and insects, which function to pollinate them. Apetalous and naked flowers are wind-pollinated; they do not need to waste their energy making showy flower parts.

Some incomplete flowers lack either the androecium or the gynoecium. These *imperfect flowers* are unisexual and fall into two categories: *staminate flowers* are male flowers, having only stamens and no pistils; *pistillate flowers* are female, having only pistils and no stamens. Forced into cross-pollination, imperfect flowers benefit the plant by preventing some of the harm inherent in self-pollination.

In the idealized flower, the parts are free down to the receptacle. Many flowers, however, exhibit *connation*, in which similar parts are fused above the receptacle. The petals of the morning glory are fused to form a funnel-shaped corolla. Carnations have connate sepals, forming a calyx tube. Many plants have pistils composed of individual fused segments, called *carpels*, while others, such as the mallow, have connate stamens, forming a stamen tube.

Other flowers show *adnation*, which involves the fusion of different parts. The stamens of phlox flowers are fused to the petals. The sepals, petals, and stamens of roses are all fused, forming a cup-shaped structure called a *hypanthium*. The presence of a hypanthium can be best observed in plum and cherry blossoms, whose individual sepals, petals, and stamens are attached to the rim of the hypanthium. Finally, many flowers have a hypanthium that is fused to the wall of the ovary. The result is that the sepals, petals, and stamens emerge from the top of the ovary, a good example being the apple blossom. Flowers of the latter category are said to have an inferior ovary, whereas the others have superior ovaries.

Flowers' corollas also vary: In flowers with a regular corolla, such as buttercups, lilies, and roses, all the petals are equal in size and shape, giving the flower a star shape. In flowers with irregular corollas, such as the snapdragon, pea, and orchid, one or more of the petals are unequal. Some irregular flowers, such as the violet, touch-me-not, and columbine, have a rounded, cone-shaped, or pointed extension of the corolla called a spur, which serves to store nectar.

Although not technically floral structures, color, shape, and inflorescences (the loose or dense clusters in which flowers appear on a plant) are other ways in which flowers differ, important because they allow certain pollinators to enter but exclude others. Bowl-shaped flowers are visited by a variety of insects, such as beetles and bees. Irregular flowers are typically pollinated by honeybees and bumblebees, and in some cases the insects fit the flower like a key fits a lock. Flowers with long spurs are pollinated by long-tongued insects such as moths. Color, determined by special molecules called pigments that occur within the cells of the plant, attracts different pollinators as well: red flowers are pollinated by birds, specifically hummingbirds and butterflies. White flowers are often open at night and are visited by moths. One group of plants have brown or maroon flowers and an odor of rotting flesh. These "carrion flowers" are pollinated by an array of insects, particularly beetles and flies. Interestingly, the way that humans perceive color is often different from the way that other animals perceive color. For example, xanthophylls reflect not only yellow but also a deep violet that bees can perceive but that humans cannot.

Kenneth M. Klemow

See also: Angiosperm cells and tissues; Angiosperm evolution; Angiosperm life cycle; Angiosperm plant formation; Angiosperms; Animal-plant interactions; Flower types; Flowering regulation; Fruit: structure and types; Garden plants: flowering; Hormones; Inflorescences; Pollination; Reproduction in plants; Seeds; Shoots; Stems.

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FLOWER TYPES

Categories: Anatomy; angiosperms

The flower is the most distinctive feature of the phylum Anthophyta*, commonly referred to as angiosperms or flowering plants, and is responsible in making them the most dominant, diverse, and widespread of all groups of plants.*

There are already about 250,000 species of flowering plants that have been discovered and named. The basis for their diversity comes from their incredible reproductive success in a wide variety of habitats. The success of this group is also reflected by the diversity of their flowers that show astonishing displays of different forms, sizes, shapes, and colors—all of these to lure pollinators and effect sexual reproduction.

Flowers are considered as an organ system because they are made up of two or more sets, or whorls, of leaflike structures. A typical flower is composed of four whorls, which are the *sepals*, *petals*, *stamens*, and a *pistil* with one or more *carpels*. Much of the variation among flowers is based on variation of these basic parts.

Complete and Incomplete Flowers

A flower that has all four whorls of floral parts is said to be a *complete flower* (such as the hibiscus and the lily). An *incomplete flower* lacks any one or more of these parts (such as those of elms, willows, oaks, and plantains). With or without sepals and petals, a flower that has both stamen and pistil is called a *perfect flower*. Thus, all compete flowers are prefect, but not all perfect flowers are complete. In contrast, flowers that have only stamens or only pistils are called *imperfect flowers*.

Unisexual and Bisexual Flowers

Unisexual flowers are either *staminate* (bearing stamens only) or *pistillate* (bearing pistils only) and are said to be imperfect. *Bisexual flowers* are perfect because they have both stamens and pistil. When staminate and pistillate flowers occur on the same individual, the plant is called *monoecious* (examples include corn and the walnut tree). When staminate and pistillate flowers are borne on separate individual flowers, the plant is said to be *dioecious* (examples include asparagus and willow).

Superior or Inferior Ovaries

The position of the ovary also varies among different flower types. A flower has a *superior ovary* when the base of the ovary is located above where the sepals, petals, and stamens are attached. This point of attachment is referred to as the *receptacle* or *hypanthium*, the fused bases of the three floral parts (tulips and St. John's wort are examples). An *inferior flower* has an ovary below where the sepals, petals, and stamens are attached (as do daffodils and sabatia). Some flowers show an *intermediate type*, where the receptacle partly surrounds the ovary; the petals and stamens branch from the receptacle about halfway up the ovary (as in cherry, peach, and almond flowers).

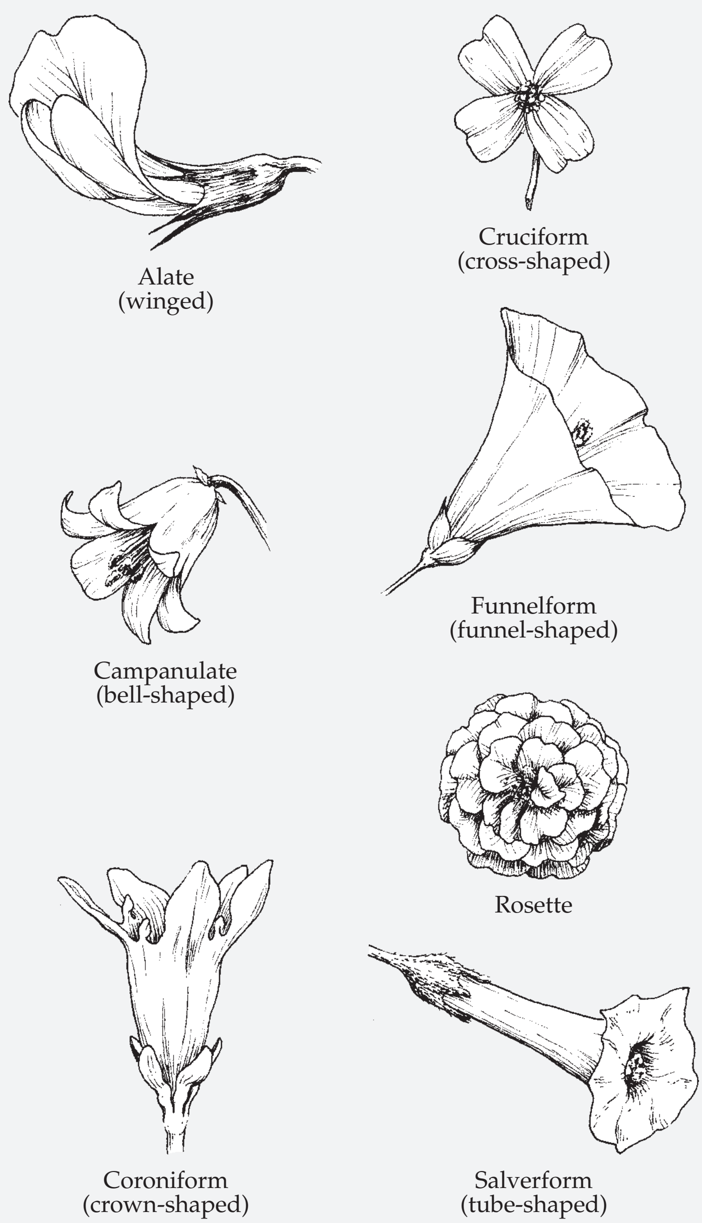
Hypogynous, Epigynous, and Perigynous Flowers

The position of the ovary in relation to the attachment of floral parts also varies from superior to inferior ovaries. Flowers in which the sepals, petals, and stamens are attached below the ovary are called *hypogynous*, and the ovaries of such flowers are said to be superior (as in pelargonium and silene). Flowers in which the sepals, petals, and stamens appear to be attached to the upper part of the ovary due to the fusion of the hypanthium are called *epigynous*, and the ovaries of such flowers are said to be inferior (as in cornus and narcissus). Flowers in which the hypanthium forms a cuplike or tubular structure that partly surrounds the ovary are called *perigynous*. In such flowers, the sepals, petals, and stamens are attached to the rim of the hypanthium, and the ovaries of such flowers are superior.

Fused and Distinct Floral Parts

The parts of a flower may be *free* or *united*. Fusion of like parts (such as petals united to petals) is called *connation*. When like parts are not fused, they are said to be *distinct* (one petal is distinct from another petal). Fusion of unlike parts (stamens united to petals) is called *adnation*, and the contrasting condition is called *free* (stamens are free from petals). Fused structures may be united from the moment of origin onward, or they may initially be separate and grow together as one later in development.

Flower Shapes: Perianth Forms



Kimberly L. Dawson Kurnizki

Regular and Irregular Flowers

In many flowers, the petals of similar shape radiate from the center of the flower and are equidistant from one another. Such flowers are said to have *regular* or *radial symmetry*. In these cases, even though there may be an uneven number of sepals and petals, any line drawn through the center of the flower will divide it into two similar halves. The halves are either exact duplicates or mirror images of each other. Flowers with radial symmetry are also called *actinomorphic flowers* (examples: stonecrop, morning glory). Flowers with *irregular* or *bilateral symmetry* have parts arranged in such a way that only one line can divide the flower into equal halves that are more or less mirror images of each other. Flowers with bilateral symmetry are also called *zygomorphic flowers* (examples: mint, pea, snapdragon). A few flowers have no plane of symmetry and are referred to as *asymmetrical*.

Corolla Shapes

Corolla is the collective term for all the petals of a single flower. This is usually the showy part of the flower. In fused corollas, any extension of the petal beyond its fused part is called the *limb*. The tubelike structure where the petals are united at the bottom of the fused corollas is called the *tube*. The opening at the top of the tube in fused corollas is called the *throat*. In the following different types of corolla shapes, numbers 1 to 6 are actinomorphic, while numbers 7 to 11 are zygomorphic.

1. *Rotate*: wheel-shaped with a short tube and large limb (example: bluets).

2. *Campanulate*: bell-shaped with an extended, flaring tube (example: bellflower).

3. *Funnelform*: funnel-shaped with a continuously expanding tube and little flaring (example: bindweeds).

4. *Tubular*: an elongated tube with minimal limb (example: trumpet vine).

5. *Salverform*: an elongated tube with a conspicuous limb, trumpet-shaped (examples: Russian olive, morning glory).

6. *Urceolate*: an inflated tube with a terminal constriction, urn-shaped (example: highbush blueberry).

7. *Bilabiate*: two-lipped, usually because of the presence of a landing platform formed by basal lobes (examples: snapdragon, salvia).

8. *Ligulate*: petals connate at the margins to form a strap-shaped corolla (example: asters).

9. *Galeate*: helmet-shaped (example: pedicularis).

10. *Spurred*: with an extension or spur that often produces nectaries (examples: impatiens, utricularia).

11. *Papilionaceous*: like a butterfly with a central standard petal and lateral wing petal (example: lupines).

Flowers of Monocots and Dicots

Floral variation provides part of the basis for dividing the flowering plants into two major groups: the *dicotyledons* and the *monocotyledons*. The informal name "dicot" is given to plants having two cotyledons (seed leaves) in each seed; "monocot" refers to plants that have one cotyledon in the seed. In monocots, the flower parts occur in threes or multiples of three; for example, three sepals, three petals, six stamens, and a pistil with three carpels. In dicots, flower parts usually occur in fours or fives or multiples of four or five. Although dicots and monocots may have other numbers of floral parts, many other features are unique to each group. Dicots include about 80 percent of all angiosperm species, including many herbaceous plants and all woody, flower-bearing trees and shrubs. Monocots are primarily herbaceous, but they also include some trees, such as palms and Joshua trees.

Types of Inflorescence

Flowers may be solitary, or they may be grouped together in an *inflorescence*, a cluster of flowers. An inflorescence has one main stalk, or *peduncle*. It may also bear numerous smaller stalks called pedicels, each with a flower at its tip. The arrangement of pedicels on a peduncle characterizes different kinds of inflorescences. Some of the common types of inflorescences are as follows:

Spike: The flowers, which are with a very short or with no pedicel, are attached along the elongate and unbranched peduncle of the inflorescence (examples: plantain, spearmint, tamarisk).

Raceme: The flowers are with pedicels of about the same length, which are attached along the elongate and unbranched peduncle of the inflorescence (examples: lily of the valley, snapdragon, mustard, currant). The oldest flowers are at the base of the inflorescence and the youngest at the apex.

Panicle: The flowers are with pedicels, which are attached along the branches arising from the peduncle of the inflorescence (examples: oats, rice, fescue).

Corymb: The flowers are with pedicels of unequal length, which are attached along an unbranched, elongate peduncle, forming a flat-topped inflorescence (examples: hawthorne, apple, dogwood).

Umbel: The flowers are with pedicles, which are all attached at about the same point at the end of the peduncle—this is specifically called a *simple umbel* (examples: onion, geranium, milkweed). A *compound umbel* is formed when the peduncle produces branches that end at approximately the same level, forming a flat top, and the ends of these branches arise from a common point (examples: carrot, dill, parsley).

Head: The flowers do not have pedicels, and they all cluster tightly on the expanded tip of the peduncle (examples: sunflower, daisy, marigold). This type of inflorescence is also referred to as *capitulum*.

Cyme: The flowers with pedicels are located at the ends of the peduncle and lateral branches as well as along the length of the lateral branches. The youngest flowers in any cluster occur farthest from the tip of the peduncle (example: chickweed).

Catkin: The flowers have no pedicels, are unisexual (either staminate or pistillate), and are attached along the length of the peduncle (examples: hazelnut, willow, birch, walnut). The flowers are usually very small and fall as a group. This type of inflorescence is also referred to as *ament*.

Spadix: The flowers have no pedicels and are attached along the length of the thickened or fleshy peduncle, which is enveloped by a conspicuously colored bract called a spathe (example: philodendron, anthurium).

Some types of inflorescences characterize different groups of plants. For example, nearly all members of the carrot family (*Apiaceae*) have compound umbels. All members of the sunflower family (*Asteraceae*) have heads, including chrysanthemums, zinnias, marigolds, and dandelions. All members of the arum family (*Araceae*) have a spadix inflorescence.

Danilo D. Fernando

See also: Angiosperms; Flower structure; Inflorescences; Plant tissues; Pollination; Shoots; Stems.

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FLOWERING REGULATION

Categories: Angiosperms; physiology; reproduction and life cycles

All flowering is regulated by the integration of environmental cues into an internal sequence of processes. These processes regulate the ability of plant organs to produce and respond to an array of signals. The numerous regulatory switches permit precise control over the time of flowering.

Control over the time of flowering is essential for the survival of flowering plants (angiosperms). Insect pollinators may be present only at certain times; unless an insect-pollinated plant is flowering at that time, pollination and the production of the next generation cannot occur. Embryo and seed development may be successful only under certain climatic conditions. The ability to respond to environmental cues is an essential factor in the regulation of flowering.

While the basic biochemical sequence of events may be common to all angiosperms, the specific regulatory steps vary greatly among species. A floral *promoter* is produced by the leaves and is transported to the shoot apex, which results in the initiation and, ultimately, the production of flowers. To analyze control points in this sequence, it is helpful to focus separately on environmental signals such as temperature and photoperiod and the way organs perceive and respond to these signals.

Chemical Communication

The regulation of flowering requires interactions between the shoot apex and other organs and thus depends heavily on chemical signals. There is strong evidence for the existence of a floral promoter called *florigen*, which may be produced in the leaves. The existence of florigen was first proposed by M. Kh. Chailakhyan, a Soviet plant physiologist, in 1937. Florigen was believed to be produced in leaves, because if leaves were removed before the photoperiod was right for flowering (a process called photoinduction), no flowering occurred. Later work by Anton Lang showed that the

The role of day length in the regulation of flowering had been recognized by 1913. The impact of photoperiod on flowering in numerous species soon became apparent, but some plants, including sunflowers, are day-neutral; they flower independently of photoperiod.

plant hormone *gibberellin* could induce flowering in certain plants, even without appropriate photoinduction. This prompted Chailakhyan to consider the possibility that florigen was actually composed of two different substances, gibberellin and a new substance he called *anthesin*.

In the late 1970's Lang, Chailakhyan, and I. A. Frolova, working with tobacco plants, discovered that there was also a floral inhibitor they called *antiflorigen*. Later, several genes controlling the production of an inhibitor in pea cotyledons and leaves were identified in other laboratories. In addition to leaf-derived inhibitors, root-derived inhibitors have been shown to regulate flowering in black currant and tobacco plants. Aside from the clear role of gibberellin in flowering, none of the other promoters and inhibitors has been identified. Nutrient levels and allocation throughout the plant may also control the time of flowering.

Photoperiod

One major role of environmental signals is to control the timing of the production of florigen and antiflorigen. This link between environmental and internal signals has been most clearly established for photoperiod. The role of day length in the regulation of flowering had been recognized by 1913. The impact of photoperiod on flowering in numerous species soon became apparent.

In the 1930's W. W. Garner and H. A. Allard found an unusually large tobacco plant growing in a field. The plant stood out because it failed to flower; they named it the Maryland Mammoth. Maryland Mammoth cuttings flowered in a greenhouse that December, and subsequent experimentation demonstrated that flowering would occur only when days were short and nights long. The Maryland Mammoth is an example of a *short-day plant*. Short-day plants generally flower in the spring or fall, when day lengths are shorter. Other examples of short-day plants are poinsettias, cockleburs, Japanese morning glories, and chrysanthemums. Plants such as spinach, lettuce, and henbane will flower only if a critical day length is exceeded; they are categorized as *long-day plants* and generally flower during long summer days.

Photoperiodic control mechanisms may be more complex, as in the case of ivy, a *short-and-long-day plant*, which requires at least a twelve-hour photoperiod followed by a photoperiod of at least sixteen hours. Still other plants, including sunflowers and maize, are *day-neutral*: They flower independent of photoperiod. By the 1940's it was established that night length, not day length, is critical in the photoperiodic control of flowering. For example, flowering in the short-day Japanese morning glory can be prevented by a brief flash of light during the critical long night. In comparing short-day and long-day plants, the distinguishing factor is not the absolute length of night required; rather, the difference is whether that night length provides the minimum (short-day plants) or maximum (long-day plants) period of darkness required to permit flowering.

How a plant perceives night length and translates this into the appropriate response in terms of flowering is not fully understood. A pigment known as *phytochrome*, however, plays a critical role. Phytochrome exists in two forms (P_r and P_{fr}) that are interconvertible. P_r absorbs red light and is converted to P_{fr}, which absorbs far-red light and is subsequently converted back to the P_r form of the pigment. Sunlight contains both red and far-red light, and thus an equilibrium between the two forms is achieved. At noon, about 60 percent of the phytochrome is in the P_{fr} form. In the dark, some P_{fr} reverts to P_r, and some breaks down. Because of the absence of red light, no new P_{fr} is generated.

The relationship between phytochrome and photoperiodic control of flowering has been established using night-break experiments with red and far-red light. (In these experiments, darkness is interrupted by momentary exposure to light.) Flowering in the Japanese morning glory, a short-day plant, can be inhibited by a flash of red light (as well as light equivalent to sunlight) in the middle of a long night. Far-red light has no effect. A flash of far-red light following a flash of red negates the inhibitory effect of the red light. In long-day plants, flowering can be induced when the dark period exceeds the critical night length with a red-light night break. Far-red light flashes do not result in flowering. The effect of the red flash can be negated by a subsequent far-red flash. In these experiments, the light flashes alter the relative amounts of P_r and P_{fr}.

Circadian Rhythms

How the perception of light by phytochrome is linked to the production of gibberellin and anthesin in long-day and short-day plants is not clear. One idea is that plants measure the amount of P_{fr} present. Flowering in short-day plants would be inhibited by P_{fr}, and these plants would not flower until very little or no P_{fr} remained after a long night. To flower, long-day plants would require some minimum level of P_{fr}, which would not be available if the nights were too long—but this explanation is not viable because P_{fr} vanishes within a few hours after the dark period begins.

Alternately, levels of phytochrome may influence an internal biological clock that keeps track of time. The clock establishes a free-running *circadian rhythm* of about twenty-four hours; this clock needs to be constantly reset to parallel the natural changes in photoperiod as the seasons change. Phytochrome interacts with the clock to synchronize the rhythm with the environment, a prospect that is strengthened by night-break experiments, where the time of the light flash during the night is critical. In the case of the Japanese morning glory, there are times during the night that a red light flash completely inhibits flowering and other times when it has no effect. In these experiments, the phase of the rhythm of the clock defines the nature of the interaction with phytochrome.

Studies on the relationship between flowering and day length have focused on the production of gibberellin and anthesin. There is evidence that the production of inhibitors by leaves is also under photoperiodic control. This has been demonstrated for photoperiodic tobacco plants and for some peas. In the case of the pea, the inhibitory effect is most obvious for short days, but lower levels of inhibitors continue to be produced as the days grow longer.

Temperature

Plants also use temperature as an environmental clue to ensure flowering. Assessing two environmental factors provides added protection. Some plants have a *vernalization* requirement—a chill that promotes or is essential for flowering. The control point regulated by vernalization may be different for different species. Vernalization has been shown to affect the sensitivity of leaves to respond to photoperiod. In some plants, only leaves initiated after the shoot apex has been chilled will induce flowering after the appropriate photoperiod.

Clearly, the competence of the leaves and shoot apex to respond to environmental and internal signals is crucial to the regulation of flowering. Pea mutants have been identified that have shoot apexes with differential sensitivity to floral induction or inhibition. Another pea mutant has an apex that is not competent to initiate flowers and remains perpetually vegetative. The competence of a day-neutral tobacco apex changes with age. In another species, the apexes of shoots cannot respond to vernalization early in development; this period of time is considered to be the juvenile phase.

A juvenile phase of development is most common in woody perennials. During this time, flowering cannot occur even under optimal environmental conditions. Maturation occurs gradually and may be accompanied by changes in leaf morphology and the ability of cuttings to root. The most significant occurrence is that the plant becomes competent to flower.

Genetic Control of Flowering

The Maryland Mammoth, discussed above, is an example of a short-day plant resulting from a mutation. Mutations that affect flowering time can lead to delayed flowering or to rapid flowering, regardless of photoperiod. Harmful effects of such mutations may include inadequate photosynthetic capability to sustain the crop (when flowering occurs too soon) or susceptibility to pests or cold temperatures at the end of the season (because of flowering too late). A focus of work on genetic modification of plants is the achievement of optimal flowering times.

Susan R. Singer, updated by Bryan Ness

See also: Angiosperm life cycle; Circadian rhythms; Dormancy; Genetics: mutations; Germination and seedling development; Hormones; Leaf abscission; Photoperiodism.

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FLUORESCENT STAINING OF CYTOSKELETAL ELEMENTS

Categories: Cellular biology; methods and techniques

Fluorescent antibody staining is a precise technique for marking elements of the cytoskeleton so they become visible under a microscope. The technique has revealed much about the location and functions of the cytoskeleton within a cell. It also offers some of the most visually appealing of the microscopic images available to biologists.

Cells require an internal system of fibers in order to maintain and change their shape. Perhaps the most straightforward function of the cytoskeleton is to provide cell support, a scaffolding that gives each cell a distinctive three-dimensional shape. Without such support every cell would be shaped like a fried egg. The fibers found in the cytoskeleton serve other functions as well: for example, as rails along which substances shuttle from one part of the cell to another. Equally important is the role of the cytoskeleton in cell movement and change in cell shape. The various cytoskeletal fibers can be rearranged, dissolved, and reconstructed at new locations when need be. The cytoskeleton is also a key component of some highly specialized cell structures, such as *cilia* and *flagella*.

Fluorescent antibody staining techniques allow scientists to observe exactly how various cytoskeletal fiber types are oriented within the cell. This technique has greatly increased knowledge of how the cytoskeleton does its jobs. It is also among the most aesthetically beautiful of all the procedures used by cell biologists.

The Cytoskeleton

The cytoskeleton is composed of three different kinds of fibers, each with different, specialized functions. *Microfilaments* are the smallest (6 nanometers in diameter). They are made up of a protein similar to the actin protein in muscle. It is thus not surprising that microfilaments participate in cell movement and shape changes. They usually are found in bundles just inside the surface of the cell, where they are best situated to help the cell change shape.

Intermediate filaments are somewhat larger. Unlike microfilaments, they seem to serve as passive scaffolding elements within the cell. They typically form an interlaced meshwork in the cytoplasm. The proteins that make up these fibers are subtly different in different kinds of cells; the significance of such variation is not clear.

The largest fibers are called *microtubules* (25 nanometers in diameter). They are hollow spirals of protein building blocks. The microtubules have important, specialized roles in particular regions of cells and at certain times in a cell's life. For example, they help move the chromosomes around during division of one cell into two. They are important components of both cilia and flagella—whiplike structures on the surfaces of some cells that serve as oars to help them swim about or to move substances along their surfaces.

Technique

The properties of the cytoskeleton depend upon its precise three-dimensional architecture within the intact cell. Thus, it is important that the researcher use methods designed to analyze the intact cytoskeleton inside whole cells. The most popular method is to fasten a fluorescent dye onto an antibody. The most commonly used dyes are *rhodamine* (for red fluorescence) and *fluorescein* (for greenish-yellow fluorescence). When such a fluorescent antibody is then added to cells, it can be located using a special *fluorescence microscope*.

Although this procedure works reasonably well, it can be improved by amplifying the signal—that is, by devising a method to add more than one molecule of fluorescent dye to each anticytoskeleton antibody molecule, which will increase the amount of fluorescent light emitted. The brighter light is much easier to see. This can be done using the so-called *secondary-antibody procedure*. A "secondary antibody" must be prepared using the first antibody (against the cytoskeletal protein) as an antigen. This time, the secondary antibody is made fluorescent. The cytoskeletal proteins are then tagged in two steps: First, the primary antibody is added to cells, then the fluorescent secondary antibody is added. Because of the nature of the secondary antibody, numerous molecules of it can adhere to each molecule of primary antibody. In this way, many fluorescent molecules can be attached to each molecule of primary antibody. The result is that the researcher can now see strikingly beautiful images in the fluorescence microscope: brilliantly colored glowing strands of the cytoskeleton, arranged in various patterns depending on what is happening inside the cell.

What Biologists Have Learned

Fluorescent antibody techniques have helped scientists learn that microfilaments and microtubules are dynamic fibers, made up of many kinds of protein (perhaps as many as several hundred), which grow and shrink as necessary. (Intermediate fibers are more stable.) In addition to proteins, whose primary role is to construct the filament itself, there are proteins associated with each fiber type whose role is to make the decisions about when, where, and how fast to assemble or disassemble the filaments. They can be assembled or disassembled like a set of building blocks. The building blocks can be moved from one part of a cell to another quite rapidly if required. Within a few seconds, the distribution of fibers can change dramatically within a living cell. This phenomenon occurs, for example, if a moving cell encounters an obstacle and changes direction. Under certain conditions, microtubule proteins can be added to one end of a microtubule at the same time that they are removed from the opposite end. The result is that the microtubule appears to "move" toward the growing end. This process has been likened to the movement of the tread on a Caterpillar-type tractor.

The first cell function to be definitely attributed to the cell's cytoskeleton was cell division. This process is an elaborate, highly choreographed minuet in which the microtubules move two sets of *chromosomes* (the structures that carry the genetic information) apart from one another and the microfilaments squeeze the cell in two between the chromosome sets. The result is two cells where there was only one, and each has a complete set of genes. How are the activities of the two kinds of fibers coordinated in both time and space, so that this elegant process occurs properly? It is now understood that changing concentrations of calcium atoms inside cells help to coordinate the actions of the several fiber types. Fluorescent antibody staining has revealed that the chromosome-moving microtubules change in length during movement and that they generate a force sufficient to drag the chromosomes through the cell.

Howard L. Hosick

See also: Cytoskeleton; Flagella and cilia.

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FOOD CHAIN

Categories: Ecology; food; nutrients and nutrition

The food chain concept allows ecologists to interconnect the organisms living in an ecosystem and to trace mathematically the flow of energy from plants through animals to decomposers.

The food chain concept provides the basic framework for production biology and has major implications for agriculture, wildlife biology, and calculating the maximum amount of life that can be supported on the earth. As early as 1789, naturalists such as Gilbert White described the many sequences of animals eating plants and themselves being eaten by other animals. However, the use of the term "food chain" dates from 1927, when Charles Elton described the implications of the food chain and food web concept in a clear manner. His solid exposition advanced the study of two important biological concepts: the complex organization and interrelatedness of nature, and energy flow through ecosystems.

Food Chains in Ecosystem Description

Stephen Alfred Forbes, founder of the Illinois Natural History Survey, contended in 1887 that a lake comprises a system in which no organism or process can be understood unless its relationship to all the parts is understood. Forty years later, Elton's food chains provided an accurate way to diagram these relationships. Because most organisms feed on several food items, food chains were cross-linked into complex webs with predictive power. For instance, algae in a lake might support an insect that in turn was food for bluegill. If unfavorable conditions eliminated this algae, the insect might also disappear. However, the bluegill, which fed on a wider range of insects, would survive because the loss of this algae merely increases the pressure on the other food sources. This detailed linkage of food chains advanced agriculture and wildlife management and gave scientists a solid overview of living systems. When Arthur George Tansley penned the term *ecosystem* in the 1930's, it was food-chain relationships that described much of the equilibrium of the ecosystem.

Digital Stock

Unlike calories, which are reduced at each step in a food chain, some toxic substances become more concentrated as the molecules are passed along. The pesticide DDT provides the most notorious example of biological magnification: DDT was found to be deposited in animal body fat in ever-increasing concentrations as it moved up the food chain to species such as pelicans. High levels of DDT in these birds broke down steroid hormones and interfered with eggshell formation.

Today most people still think of food chains as the basis for the "balance of nature." This phrase dates from the controversial 1960 work of Nelson G. Hairston, Frederick E. Smith, and Lawrence B. Slobodkin. They proposed that if only grazers and plants are present, grazing limits the plants. With predators present, however, grazers are limited by predation, and the plants are free to grow to the limits of the nutrients available. Such explanations of the "balance of nature" were commonly taught in biology books throughout the 1960's and 1970's.

Food Chains in Production Biology

Elton's explanation of food chains came just one year after Nelson Transeau of Ohio State University presented his calculations on the efficiency with which corn plants converted sunlight into plant tissue. Ecologists traced this flow of stored chemical energy up the food chain to herbivores that ate plants and on to *carnivores* that ate *herbivores*. Food chains therefore undergirded the new "production biology" that placed all organisms at various *trophic levels* and calculated the extent to which energy was lost or preserved as it passed up the food chain.

With data accumulating from many ecologists, Elton extended food chains into a pyramid of numbers. The *food pyramid*, in which much plant tissue supports some herbivores that are in turn eaten by fewer carnivores, is still referred to as an *Eltonian pyramid*. In 1939 August Thienemann added *decomposers* to reduce unconsumed tissues and return the nutrients of all levels back to the plants. Early pyramids were based on the amount of living tissues, or *biomass*.

Calculations based on the amount of chemical energy at each level, as measured by the heat released when food is burned (calories), provided even more accurate budgets. Because so much energy is lost at each stage in a food chain, it became obvious that this inefficiency was the reason food chains are rarely more than five or six links long and why large, fierce animals are uncommon. It also became evident that because the earth intercepts a limited amount of sunlight energy per year, there is a limit on the amount of plant life—and ultimately upon the amount of animal life and decomposers—that can be fed. Food chains are also important in the accounting of carbon, nitrogen, and water cycling.

Value of Food Chains in Environmental Science

Unlike calories, which are dramatically reduced at each step in a food chain, some toxic substances become more concentrated as the molecules are passed along. The concentration of molecules along the food chain was first noticed by the Atomic Energy Commission, which found that radioactive iodine and strontium released in the Columbia River were concentrated in tissue of birds and fish. However, the pesticide DDT provided the most notorious example of biological magnification: DDT was found to be deposited in animal body fat in ever-increasing concentrations as it moved up the food chain to ospreys, pelicans, and peregrine falcons. High levels of DDT in these birds broke down steroid hormones and interfered with eggshell formation.

Because humans are *omnivores*, able to feed at several levels on the food chain (that is, both plants and other animals), it has been suggested that a higher world population could be supported by humans moving down the food chain and becoming vegetarians. A problem with this argument is that much grazing land worldwide is unfit for cultivation, and therefore the complete cessation of pig or cattle farming does not necessarily free up substantial land to grow crops.

While the food chain and food web concepts are convenient theoretical ways to summarize feeding interactions among organisms, real field situations have proved far more complex and difficult to measure. Animals often switch diet between larval and adult stages, and they are often able to shift food sources widely. It is often difficult to draw the boundaries of food chains and food webs.

John Richard Schrock

See also: Animal-plant interactions; Biomass related to energy; Community-ecosystem interactions; Community structure and stability; Ecology: concept; Ecosystems: overview; Ecosystems: studies; Trophic levels and ecological niches.

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FOREST AND RANGE POLICY

Categories: Economic botany and plant uses; ecosystems; forests and forestry

Forest and range policies are laws protecting forests and rangelands. Such policies usually seek to sustain and protect biodiversity while setting guidelines for the sustainable use of natural resources.

Many national governments have established forest and range policies. *Rangeland*, land that supplies forage for grazing and browsing animals, covers almost one-half of the ice-free land on earth. More than three billion cattle, sheep, goats, camels, buffalo, and other domestic animals graze on rangelands. These animals are important in converting forages into milk and meat, which provide nourishment for people around the world. Forests cover almost 30 percent of the earth and provide humans with lumber, fuel woods, food products, latex rubber, and valuable chemicals that constitute prescription and nonprescription drugs. Rangelands and forests also function as important ecosystems that help provide food and shelter for wildlife, control erosion, and purify the atmosphere. Forests and rangelands have been undergoing destruction and degradation at alarming rates at the hands of humans.

Protecting Forests and Rangelands

The nearly 15 billion acres of forest that originally existed on the earth have been reduced to approximately 11 billion acres by human conversion of land to cropland, pastureland, cities, and nonproductive land. Forests, if properly maintained or left alone, are the most productive and self-sustaining ecosystems that land can support. Tropical rain forests are the natural habitat for at least 50 percent, and possibly up to 90 percent, of the species on earth. In the late 1990's, Harvard biologist Edward O. Wilson stated that 25 percent of the earth's species could become extinct by the year 2050 if the current rate of tropical forest destruction were not stopped.

Many national governments have established policies for protecting forest habitats and the biological diversity found within them. National parks and reserves provide protection for both forests and rangelands. Some countries have laws that prohibit clearing, burning, or logging of particular forests.

China, which suffered from erosion and floods as a result of centuries of deforestation, began an impressive *reforestation* campaign during the 1990's, planting almost 11 million acres of new trees. Korea attained 70 percent reforestation after losing almost all its forested land in a civil war during the 1950's. Japan has enacted strict environmental laws, which have allowed it to reforest 68 percent of its land area. Japan has relied upon imported timbers in order to allow its new forest projects to flourish. Even with such worldwide success in reforestation, it is estimated that protection and sustainable management of forests and rangelands still need to be increased by a factor of three if forests are to be saved.

Multiple Use

Protecting forestland involves an interdisciplinary approach. In the United States, 191 million acres of forestland are managed by the U.S. Forest Service. The Forest and Rangeland Renewable Resource Planning Act (RPA) of 1974 and the National Forest Management Act (NFMA) of 1976 mandated management plans for forests and rangelands to ensure that resources would be available on a sustained basis. Management policies must sustain and protect biodiversity; old-growth forests; riparian areas; threatened, endangered, and sensitive species; rangeland; water and air quality; access to forests; and wildlife habitat.

The Forest Service provides inexpensive grazing lands for more than three million cattle and sheep every year, supports multimillion-dollar mining operations, maintains a network of roads eight times longer than the U.S. interstate highway system, and allows access to almost one-half of all national forest land for commercial logging. The Forest Service is responsible for producing plans for the multiple use of national lands.

Sustainability policies require that the net productive capacity of the forest or rangeland does not decrease with multiple use. This involves making sure that soil productivity is maintained by keeping erosion, compaction, or displacement by mining or logging equipment or other motorized vehicles within tolerable limits. It further requires that a large percentage of the forest remains undeveloped so that soils and habitats, as well as tree cover, will remain undisturbed and in their natural state.

The RPA and NFMA, along with the Endangered Species Act (ESA) of 1973, mandate policies that encourage the proliferation of species native to and currently living in the forest. Natural ecosystem processes are followed to ensure their survival. Even though forests and rangelands are required to be multiple-use areas, policy maintains that there can be no adverse impact to threatened, endangered, or sensitive species. Species habitats within the forest are to remain well distributed and free of barriers that can cause fragmentation of animal populations and ultimately species loss. If a forest contains fragmented areas created by human activity, corridors that connect the forest patches are constructed. In this way species are not isolated from one another, and viable populations can exist.

The Forest Service creates artificial habitats to encourage the survival of species in cases of natural disaster. When Hurricane Hugo devastated the Francis Marion National Forest in South Carolina in 1989, winds snapped 90 percent of the trees with active woodpecker cavities in some areas of the forest. The habitat destruction caused 70 percent of the red-cockaded woodpecker population to disappear. The Forest Service and university researchers created nesting and roosting cavities to save the woodpeckers. Within a four-year period, the population had dramatically recovered.

Image Not Available

Timber, Oil, and Mineral Leasing

Logging activities in forests are covered by the Resource Planning Act of 1990. Forested land must be evaluated for its ability to produce commercially usable timber without negative environmental impact. There must be reasonable assurance that stands managed for timber production can be adequately restocked within five years of the final harvest. Further, no irreversible resource damage is allowed to occur. Policy further requires use of the *silviculture* practices that are best suited to the land management objectives of the area. Cutting practices are then monitored. The 1990's were characterized by a trend toward restricting logging methods in order to protect habitats and preserve older stands of trees. In the 1993 Renewable Resource Assessment update, the Forest Service found that timber mortality, at 24.3 percent, was still interfering with biological diversity. Some forested areas were withdrawn from timber production because of their fragility.

Multiple use under the NFMA allowed forests to be available for oil and gas leasing. Certain lands were exempted from mineral exploration by acts of Congress or executive authority. However, the search for and production of mineral and energy sources remained under the jurisdiction of the Forest Service, which was charged to provide access to national forests for mineral resources activities. The Federal On-Shore Oil and Gas Leasing Reform Act of 1987 gave the Forest Service more authority in making lease decisions.

Pest and Weed Control

Pesticides are sometimes used during attempts to ensure the health of forestland. Policy in the United States requires the use of safe pesticides and encourages the development of an *integrated pest management* (IPM) plan. Any decision to use a particular pesticide must be based on an analysis of its effectiveness, specificity, environmental impact, economic efficiency, and effects on humans. The application and use of pesticides must be coordinated with federal and state fish and wildlife management agencies. Pesticides can be applied only to areas that are designated as wilderness when their use is necessary to protect or restore resources in the area. Other methods of controlling disease include removing diseased trees and vegetation from the forest, cutting infected areas from plants and removing the debris, treating trees with antibiotics, and developing disease-resistant plant varieties.

Forest Service policy on integrated pest management was revised in 1995 to emphasize the importance of integrating noxious weed management into the forest plan for ecosystem analysis and assessment. Noxious weed management must be coordinated in cooperation with state and local government agencies as well as private landowners. Noxious weeds include invasive, aggressive, or harmful nonindigenous or exotic plant species. They are generally opportunistic, poisonous, toxic, parasitic, or carriers of insects or disease. The Forest Service is responsible for the prevention, control, and eradication of noxious weeds in national forests and grasslands.

In North Dakota, one strategy for promoting weed-free forests uses goats to help control leafy spurge. The goats graze on designated spurge patches during the day and return to portable corrals during the night. A five-year study found that the goats effectively reduced stem densities of spurge patches to the extent that native livestock forage plants were able to reestablish themselves.

A strategy that has been implemented in Wyoming, Colorado, Idaho, Utah, and Montana requires pack animals on national forest land to eat state-certified weed-free forage. Another strategy involves the use of certified weed-free straw and gravel in construction and rehabilitation efforts within national forests. *Biocontrols*, *herbicides*, and *controlled burning* are also commonly used during IPM operations in forests.

Other Protection Issues

Natural watercourses and their banks are referred to as *riparian areas*. The plant communities that grow in these areas often serve as habitats for a large variety of animals and birds and also provide shade, bank stability, and filtration of pollution sources. It is therefore important that these areas remain in good ecological condition. Riparian areas and streams are managed according to legal policies for *wetlands*, floodplains, water quality, endangered species, and wild and scenic rivers.

Dirt roads in national forests are often closed when road sediment pollutes riparian areas and harms fish populations. Forest and rangeland roads are also closed to prevent disruption of breeding or nesting colonies. Seemingly harmless human endeavors—such as seeking mushrooms, picking berries, or hiking in the forest—can cause problems for calving elk and nesting eagles. Therefore, the amount of open roads in the forest is being reduced in order to preserve habitat and return land to a more natural state.

Fire management is important to healthy forests. In many cases fires are prevented or suppressed, but prescribed fires are used to protect and maintain ecosystem characteristics. Some conifers, such as the giant sequoia and the jack pine, will release their seeds for germination only after being exposed to intense heat. Lodgepole pines will not release their seeds until they have been scorched by fire. Ecosystems that depend on the recurrence of fire for regeneration and balance are called *fire climax ecosystems*. Prescribed fires are used as a management tool in these areas, which include some *grasslands* and pine habitats.

In 1964 the U.S. Congress passed the Wilderness Act, which mandates that certain federal lands be designated as wilderness areas. These lands must remain in their natural condition, provide solitude or primitive types of recreation, and be at least 5,000 acres in area. They usually contain ecological or geological systems of scenic, scientific, or historical value. No roads, motorized vehicles, or structures are allowed in these areas. Furthermore, no commercial activities are allowed in wilderness areas except livestock grazing and limited mining endeavors that began before the area received wilderness designation.

Grazing Practices and Problems

Approximately 42 percent of the world's rangeland is used for grazing livestock; much of the rest is too dry, cold, or remote to serve such purposes. It is common for these rangelands to be converted into croplands or urban developments. The rate of loss for grazing lands worldwide is three times that of tropical forests, and the area lost is six times that of tropical forests. There are more threatened plant species in North American rangelands than any other major biome.

Rangeland grasses are known for their deep, complex root systems, which makes the grasses hard to uproot. When the tip of the leaf is eaten, the plant quickly regrows. Each leaf of grass on the rangeland grows from its base, and the lower half of the plant must remain for the plant to thrive and survive. As long as only the top half of the grass is eaten, grasses serve as renewable resources that can provide many years of grazing. Each type of grassland is evaluated based on grass species, soil type, growing season, range condition, past use, and climatic conditions. These conditions determine the herbivore *carrying capacity*, or the maximum number of grazing animals a rangeland can sustain and remain renewable.

Overgrazing occurs when herbivore numbers exceed the land's carrying capacity. Grazing animals tend to eat their favorite grasses first and leave the tougher, less palatable plants. If animals are allowed to do this, the vegetation begins to grow in patches, allowing cacti and woody bushes to move into vacant areas. As native plants disappear from the range, weeds begin to grow. As the nutritional level of the forage declines, hungry animals pull the grasses out by their roots, leaving the ground bare and susceptible to damage from hooves. This process initiates the desertification cycle. With no vegetation present, rain quickly drains off the land and does not replenish the groundwater. This makes the soil vulnerable to erosion. Almost one-third of rangeland in the world is degraded by overgrazing. Among the countries suffering severe range degradation are Pakistan, Sudan, Zambia, Somalia, Iraq, and Bolivia.

The United States has approximately 788 million acres of rangeland. This represents almost 34 percent of the land area in the nation. More than one-half of the rangeland is privately owned, while approximately 43 percent is publicly owned and managed by the Forest Service and the Bureau of Land Management (BLM). State and local governments manage the remaining 5 percent. Efforts to preserve rangelands include close monitoring of carrying capacity and removal of substandard ranges from the grazing cycle until they recover. New grazing practices, such as cattle and sheep rotation, help to preserve the renewable quality of rangelands. Grazing is managed with consideration to season, moisture, and plant growth conditions. Noxious weed encroachment is controlled, and native forages and grasses are allowed to grow.

Most rangelands in the United States are shortgrass prairies located in the western part of the nation. These lands are further characterized by thin soils and low annual precipitation. They undergo numerous environmental stresses. Woody shrubs, such as mesquite and prickly cactus, often invade and take over these rangelands as overgrazing or other degradation occurs. Such areas are especially susceptible to desertification. Recreational vehicles, such as motorcycles, dune buggies, and four-wheel-drive trucks, can damage the vegetation on ranges. According to the 1993 Renewable Resource Assessment update, many of the rangelands in the United States were in unsatisfactory condition.

Steps to restore healthy rangelands include restoring and maintaining riparian areas and priority watersheds. These areas are monitored on a regular basis, and adjustments are made if their health is jeopardized by sediment from road use or degradation of important habitats caused by human activity. The Natural Resources Conservation program is teaching private landowners how to burn unwanted woody plants on rangelands, reseed with perennial grasses that help hold water in the soil, and rotate grazing of cattle and sheep on rangelands so that the land is able to recover and thrive. Such methods have proven to be successful.

Toby R. Stewart and Dion Stewart

See also: Biological invasions; Deforestation; Desertification; Erosion and erosion control; Forest fires; Forest management; Grasslands; Grazing and overgrazing; Integrated pest management; Logging and clear-cutting; Sustainable agriculture; Sustainable forestry.

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FOREST FIRES

Categories: Ecology; ecosystems; environmental issues; forests and forestry

Whether natural or caused by humans, fires destroy life and property in forestlands but are also vital to the health of forests.

Evidence of forest fires is routinely found in soil samples and tree borings. The first major North American fires in the historical record were the Miramichi and Piscataquis fires of 1825. Together, they burned 3 million acres in Maine and New Brunswick. Other U.S. fires of significance were the Peshtigo fire in 1871, which raged over 1.28 million acres and took fourteen hundred human lives in Wisconsin; the fire that devastated northern Idaho and northwestern Montana in 1910 and killed at least seventy-nine firefighters; and a series of fires that joined forces to sweep across one-third of Yellowstone National Park in 1988.

Fire Behavior

Fires need heat, fuel, and oxygen. They spread horizontally by igniting particles at their edge. At first, flames burn at one point, then move outward, accumulating enough heat to keep burning on their own. Topography and weather affect fire behavior. Fires go uphill faster than downhill because warm air rises and preheats the uphill fuels. Vegetation on south- and west-facing slopes receives maximal sunlight and so is drier and burns more easily. Heat is pulled up steep, narrow canyons, as it is up a chimney, increasing heat intensity. For several reasons, only one-third of the vegetation within a large fire usually burns. This mosaic effect may be caused by varied tree species that burn differently, old burns that stop fire, strong winds that blow the fire to the leeward side of trees, and varied fuel moisture.

Forest Management

One of the early criteria of forest management was fire protection. In the second quarter of the twentieth century, lookout towers, firebreaks, and trails were built to locate fires as quickly as possible. Low fires that otherwise would have burned through the forest at ground level and cleared out brush every five to twenty-five years were suppressed. As a result, the natural cycle of frequent fires moving through an area was broken. Fallen trees, needles, cones, and other debris collected as kindling on the forest floor, rather than being incinerated every few years.

It took foresters and ecologists fifty years to realize that too much fire suppression was as bad as too little. Infrequent fires cause accumulated kindling to burn hot and fast and explode into treetops. The result is a devastating *crown fire*, a large fire that advances as a single front. Burning embers of seed cones and sparks borne by hot, strong winds created within the fire are tossed into unburned areas to start more fires.

In the 1970's *prescribed burning* was added to forest management techniques used to keep forests healthy. Fires set by lightning are allowed to burn when the weather is cool, the area isolated, and the risk of the fire exploding into a major fire low. More than 70 percent of prescribed burning takes place in the southeastern states, where natural fires burn through an area more frequently than in the West.

Causes of Fires

Forest fires may be caused by natural events or human activity. Most natural fires are started by lightning strikes. Dozens of strikes can be recorded from one lightning storm. When a strike seems likely, fire spotters watch for columns of smoke, and small spotter planes will fly over the area, looking for smoke. Many of the small fires simply smoulder and go out, but if the forest is dry, multiple fires can erupt from a single lightning storm.

The majority of forest fires are human-caused, and most are the result of carelessness rather than arson. Careless campers may leave a campsite without squelching their campfire completely, and winds may then whip the glowing embers into flames. A smoker may toss a cigarette butt from a car window. Sparks from a flat tire riding on the rim may set fire to vegetation alongside the highway. The sun shining through a piece of broken glass left by litterers may ignite dry leaves.

In some areas, prescribed fires are set in an attempt to re-create the natural sequence of fire. In Florida, prescribed burns provide wildlife habitat by opening up groves to encourage healthy growth. Other fires start accidentally but are allowed to burn until they reach a predetermined size.

Benefits of Fire

Some plant species require very high temperatures for their seed casings to split for germination. After fire periodically sweeps through the forest, seeds will germinate. Other species, such as the fire-resistant ponderosa pine, require a shallow layer of decaying vegetable matter in which to root. Fires burn excess debris and small trees of competing species and leave an open environment suitable for germination. Dead material on the forest floor is processed into nutrients more quickly by fire than by decay, and in a layer of rich soil, plants will sprout within days to replace those destroyed in the fire.

Fire's Disadvantages

Erosion is one of the devastating effects of a fire. If the fuels burn hot, tree oils and resins can be baked into the soil, creating a hard shell that will not absorb water. When it rains, the water runoff gathers mud and debris, creating flash floods and extreme stream *sedimentation*. Culverts and storm drains fill with silt, and streams flood and change course. Fish habitat is destroyed, vegetation sheltering stream banks is ripped away, and property many miles downstream from the forest is affected.

When a fire passes through timber it generally leaves pockets of green, although weakened, stands. Forest pests, such as the bark beetle, are attracted to the burned trees and soon move to the surviving trees, weakening them further. Healthy trees outside the burn area may also fall to pest infestation unless the burned trees are salvaged before pests can take hold. The ash and smoke from hot, fast-burning forest fires can be transported for

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miles, affecting air quality many miles from the actual fire.

Relationship to Timber Resources

Although a prescribed fire is an attempt to duplicate natural fire, it is not as efficient, because private and commercial property within the fire path must be protected. Once a fire has occurred, burned timber deteriorates quickly, either through insect infestation or blueing—a mold that stains the wood. Private landowners can move quickly to salvage fire-damaged trees and plant new seedlings to harness erosion. On federal land, regulations governing the salvage of trees can delay logging of the burned snags until deterioration makes it uneconomical to harvest them.

Fire Fighting

In fire fighting, bulldozers are used to cut fire lines ahead of the approaching fire, and fuels between fire lines and the fire are backburned. Helicopters and tanker planes drop water with a fire-retardant additive, or bentonite, a clay, at the head of the fire to smother fuels. Firefighters are equipped with fire shelters in the form of aluminized pup tents, which they can pull over themselves if a fire outruns them. Despite technological advances, one of the best tools for fighting fires—along with the shovel—remains the pulaski, a combination ax and hoe, first produced commercially in 1920. This tool, in the hands of on-the-ground firefighters, is used to cut fire breaks and to throw dirt on smoldering debris.

Public Policy and Public Awareness

Since the early twentieth century, forest fires have engendered public policy in the United States. In the aftermath of major fires in 1903 and 1908 in Maine and New York, state fire organizations and private timber protective associations were formed to provide fire protection. These, in turn, contributed to the Weeks Act of 1911, which permitted cooperative fire protection between federal and state governments.

People who make their homes in woodland settings in or near forests face the danger of forest fire, and government agencies provide information to help people safeguard themselves and their property. Homes near forests should be designed and landscaped with fire safety in mind, using fire-resistant or noncombustible materials on the roof and exterior. Landscaping should include a clear safety zone around the house. Hardwood trees, less flammable than conifers, and other fire-resistant vegetation should be planted.

J. A. Cooper

See also: Forests; Forest management; Sustainable forestry; Timber industry; Wood and timber.

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FOREST MANAGEMENT

Categories: Disciplines; economic botany and plant uses; forests and forestry

Forest management includes reforestation programs as well as techniques to manage logging practices, provide grazing lands, support mining operations, maintain infrastructure networks, or slow the destruction of rain forests.

Forests provide lumber for buildings, wood fuel for cooking and heating, and raw materials for making paper, latex rubber, resin, dyes, and essential oils. Forests are also home to millions of plants and animal species and are vital in regulating climate, purifying the air, and controlling water runoff. A 1993 global assessment by the United Nations Food and Agriculture Organization (FAO) found that three-fourths of the forests in the world still have some tree cover, but less than one-half of these have intact forest ecosystems. *Deforestation* is occurring at an alarming rate, and management practices are being sought to try to halt this destruction.

Thousands of years ago, forests and woodlands covered almost 15 billion acres of the earth. Approximately 16 percent of the forests have been cleared and converted to pasture, agricultural land, cities, and nonproductive land. The remaining 11.4 billion acres of forests cover about 30 percent of the earth's land surface. Clearing forests has severe environmental consequences. It reduces the overall productivity of the land, and nutrients and biomass stored in trees and leaf litter are lost. Soil once covered with plants, leaves, and snags becomes prone to erosion and drying. When forests are cleared, habitats are destroyed and biodiversity is greatly diminished. Destruction of forests causes water to drain off the land instead of being released into the atmosphere by transpiration or percolation into groundwater. This can cause major changes in the hydrologic cycle and ultimately in the earth's climate. Because forests remove a large amount of carbon dioxide from the air, the clearing of forests causes more carbon dioxide to remain, thus upsetting the delicate balance of atmospheric gases.

Rain Forests

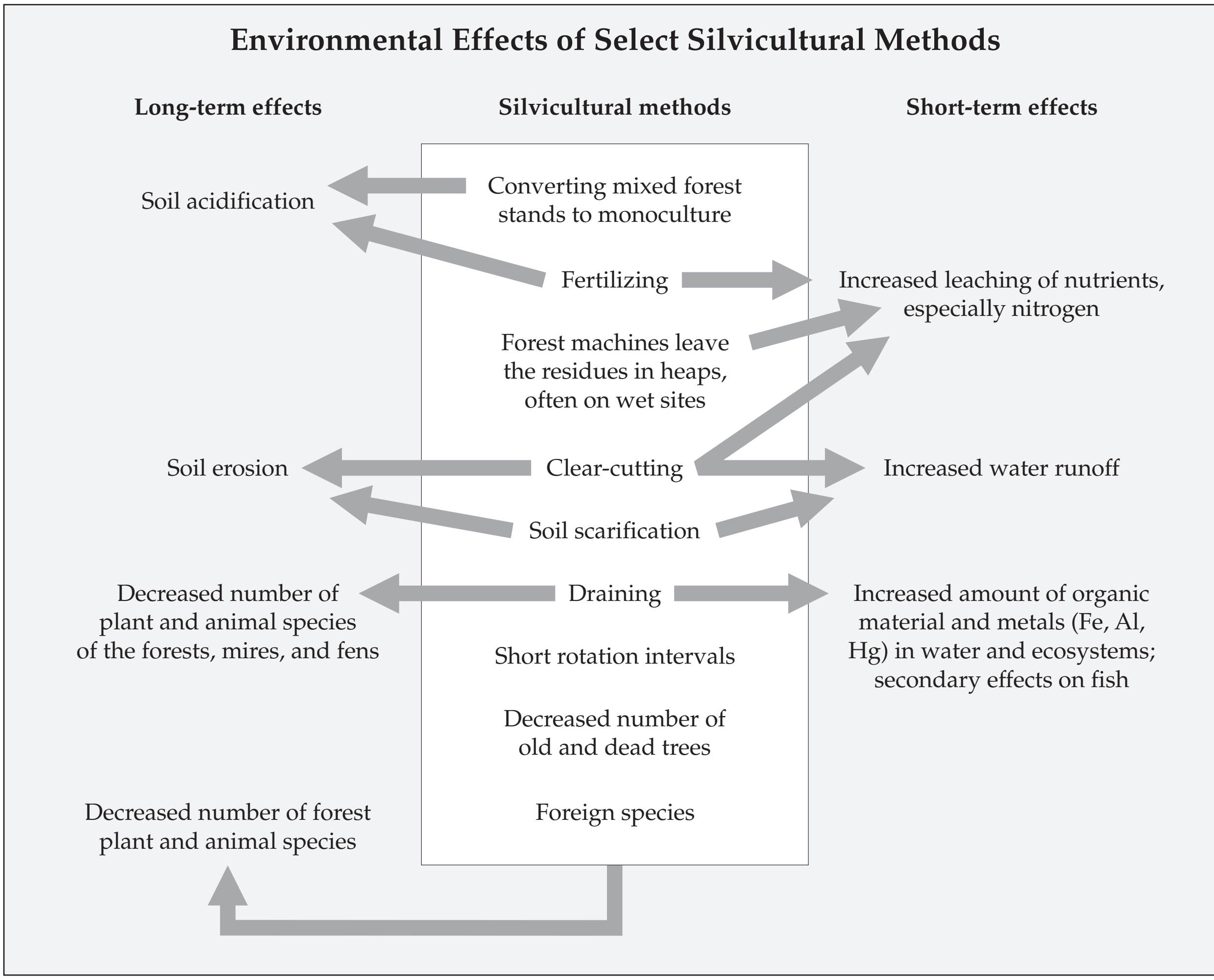
Rain forests provide habitats for at least 50 percent (some estimates are as high as 90 percent) of the total stock of plant, insect, and other animal species on earth. They supply one-half of the world's annual harvest of hardwood and hundreds of food products, such as chocolate, spices, nuts, coffee, and tropical fruits. Tropical rain forests also provide the main ingredients in 25 percent of prescription and nonprescription drugs, as well as 75 percent of the three thousand plants identified as containing chemicals that fight cancer. Industrial materials, such as natural latex rubber, resins, dyes, and essential oils, are also harvested from tropical forests.

Tropical forests in Asia, Africa, and Latin America are rapidly being cleared to produce pastureland for large cattle ranches, establish logging operations, construct large plantations, grow narcotic plants, develop mining operations, or build dams to provide power for mining and smelting operations. In 1985 the FAO's Committee on Forest Development in the Tropics developed the Tropical Forestry Action Plan to combat these practices, develop sustainable forest methods, and protect precious ecosystems. Fifty nations in Asia, Africa, and Latin America have adopted the plan.

Several management techniques have been successfully applied to slow the destruction of tropical forests. *Sustainable logging* practices and *reforestation* programs have been established on lands that allow timber cutting, with complete bans of logging on virgin lands. Certain regions have set up extractive reserves to protect land for the native people who live in the forest and gather latex rubber and nuts from mature trees. Sections of some tropical forests have been preserved as *national reserves*, which attract tourists while preserving trees and biodiversity.

Developing countries have been encouraged to protect their tropical forests by using a combination of *debt-for-nature swaps* and *conservation easements*. In debt-for-nature swaps, tropical countries act as custodians of the tropical forest in exchange for foreign aid or relief from debt. Conservation easement involves having another country, private organization, or consortium of countries compensate a tropical country for protecting a specific habitat.

Another management technique involves putting large areas of the forest under the control of indigenous people who use *slash-and-burn agriculture* (also known as swidden or milpa agriculture). This traditional, productive form of agriculture follows a multiple-year cycle. Each year farmers clear a forest plot of several acres in size to allow the sun to penetrate to the ground. Leaf litter, branches, and fallen trunks are burned, leaving a rich layer of ashes. Fast-growing crops, such as bananas and papayas, are planted and provide shade for root crops, which are planted to anchor the soil. Finally, crops such as corn and rice are planted. Crops mature in a staggered sequence, thus providing a continuous supply of food. Use of mixed perennial *polyculture* helps prevent insect infestations, which can destroy *monoculture* crops. After one or two years, the forest begins to take over the agricultural plot. The farmers continue to pick the perennial crops but essentially allow the forest to reclaim the plot for the next ten to fifteen years before clearing and planting the area again. Slash-and-burn agriculture can, however, post hazards: A drought in Southeast Asia in 1997 caused fires to burn for months when monsoon rains did not materialize, polluting the air and threatening the health of millions of Indonesians. In 1998, previous abuse of the technique resulted in flooding and mudslides in Honduras after the onset of Hurricane Mitch.



Source: Adapted from I. Stjernquist, "Modern Wood Fuels," in *Bioenergy and the Environment*, edited by Pasztor and Kristoferson, 1990.

U.S. Forest Management

Forests cover approximately one-third of the land area of the continental United States and comprise 10 percent of the forests in the world. Only about 22 percent of the commercial forest area in the United States lies within national forests. The rest is primarily managed by private companies that grow trees for commercial logging. Land managed by the U.S. Forest Service provides inexpensive grazing lands for more than three million cattle and sheep every year, supports multimillion-dollar mining operations, and consists of a network of roads eight times longer than the U.S. interstate highway system. Almost 50 percent of national forest land is open for commercial logging. Nearly 14 percent of the timber harvested in the United States each year comes from national forest lands. Total wood production in the United States has caused the loss of more than 95 percent of the old-growth forests in the lower forty-eight states. This loss includes not only high-quality wood but also a rich diversity of species not found in early-growth forests.

National forests in the United States are required by law to be managed in accordance with principles of *sustainable yield*. Congress has mandated that forests be managed for a combination of uses, including grazing, logging, mining, recreation, and protection of watersheds and wildlife. Healthy forests also require protection from pathogens and insects. *Sustainable forestry*, which emphasizes biological diversity, provides the best management. Other management techniques include removing only infected trees and vegetation, cutting infected areas and removing debris, treating trees with antibiotics, developing disease-resistant species of trees, using insecticides and fungicides, and developing integrated pest management plans.

Two basic systems are used to manage trees: even-aged and uneven-aged. *Even-aged management* involves maintaining trees in a given stand that are about the same age and size. Trees are harvested, then seeds are replanted to provide for a new even-aged stand. This method, which tends toward the cultivation of a single species or monoculture of trees, emphasizes the mass production of fast-growing, low-quality wood (such as pine) to give a faster economic return on investment. Even-aged management requires close supervision and the application of both fertilizer and pesticides to protect the monoculture species from disease and insects.

Uneven-aged management maintains trees at many ages and sizes to permit a natural regeneration process. This method helps sustain biological diversity, provides for long-term production of high-quality timber, allows for an adequate economic return, and promotes a multiple-use approach to forest management. Uneven-aged management also relies on selective cutting of mature trees and reserves *clear-cutting* for small patches of tree species that respond favorably to such logging methods.

Harvesting Methods

The use of a particular tree-harvesting method depends on the tree species involved, the site, and whether even-aged or uneven-aged management is being applied. *Selective cutting* is used on intermediate-aged or mature trees in uneven-aged forests. Carefully selected trees are cut in a prescribed stand to provide for a continuous and attractive forest cover that preserves the forest ecosystem.

Shelterwood cutting involves removing all the mature trees in an area over a period of ten years. The first harvest removes dying, defective, or diseased trees. This allows more sunlight to reach the healthiest trees in the forest, which will then cast seeds and shelter new seedlings. When the seedlings have turned into young trees, a second cutting removes many of the mature trees. Enough mature trees are left to provide protection for the younger trees. When the young trees become well established, a third cutting harvests the remaining mature trees, leaving an even-aged stand of young trees from the best seed trees to mature. When done correctly, this method leaves a natural-looking forest and helps reduce soil erosion and preserve wildlife habitat.

Seed-tree cutting harvests almost every tree at one site, with the exception of a few high-quality seed-producing and wind-resistant trees, which will function as a seed source to generate new crops. This method allows a variety of species to grow at one time and aids in erosion control and wildlife conservation.

Clear-cutting removes all the trees in a single cutting. The clear-cut may involve a strip, an entire stand, or patches of trees. The area is then replanted with seeds to grow even-aged or tree-farm varieties. More than two-thirds of the timber produced in the United States, and almost one-third of the timber in national forests, is harvested by clear-cutting. A clear-cut reduces biological diversity by destroying habitat. It can make trees in bordering areas more vulnerable to winds and may take decades to regenerate.

Forest Fires

Forest fires can be divided into three types: surface, crown, and ground fires. *Surface fires* tend to burn only the undergrowth and leaf litter on the forest floor. Most mature trees easily survive, as does wildlife. These fires occur every five years or so in forests with an abundance of ground litter and help prevent more destructive crown and ground fires. Such fires can release and recycle valuable mineral nutrients, stimulate certain plant seeds, and help eliminate insects and pathogens.

Crown fires are very hot fires that burn both ground cover and tree tops. They normally occur in forests that have not experienced fires for several decades. Strong winds allow these fires to spread from deadwood and ground litter to treetops. They are capable of killing all vegetation and wildlife, leaving the land prone to erosion.

Ground fires are more common in northern bogs. They can begin as surface fires but burn peat or partially decayed leaves below the ground surface. They can smolder for days or weeks before anyone notices them, and they are difficult to douse.

Natural forest fires can be beneficial to some plant species, including the giant sequoia and the jack pine trees, which release seeds for germination only after being exposed to intense heat. Grassland and coniferous forest ecosystems that depend on fires to regenerate are called fire climax ecosystems.

They are managed for optimum productivity with prescribed fires.

The Society of American Foresters has begun advocating a concept called *new forestry*, in which ecological health and biodiversity, rather than timber production, are the main objectives of forestry. Advocates of new forestry propose that any given site should be logged only every 350 years, wider buffer zones should be left beside streams to reduce erosion and protect habitat, and logs and snags should be left in forests to help replenish soil fertility. Proponents also wish to involve private landowners in the cooperative management of lands.

Toby R. Stewart and Dion Stewart

See also: Agriculture: traditional; Deforestation; Forest fires; Forests; Old-growth forests; Rainforest biomes; Rain forests and the atmosphere; Reforestation; Savannas and deciduous tropical forests; Sustainable forestry.

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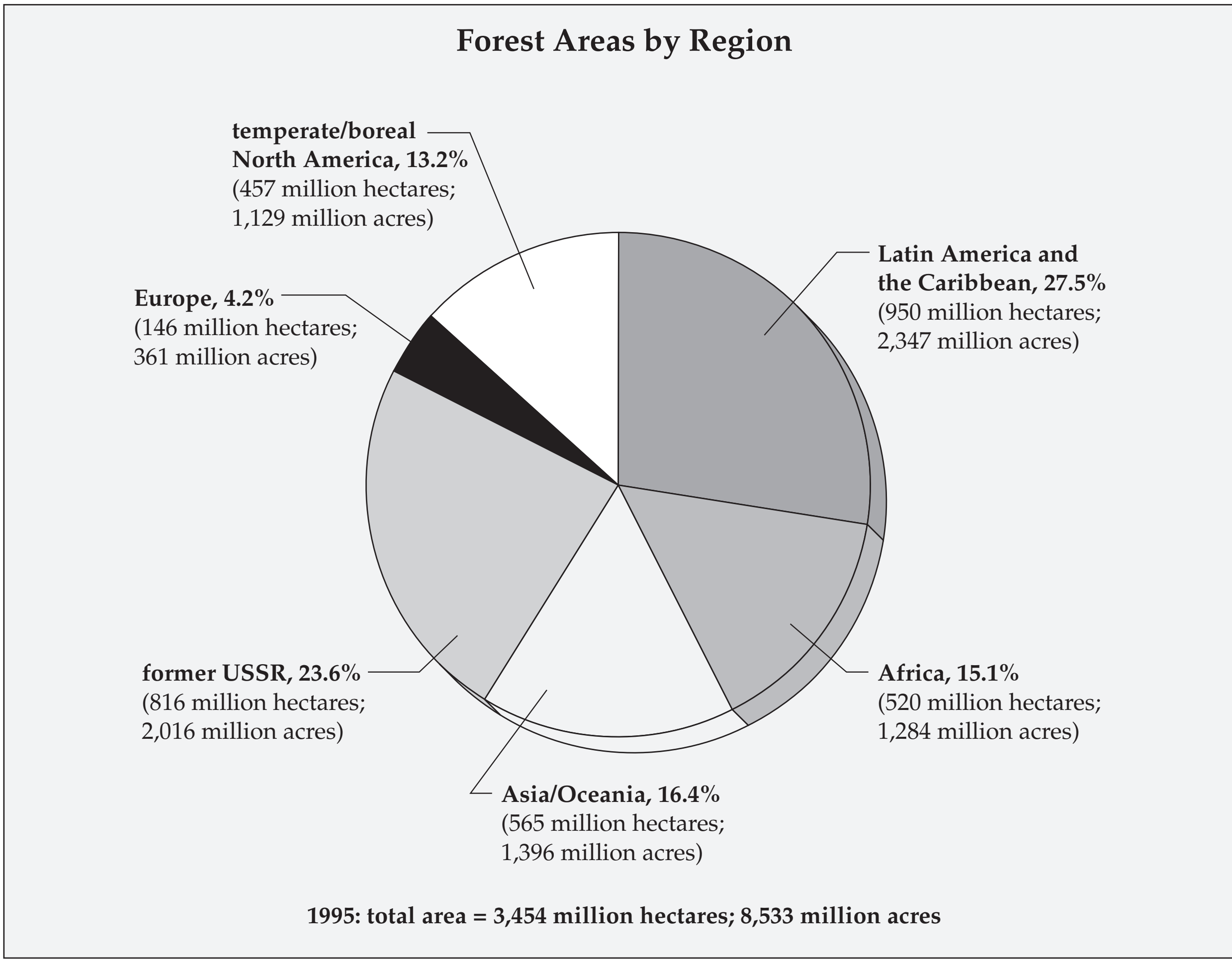
FORESTS

Categories: Ecosystems; forests and forestry

Forests are complex ecosystems in which trees are the dominant type of plant. There are three main forest biomes: tropical, temperate, and boreal.

Both humans and animals depend on forests for food, shelter, and other resources. Forests once covered much of the world and are still found from the equator to the Arctic regions. A forest may vary in size from only a few acres to thousands of square miles, but generally any natural area in which trees are the dominant type of plant can be considered a forest. For a plant to be called a tree, the standard



Source: Data are from United Nations Food and Agriculture Organization (FAOSTAT Database, 2000).

definition requires that the plant must attain a mature height of at least 8 feet (about 3 meters), have a woody stem, and possess a distinct crown. Thus, size makes roses shrubs and apples trees, even though apples and roses are otherwise close botanical relatives. Foresters generally divide the forests of the world into three general categories: *tropical*, *temperate*, and *boreal*.

Tropical Rain Forest

The tropical rain forest is discussed in depth elsewhere (see "Rain-forest biomes"). In brief, it is a forest consisting of a dizzying variety of trees, shrubs, and other plants that remain green year-round. The growth is lush and usually includes both a dense *canopy* formed by the crowns of the largest trees and a thick *understory* of smaller trees and shrubs. Growth is often continuous, rather than broken into periods of dormancy and active growth, so that fruiting trees are occasionally seen bearing blossoms and mature fruit simultaneously.

Temperate Forest

The temperate forest lies between the tropical forest and the boreal, or northern, forest. The forests of the Mediterranean region of Europe as well as the forests of the southern United States are temperate forests. Trees in temperate forests can be either *deciduous* or *coniferous*. Although coniferous trees are generally thought of as evergreen, the distinction between types is actually based on seed production and leaf shape. Coniferous trees, such as spruces, pines, and hemlocks, produce seeds in cones and have needle-like leaves. Deciduous trees, such as maples, poplars, and oaks, have broad leaves and bear seeds in other ways. Some conifers, such as tamarack, do change color and drop their needles in the autumn, while some deciduous trees, particularly in the southerly regions of the temperate forest, are evergreen.

Deciduous trees are also referred to as *hardwoods*, while conifers are *softwoods*, a classification that refers more to the typical density of the wood than to how difficult it is to nail into it. Softwoods are lower in density and will generally float in water while still green. Hardwoods are higher in density on average and will sink.

Like tropical forests, temperate forests can be quite lush. While the dominant species vary from area to area, depending on factors such as soil types and available rainfall, a dense understory of shade-tolerant species often thrives beneath the canopy. Thus, a mature temperate forest may have thick stands of rhododendrons 20 to 30 feet (6 to 9 meters) high thriving in the shade of 80-foot (24-meter) oaks and tulip poplars. As the temperate forest approaches the edges of its range and the forest makes the transition to boreal, the understory thins out, disappearing almost completely or consisting only of low shrubs. Even in temperate forests, the dominant species may prevent an understory from forming. Stands of southern loblolly pine, for example, often have a parklike feel, as the thick mulch created by fallen needles chokes out growth of other species.


Digital Stock

A rain forest in Washington State.

Boreal Forest

The boreal forest, which lies in a band across the northern United States, Canada, northern Europe, and northern Asia, is primarily a coniferous forest. The dominant species are trees such as white spruce, hemlock, and white pine. Mixed stands of northern hardwoods, such as birch, sugar maple, and red oak, may be found along the southern reaches of the boreal forest. As the forest approaches the Arctic, trees are fewer in type, becoming primarily spruce, birch, and willows, and smaller in size. The understory is generally thin or nonexistent, consisting of seedlings of shade-tolerant species, such as maple, and low shrubs. Patches of boreal-type forest can be found quite far south in higher elevations in the United States, such as the mountains of West Virginia. The edge of the temperate forest has crept steadily northward following the retreat of the glaciers at the end of the Ice Age twenty thousand years ago.

Forest Ecology and Resources

In all three types of forest a complex system of interrelationships governs the ecological well-being of the forest and its inhabitants. Trees and animals have evolved to fit into particular environmental niches. Some wildlife may need one resource provided by one species of tree in the forest during one season and a resource provided by another during a different time of year, while other animals become totally dependent on one specific tree. Whitetail deer, for example, browse on maple leaves in the summer, build reserves of fat by eating acorns in the fall, and survive the winter by eating evergreens. Deer are highly adaptable in contrast with other species, such as the Australian koala, which depends entirely on eucalyptus leaves for its nutritional needs. Just as the animals depend on the forest, the forest depends on the animals to disperse seeds and thin new growth. Certain plant seeds, in fact, will not sprout until being abraded as they pass through the digestive tracts of birds.

Humans also rely on the forest for food, fuel, shelter, and other products. Forests provide wood for fuel and construction, fibers for paper, and chemicals for thousands of products often not immediately recognized as deriving from the forest, such as plastics and textiles. In addition, through the process of transpiration, forests regulate the climate by releasing water vapor into the atmosphere while removing harmful carbon compounds. Forests play an important role in the hydrology of watersheds. Rain that falls on a forest will be slowed in its passage downhill and is often absorbed into the soil rather than running off into rivers and lakes. Thus, forests can moderate the effects of severe storms, reducing the dangers of flooding and preventing soil erosion along stream and river banks.

Threats to the Forest

The primary threat to the health of forests around the world comes from humans. As human populations grow, three types of pressure are placed on forests. First, forests are cleared to provide land for agriculture or for the construction of new homes. This process has occurred almost continuously in the temperate regions for thousands of years, but it did not become common in tropical regions until the twentieth century. Often settlers level the forest and burn the fallen trees to clear land for farming (*slash-and-burn agriculture*) without the wood itself being used in any way. Tragically, the land thus exposed can become infertile for farming within a few years. After a few years of steadily diminishing crops, the land is abandoned. With the protective forest cover removed, it may quickly become a barren, eroded wasteland.

Second, rising or marginalized populations in developing nations often depend on wood or charcoal as their primary fuel for cooking and for home heat. Forests are destroyed as mature trees are removed for fuel wood faster than natural growth can replace them. As the mature trees disappear, younger and younger growth is also removed, and eventually the forest is gone completely.

Finally, growing populations naturally demand more products derived from wood, which can include everything from lumber for construction to chemicals used in cancer research. Market forces can drive forest products companies to harvest more trees than is ecologically sound as stockholders focus on short-term individual profits rather than long-term environmental costs. The challenge to foresters, ecologists, and other scientists is to devise methods that allow humanity to continue to utilize the forest resources needed to survive without destroying the forests as complete and healthy ecosystems.

Nancy Farm Männikkö

See also: Forest and range policy; Forest fires; Forest management; Old-growth forests; Rain-forest biomes; Rain forests and the atmosphere; Slash-and-burn agriculture; Sustainable forestry; Timber industry; Wood; Wood and charcoal as fuel resources.

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FOSSIL PLANTS

Categories: Evolution; paleobotany

Fossil plants are remnants, impressions, or traces of plants from past geologic ages preserved in the earth's crust.

The rise of land-dwelling animals paralleled the rise of plants, which have always been the basis for animal life. Fossil plants are a valuable source of information regarding such phenomena as changes in climate, ancient geography, and the evolution of life itself.

Thallophytes

The earliest fossil plants are represented by a phylum called the *thallophytes*. The geological record of the thallophytes is incomplete. Of seven large groups, only a few are represented by fossils. Although some records from the Paleozoic era have been found, the earliest identifiable specimens found are from the Jurassic period. The dearth of fossils from this group of plants can be attributed to their minute size and the fragile nature of their remains.

The thallophytes are in the most primitive plants, lacking roots, stems, leaves, and conducting cells. The simplest thallophytes are in the subphylum of *autophytic thallophytes*, which include blue-green bacteria (or cyanobacteria, formerly known as blue-green algae), diatoms, and algae. All these plants produce chlorophyll. Cyanobacteria are unicellular organisms occurring in colonies held together by a jellylike material. Diatoms are one-celled plants enclosed in a wall consisting of two overlapping valves. The next class, called simply algae, consists of several different types of seaweed, such as chara, or stonewort, which secretes lime with which it encrusts its leaves and is responsible for many freshwater limestones of the past. Many fossils that have been described as algae were actually molds of burrows or tracks of animals.

The second subphylum of the thallophytes is called the *heterophytic thallophytes*. These plants are distinguished by the absence of chlorophyll; as in animals, their principal source of energy is organic. The heterophytic thallophytes are subdivided into three classes. *Bacteria*, one-celled plants without definite nuclei, are the chief agents of the decomposition of organic matter; without bacteria, more prehistoric plant and animal remains would have been preserved. The next class, *slime fungi*, are sticky masses enclosing many nuclei but without cell walls. Slime fungi have never been found as fossils. The final class is the *fungi*, which are composed essentially of a branching mass of threads called the mycelium, which penetrate the cell walls of their "host"—plant or animal—and live upon its substance. *Lichens* are made up of a fungus and an alga living together in symbiosis. Fossil lichens have been recognized only from very recent formations.

Bryophytes

The next phylum to emerge, the *bryophytes*, exhibits a distinct advance over the thallophytes: Bryophytes adapted more successfully to the terrestrial environment. They were able to take water and other necessary substances from the soil by means of rootlike hairs called rhizoids. The most distinct advance of the bryophytes over the thallophytes is in their method of reproduction. The spores produced by these plants germinate by sending out a mass of green threads, the protonema.

The simplest bryophytes are the *liverworts*. The *mosses*, which are more abundant today than the liverworts, possess leaves consisting of many small chlorophyll-bearing cells. Because the ancient members of the bryophyte group were more delicate than the modern forms, they have been preserved only under exceptional conditions, such as those provided by the silicified peat beds at Rhynie, Scotland, which contain fossils from the Devonian period.

Pteridophytes

The *pteridophytes* were much more advanced than the bryophytes. While the structure of the bryophytes was primarily cellular, that of the fern plant is vascular. Unlike the bryophytes, the pteridophytes originate from a fertilized egg and produce spores. Pteridophytes are well represented by the ferns, which have existed from the Devonian period. Another class of pteridophytes is the horsetails (*Equisetales*), which also have existed from the Devonian to the present.

The third class of pteridophytes is the club mosses, which are largely creeping, many-branched plants with numerous tiny, mosslike leaves spirally arranged on the stem. The final class of pteridophytes, *Sphenophyllales*, consisted of slender plants with jointed stems and leaves in whorls. These climbing plants are known from the Devonian to the Permian periods.

Spermatophytes: Gymnosperms

The fourth phylum, the *spermatophytes*, are distinguished by the production of seeds, although the lower groups have the same alternation of the vegetative (asexual) and reproductive (sexual) generations as is seen in the pteridophytes. The chief distinguishing characteristics of the spermatophytes are the formation of a pollen tube and the production of seeds.

The first class, the *gymnosperms*, are typified by the pines, mostly evergreens. Members of one order of gymnosperms, *Cycadofilicales*, were fernlike in habit but were not actually ferns. Because the leaf and stem remained practically unchanged, it is very easy to mistake the early seed plants for ferns. One of the most familiar of the fernlike fronds of the Pennsylvanian coal deposits is *Neuropteris*, which had large, compound leaflets.

The stem in most forms was thick and short and covered with an armor of leaf bases. It represents an advance over previous plants in that it had a true flower because both male and female organs were borne on the same axis and were arranged in the manner of later flowering plants. Thus *Cycadales* is an intermediary in the line of development of the angiosperms (flowering plants) from their fern ancestors. This order formed the dominant vegetation of the Mesozoic, ranging from the Triassic into the Lower Cretaceous.

The next order of gymnosperms, *Cordaitales*, is an extinct group of tall, slender trees that thrived throughout the world from the Devonian to the Permian period. The leaves of these trees were swordlike and distinguished by their parallel veins and great size, reaching up to 1 meter. The *Cordaitales* were the dominant members of the gymnosperm forests during the Devonian period. The fourth order of gymnosperms, *Ginkgoales*, resembles the conifers in general appearance. The leaves, however, are fanlike and are shed each year. Like the cycads and ferns, the male cells are motile in fertilization.

The order *Coniferales* includes mostly evergreen trees and shrubs, with needles or scalelike leaves and with male and female cones. Derived from *Cordaitales* of the Paleozoic, *Coniferales* possesses fewer primitive characters than *Ginkgoales*. The yews, which are comparatively modern, have fruit with a single seed surrounded by a scarlet, fleshy envelope. Another family, *Pinaceae*, having cones with woody or membranous scales, are represented by *Araucaria*, which is very common in the Petrified Forest in eastern Arizona.

The *Abietae*, one of the more common families of evergreens, includes pines, cedars, and hemlocks dating back to the Lower Cretaceous. One of the most extraordinary members of the conifers was the family *Taxodiaceae*, which includes the genus *Sequoia*, represented today only by the redwood and the *Sequoia gigantea*, which grow in California. These species' twigs, cones, and seeds were abundant in the Lower Cretaceous of North America. Finally, the family *Cupressaceae* includes the junipers and is known from the Jurassic.

Spermatophytes: Angiosperms

The second class of spermatophytes is the *angiosperms*, commonly known as flowering plants. The angiosperms contain the plants of the highest rank. This group comprises well over one-half of all known living species of plants. The typical flower is composed of an outer bud-covering portion, the stamens, and the pistil. When the wind or an insect brings the pollen into contact with the pistil, the pollen is held in place by a sugary solution. After the pollen penetrates an ovule, the nucleus divides several times. This fusion is called fertilization. The embryo, consisting of a stem with seedling leaves, is called a seed.

Both subclasses of the angiosperms first appeared in the upper part of the Lower Cretaceous. *Dicotyledoneae* (the dicotyledones, or dicots) comprises a primitive subclass that begins with two seedling leaves that are usually netted-veined. The stem is usually thicker below than above, with the vascular bundles arranged to form a cylinder enclosing a pith center. As growth proceeds, new cylinders are formed. The last of the dicots to appear was the sassafras tree, flourishing throughout North America and Europe since the Lower Cretaceous.

The second subclass, *Monocotyledoneae* (monocotyledones, or monocots), descended from the dicots. These plants are distinguished by the fact that they begin with a single leaflet, or *cotyledon*. The veins of the leaves are parallel, the stem is cylindrical, and the roots are fibrous. This subclass is represented by the grasses and grains. Fossils from this subclass date back to the upper part of the Lower Cretaceous of eastern North America. The fossil record of the palm goes back to the mid-Cretaceous.

Evolution of Plants

The evolution of plants is the story of their struggle to adapt themselves to land. One of the changes necessary in the development of land flora was the change from a cellular structure to a vascular one, which opened up possibilities for increase in size and laid the foundation for the trees. In order to adapt to land, plants also had to develop a resistance to the dehydrating quality of the air.

The earliest plants, the thallophytes, were closely tied to water. One of the first examples of flora adapting to land were the freshwater algae. The change from a cellular to a vascular structure led to the development of roots; the pteridophytes were the first plants to take this step. The mosses and ferns adapted to land but still required rain or dew for the union of the gametes. It is only the spermatophytes that developed a device that freed them from the necessity of external water for fertilization to occur. This ability permitted the spermatophytes to proliferate throughout the earth.

Alan Brown

See also: Angiosperm evolution; Cycads and palms; Evolution of plants; Paleobotany; Paleoecology; Petrified wood.

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FRUIT CROPS

Categories: Agriculture; economic botany and plant uses; food

Fruits are mature, or ripened, ovaries of angiosperms, their contents, and any accompanying accessory structures. From a botanical point of view, common foods such as grains, nuts, dried beans, squash, eggplant, and tomatoes are fruits, but in common usage the term is usually restricted to fleshy fruits that are commonly grown commercially as crops and are eaten, primarily raw, for their fleshy and juicy pulp.

Fertilization of ovules and the initiation of seed development lead to hormone production that triggers fruit development. Consequently, fruits usually contain seeds, but seeds can form without fertilization (*parthenogenesis*), and fruits can develop without seeds (*parthenocarpy*). Many fruits that are cooked or eaten as part of a main course are usually classed as vegetables. This dichotomy is reflected in the origins of the two words: fruit, from the Latin *fruor*, "to enjoy," and vegetable, from the Latin *vegetare*, "to enliven."

Ecology of Fruits

In nature, fleshy fruits serve as a reward for seed-dispersing animals. In keeping with the evolutionary principle that selection tends to minimize the cost of structures while maximizing their function, the flesh of these fruits contains comparatively few calories and basically consists of colored, flavored sugar water. Using animals as dispersal agents carries a risk, however, of seed destruction. Consequently, fleshy fruits that are dispersed by animals exhibit a number of mechanisms that protect seeds. One of these is the production of a large, hard seed that an animal cannot eat, such as a peach pit or a mango seed. Another protective characteristic is small seeds that go through an animal's digestive system without being crushed or digested, such as strawberry seeds. Over the last ten thousand years that humans have been practicing agriculture, many fleshy fruited species have been domesticated and bred for improved fruit production and quality. Several of the most marketed fruits worldwide are discussed below.

Temperate Fruits

The rose family (*Rosaceae*) contains a wide array of fruits grown in the cool regions of the world: apples, pears, plums, peaches, cherries, strawberries, and raspberries. Apples are the most important fruit tree crop of temperate regions. Apple and pear fruits are known as *pomes* because the edible fleshy part of the fruit is a combination of the outer ovary wall and the basal part of the flower. Cultivated apples are believed to have originated in western Asia and were enjoyed in prehistoric times. Apples were brought to North America about 1620 and are now the most widely grown fruit in the United States. Most of the apples grown today are diploids, but many are triploids. Orchards are usually planted with grafted trees, to ensure uniformity of the crop. Literally thousands of varieties of apples have been developed over the centuries since the species was domesticated.

Plums, peaches, and cherries come from different species of the genus *Prunus*. They share a fruit type known as a *drupe*, consisting of a fleshy mesocarp and a single seed inside of a hard endocarp. While there are native species of *Prunus* in the New World, the domesticated species are native to Eurasia.

The modern cultivated strawberry is a hybrid that apparently formed spontaneously in a European garden between a species of *Fragaria* from Chile and one from Virginia. Europeans had eaten native strawberries for centuries before the discovery of the New World, but the hybrid (*Fragaria ananassa*) was larger in size, as flavorful, and produced more fruit. A strawberry is actually an aggregation of fruits, or *aggregate fruit*. Each tiny seed is itself a fruit. The large, succulent, mass is the swollen top of the stem on which the flower was borne. Raspberries are also aggregated fruits, but each globular segment of the raspberry is itself a fruit, called a *drupelet*. The caps of drupelets pull free of the stem tips when the berry is picked.

Grapes are the second most widely cultivated fleshy fruit (on a tonnage-produced basis). However, the majority of grapes are not eaten as fruit but are turned into other foods, such as vinegar, liqueurs, raisins, and wine. The most widely cultivated species of grape is *Vitis vinifera* (*Vitaceae*), a woody perennial vine native to middle Asia. There are hundreds of varieties of grapes that vary in the color of the skin, flesh, flavor, and sweetness of the berries.

Nuts are dry fruits, each of which contains a single seed that is free inside the ovary wall, except for an attachment at one end called the funiculus. The pericarp (the walls of the ovary) is hard and fibrous. Commercially grown nuts include filberts, pecans, walnuts, and macadamia nuts, sold both for eating and for cooking.

Tropical Fruits

Many species of the genus *Citrus* (including sweet orange, tangerine, grapefruit, lemon, and lime) are grown for their edible fruits. Sweet oranges (*Citrus sinensis*) are the most widely grown fruit in the world, but in the nineteenth century they were considered luxuries and prescribed as cold remedies by physicians. Like other citrus fruits, the fruit of an orange is technically a *hesperidium*, a berry with a leathery rind and a juicy pulp that is formed of juice sacks borne on the inner layer of the fruit wall. The juice sacks fill the sections of the fruit and surround the seeds. The watery solution in the sacks is high in vitamin C. There are three main classes of oranges: Valencias, navels, and blood oranges. Valencias, with their deep orange color and rich flavor, are the source of most or-

PhotoDisc

Over the last ten thousand years that humans have been practicing agriculture, many fleshy fruited species have been domesticated and bred for improved fruit production and quality. Strawberries are one of the wide array of fruits grown in the cool regions of the world.

ange juice. Navel oranges, favored for eating, are the result of a mutation that produces a second ovarylike structure (the navel) instead of seeds. Because they are seedless, navel oranges are all propagated by grafting. Blood oranges are seeded oranges named for the patches of deep red-purple color in the fruit.

Bananas became a major fruit crop in the twentieth century; prior to the use of refrigerated ships, bananas spoiled before they could reach markets outside the tropics. Wild bananas, native to eastern Asia, have seeds, but the common domesticated banana (*Musa paradisiaca*) is seedless and is the product of several cycles of hybridization followed by increases in chromosome number. Whether the fruit will be a tender and sweet yellow or red or a tough, starchy green plantain depends on the particular combination of chromosomes in the hybrid. Banana plants are giant herbs, not trees, and are propagated vegetatively by planting a piece of stem. Over the course of a year, the stem grows and produces a long terminal inflorescence of many clusters of female flowers along the flowering stalk and male flowers at the tip. The female flowers spontaneously mature, with each cluster forming a hand, or bunch, of bananas. An entire inflorescence can produce more than three hundred bananas, weighing 110 pounds. After fruiting, the shoot dies and is cut, allowing a sprout from the base to produce the next flowering stem.

Mangoes (*Mangifera indica*) are extremely common and important fruits in tropical areas, particularly in their native region of Southeast Asia, where the fruit pulp and even the seeds have been used for food. Mangoes are borne on trees that can grow only within tropical regions where there is adequate water in the summer. The fruit is a berry with musky yellow flesh surrounding a single large seed. Mangoes belong to the poison ivy family; some people are allergic to the latex produced in the skins. Mangoes were introduced into Brazil by the Portuguese in the early 1700's and subsequently spread to other areas of the New World tropics.

Melons, both common melons (*Cucumis melo*) and watermelons (*Citrullus lanatus*) belong to the same family (*Cucurbitaceae*) as squashes, but the latter are all native to the New World and the former to the Old World. All these species share the same kind of fruit, a *pepo*, which consists of a hard rind derived in part from the basal parts of the flower, and an edible fleshy layer of inner ovary tissue. Melons are monoecious vines with showy male and female flowers that require pollination to set fruit. Melons are native to Africa, where they were undoubtedly prized for their high water content and fresh flavor. Selection has led to numerous varieties, including cantaloupe, Crenshaw, honeydew, Persian, musk, and a variety of other melons that differ in the color and surface of the rind, color of the flesh, taste, and degree of sweetness.

Watermelons are native to sub-Saharan Africa, but they can be grown in temperate regions because they are annuals. The flesh is 87-92 percent water and is acidic enough to curdle milk. Recently, seedless types have been produced by artificially making triploid plants. The pollen of these triploids is sterile, and the seeds abort early. Farmers plant the triploids with fertile diploids. Pollen from the diploids fertilizes the ovules of the triploids and triggers fruit production. The seeds quickly die, but the fruit continues to mature into a seedless watermelon.

Beryl B. Simpson

See also: Angiosperm life cycle; Flower structure; Fruit: structure and types; Pollination; Reproduction in plants; Vegetable crops.

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FRUIT: STRUCTURE AND TYPES

Categories: Anatomy; angiosperms; economic botany and plant uses; reproduction and life cycles

Fruits are the seed-containing reproductive organs, including nuts and grains, produced by angiosperms (flowering plants).

When most people think of a fruit, what typically comes to mind is a juicy, edible object, such as an apple, orange, or banana. To botanists, however, fruit includes many plant-derived structures, such as grains, nuts, and many vegetables. In essence, a fruit is an enlarged *ovary*, often with some accessory tissue, that develops after a flower has been pollinated. After pollination, seed development begins, and soon the peripheral parts of the flower fall away, leaving the immature fruit. The fruit subsequently enlarges and then ripens to maturity. It is then often edible.

Fruit Structure

Almost all fruits have a general structure that consists of an outer layer called the *pericarp*. The pericarp, in turn, encloses the *seed* or seeds. Usually there is a space between the seed and the pericarp, called a *locule*. The pumpkin is a good illustration of this structure, with orange rind as the pericarp, the hollow space within the locule, and the seeds inside the locule.

There are many different kinds of fruits. Some, such as cherries, tomatoes, and apples, have fleshy, juicy pericarps. Others, such as peanuts, milkweed pods, and acorns, have dry pericarps. The variability in fruits represents different seed dispersal strategies. In some plants, the seeds are dispersed while still enclosed within the fruit. Seeds in fleshy fruits are often dispersed by animals that eat the fruit and then either discard the seeds or later defecate them. Other fruits have barbs or hooks that catch on to fur or feathers and then travel with an animal until they are removed or drop off. Still other seeds, such as those of maple and ash, have "wings" for wind dispersal. A few, such as those of the coconut palm and many sedges, have fruits that float and are dispersed by water. In most instances, the fruit merely opens, and the seeds drop onto the ground. Some plants, such as witch hazel and the touch-me-not, produce fruits that open explosively and can disperse their seeds great distances.

Fruit Types

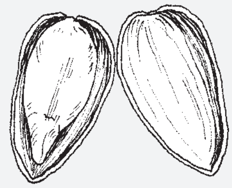
Fruits can be classified, based on the nature of the pericarp, into two groups: fleshy and dry. Fleshy fruits, in turn, are classified into several types, including *drupes*, *berries*, *pomes*, *hesperidia*, and *pepos*. Dry fruits are also subdivided into several categories, including *follicles*, *legumes*, *capsules*, *achenes*, *nuts*, *samaras*, *schizocarps*, and *caryopses*.

The three most familiar types of *fleshy fruits* are drupes, berries, and pomes. A drupe is a fleshy fruit that contains a single seed surrounded by a hard, bony inner wall of the pericarp (called the *endocarp*). The middle and outer walls of the pericarp (called the *mesocarp* and *exocarp*, respectively) are juicy and often sweet. Drupes include all the pitted fruits, such as cherries, plums, peaches, and olives. A berry typically has several seeds, and the pericarp is fleshy throughout. Familiar examples include tomatoes, eggplants, and grapes. A pome is a fleshy fruit, often with many seeds, that has a thick layer of *accessory tissue* immediately surrounding the pericarp. The accessory tissue is generally juicy, sweet, and often edible. Representative pomes include apples and pears.

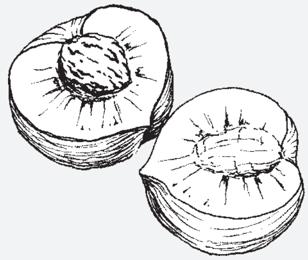
Two other fleshy fruits, the hesperidium and the pepo, are characterized by a leathery rind. Hesperidia, also known as a citrus fruits, have rinds rich in aromatic oils surrounding a juicy interior composed of wedge-shaped segments that have a sugary, acidic sap. Hesperidia include oranges, grapefruits, lemons, and limes. The pepo has a tough exocarp which is either smooth or variously sculptured and normally contains many seeds. Examples include cucumbers, cantaloupes, and squash.

Some common *dry fruits* are follicles, legumes,

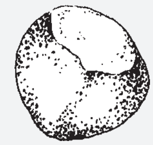
Fruit Types



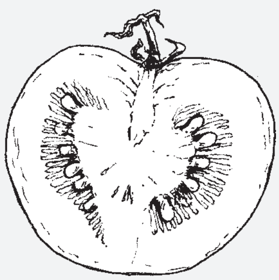
Achene: small, dry, indehiscent, single locule, single seed



Drupe: fleshy, indehiscent, stony endocarp around single seed; e.g., peach, cherry

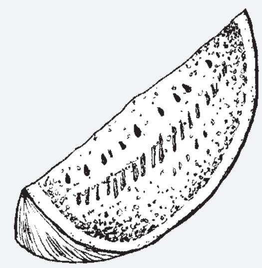


Nut: hard, dry, indehiscent, usually a single seed

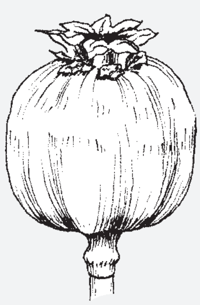


Berry: fleshy, from a single pistil, several seeds; e.g., tomato

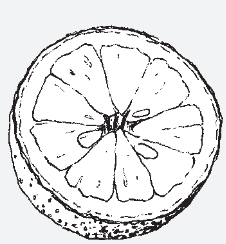
Follicle: dry, dehiscent with single-sided opening, single carpel; e.g., milkweed pod



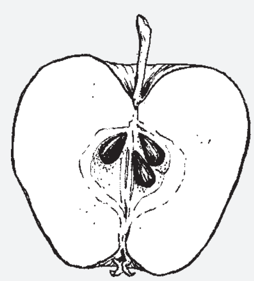
Pepo: fleshy, indehiscent, many-seeded, tough-rinded; e.g., melon, cucumber



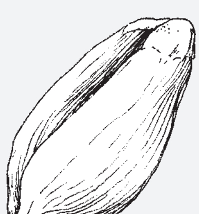
Capsule: dry, dehiscent, more than one carpel



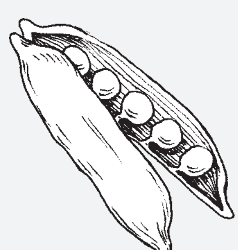
Hesperidium: fleshy fruit with tough rind; e.g., orange



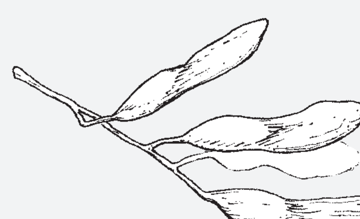
Pome: fleshy, indehiscent, growing from compound ovary, modified floral tube around core; e.g., apple



Caryopsis: dry, indehiscent, single seed with coat fused to pericarp—a grain



Legume: dry, dehiscent with two sides, single carpel; e.g., pea pod



Samara: dry, indehiscent, winged

Kimberly L. Dawson Kurnizki

capsules, achenes, nuts, samaras, schizocarps, and caryopses. Follicles are podlike fruits that open up along one side, revealing numerous seeds. Examples include milkweed pods and the aggregate follicles of magnolias. In contrast, legumes are podlike fruits that open up along two lines, releasing several seeds. They are produced by many members of the legume family, such as peas, beans, and peanuts.

The capsule opens along three or more lines or by pores at the top of the fruit. Lilies and poppies are good examples of plants that produce capsules. Achenes each contain a single seed that is free inside the cavity, except for an attachment at one end called the *funiculus*, and are typically small. A good example is a sunflower "seed." A nut is similar to an achene, except that the pericarp is hard and fibrous and is derived from a compound ovary. Representative nuts include acorns, hazelnuts, and hickory nuts. A samara is a modified achene that has part of the pericarp flattened to form a wing. Examples of plants that produce samaras include ashes and elms.

Maples have a winged fruit, called a *schizocarp*, which is often mistaken for a samara. Close observation reveals that the schizocarps come in attached pairs that later split into single-seeded portions. Schizocarps, which are generally not winged, also occur in the parsley family, where they may split into more than two parts. Finally, a *caryopsis* is a single-seeded fruit whose seed coat is fused to the

Fruit Types and Characteristics

Classification	*Examples*	*Type*[1]	*Fleshy/ Dry*[2]	*Dehiscent/ Indehiscent*[3]	*Comments*
Accessory	Strawberry	Accessory	F	—	Develops from receptacle; ovaries are achenes on surface.
Achene	Dandelion, sunflower	Simple	D	I	Single locule with single seed; not especially hard.
Aggregate	Raspberry	Aggregate	F	—	Drupelets from several pistils on a single flower.
Berry	Grape, tomato	Simple	F	—	Not enclosed by a receptacle, many seeds, soft skin.
Capsule	Lily, poppy	Simple	D	D	Formed by two or more carpels not separated by a septum.
Caryopsis (grain)	Wheat, corn, other grains	Simple	D	I	Single seed fused to pericarp.
Drupe	Peach, plum, cherry	Simple	F	—	Larger fruit with single seed (stone).
Drupelet	Raspberry drupelet	Simple on aggregate	F	I	Small, single seeded; occurs as a segment of an aggregate fruit.
Follicle	Milkweed pod	Simple	D	D	Single carpel opening on one side.
Hesperidium	Orange, other citrus	Simple	F	—	Berry-shaped, with several seeds and a tough rind.
Hip	Rose hips	Simple	F/D	—	Enlarged hypanthium surrounding many achenes.
Legume	Bean, pea pod	Simple	D	D	Composed of one carpel with seeds.

pericarp. Caryopses are produced only by plants in the grass family and include the familiar grains wheat, corn, rice, and oats.

The fruits listed above commonly fall under the category of *simple fruits*. In other words, they are identifiable as individual structures. Other plants produce fruits in dense clusters, and these are termed either *aggregate fruits* or *multiple fruits*. Aggregate fruits are produced by a single flower that has numerous pistils. One example is a raspberry, which is an aggregate of drupes which are often referred to as drupelets because of their small size. Another is the strawberry, not a berry in the botanical sense, which is an aggregate of tiny achenes attached to the surface of a swollen, juicy, *receptacle* (originally the base of the flower where all the flower parts were attached). In contrast, multiple fruits are produced by clusters of small flowers, each of which produces a single fruit. Representative multiple fruits include mulberries, figs, and pineapples.

Development and Maturation

In nature, fruits develop only after the flower is effectively pollinated. If pollination does not occur, the entire flower shrivels up, and no fruit is formed. Fruit development is apparently stimulated when the developing seeds produce hormones that diffuse into the ovary wall, causing it to enlarge. Two hormones are particularly implicated in fruit for-

Classification	*Examples*	*Type*[1]	*Fleshy/ Dry*[2]	*Dehiscent/ Indehiscent*[3]	*Comments*
Loment	Tick trefoil, sweet vetch	Simple	D	I	Legume but with individual seeds constricted by the pod.
Multiple	Pineapple, mulberry	Multiple	F	—	Formed by many flowers and ovaries on one receptacle.
Nut, nutlet	Acorn, hazelnut	Simple	D	I	Usually single seed inside a hard, woody pericarp.
Pepo	Melon, cucumber	Pepo	F	—	Not enclosed by receptacle; many seeds; tough rind.
Pome	Apple	Simple	F	—	Floral tube (core) containing multiple seeds, surrounded by fruit.
Samara	Maple, ash, elm fruits	Simple	D	I	Not splitting; winged.
Schizocarp	Carrot, geranium fruits	Simple	D	I	Fruit splitting but not releasing seeds.
Silicle (silique)	Mustard (*Brassicaceae*) fruits	Simple	D	D	Two carpels separated by septum, less than twice longer than wide.
Synconium	Fig	Multiple	F	—	From entire inflorescence (many flowers) with inverted receptacle bearing flowers internally; fruit formed of ripened ovaries (receptacle tissue).

— Not applicable.

1. Four main types: Simple (formed from a single mature ovary from a single flower); aggregate (several mature ovaries from a single flower); multiple (several mature ovaries from several flowers united on one receptacle, forming a mass); accessory (from tissues surrounding the ovary or ovaries, generally from flowers with inferior ovaries).
2. All fruits are either dry or fleshy, characterizing the pericarp at maturity.
3. Dehiscent fruits are dry fruits that split open when mature to release their contents, along either one or two sides. Indehiscent fruits are dry fruits that do not split open at maturity; often they are single-seeded.

mation: *auxin* and *gibberellin*. Many fruit growers routinely spray their plants with auxin to induce the formation of seedless, or *parthenocarpic*, fruits.

Fruit ripening is an important process that must occur properly in order for the seeds to be effectively dispersed. In fleshy fruits, such as tomatoes, cherries, apples, oranges, and bananas, fruit ripening involves several important changes in the pericarp that make the fruit more visible and palatable to a potential animal disperser. Perhaps the most visible change is in the color of the fruit. Immature fruits are green because of the presence of the pigment *chlorophyll* in the cells of the outer layer. Potential dispersers fail to notice the immature fruit because it blends in with the surrounding leaves. As fruits ripen, the chlorophyll breaks down, and other colors, such as orange, yellow, red, or blue, become evident. Those colors are the result of pigments that either are present in the unripe fruit and masked by the chlorophyll or develop as the fruit ripens. The texture and chemical composition of the pericarp change as well. Most fruits soften as they ripen, a result of the degradation of the cell walls in the pericarp. At the same time, starches or oils in the pericarp are chemically transformed into simple sugars such as *fructose*. That change causes the fruit to become better-tasting, more digestible, and thus more attractive to a hungry animal.

The physiology of fruit ripening has been well studied. Fruits such as grapes, citrus fruits, and strawberries ripen gradually. Others, such as tomatoes, apples, and pears, exhibit a transitional event called *climacteric*, which is marked by a dramatic increase in the rate at which oxygen is absorbed by the fruit, followed by a rapid change in the color and physical nature of the pericarp. Studies of climacteric fruit have shown that the onset of ripening can be delayed by storing the fruit at low temperatures or in an atmosphere devoid of oxygen. On the other hand, climacteric can be induced by exposing the fruit to *ethylene*, a plant hormone. Interestingly, ethylene is produced by ripening fruits, and thus a ripe fruit promotes the development of any unripe fruits nearby.

Finally, many plants drop their fruits at some point after they become ripened. Botanists use the term *abscission* to refer to the dropping process. Fruit abscission, like leaf abscission, occurs when a layer of cells at the base of the *pedicel* (the stem that attaches to the plant) become weakened. Studies have shown that abscission is influenced by two hormones: ethylene and auxin. Ethylene promotes abscission of fruits in many plant species, such as cherries, blueberries, and blackberries. Auxin, on the other hand, has effects that vary depending on the dose: Low concentrations promote fruit retention, while high doses cause fruits to drop.

Kenneth M. Klemow

See also: Hormones; Pigments in plants.

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FUNGI

Categories: Fungi; taxonomic groups

The kingdom of nonphotosynthetic eukaryotic organisms, fungi are heterotrophic organisms, feeding on other materials rather than making their own food. They live on dead organisms by secreting digestive enzymes and absorbing the breakdown products. Although these organisms are stationary like plants and thus traditionally studied in botany courses, the heterotropic fungi are fundamentally different from plants, which are autotrophic organisms.

Although some unicellular forms of fungi exist, most fungi are characterized by a mycelial growth form; that is, they generally are made up of a mass of *hyphae* (tubular filaments). All fungi live in their food and have an absorptive mode of nutrition by which they secrete digestive enzymes and absorb the breakdown products. They are therefore heterotrophs. Fungi are also characterized by possession of cell walls made of chitin, synthesis of the amino acid lysine via the amino adipic acid (AAA) pathway, and possession of a ribosomal DNA sequence that classifies them more closely with other fungi than with any other group of organisms. Fungi produce spores by either asexual or sexual means. The way they produce their spores constitutes one of the main taxonomic criteria for classifying them within the kingdom *Fungi*.

Ecology and Habitats

Because of their absorptive, heterotrophic mode of acquiring nutrients, fungi are important members of the *decomposer* community in ecosystems. Because fungi break down dead organic matter (that is, because they live as *saprophytes*), they simultaneously release nutrients that are taken up by other members of their ecosystem. Fungi exist in terrestrial and aquatic habitats. Because the saprophytic fungi grow in a radial fashion from a point of origin, the mushroom types of fungi sometimes form so-called fairy rings: At the advancing edge of the mycelia, mushroom fruiting bodies appear in the shape of an irregular ring. One mass of mycelia, for example, became so large that it occupied 37 acres (15 hectares) in the Upper Peninsula of Michigan and became known as the Humongous Fungus.

Fungi are major *parasites*, living on live plants, animals, and other fungi. Fungal plant pathogens have evolved a variety of mechanisms to enable the fungus to penetrate the host plant and overcome the host's defenses. Next, the pathogen absorbs food from the host by establishing *haustoria*, which form a highly specialized absorbing system. These structures do not actually penetrate the host plasma membrane, but they reside within pockets of the host cell, where they secrete extrahyphal enzymes and absorb the soluble result. Consequently, the host plant develops a series of symptoms characteristic of the infection. Farmers can suffer severe loss of crops if an infestation is left unchecked. Plant breeders attempt to breed disease resistance into crop plants as a means of combating fungal diseases.

In contrast to plant fungal pathogens, some fungi grow within plants and do not cause disease symptoms. These fungi are called *endophytes*. They appear to protect host plants from herbivores and from certain pathogenic microbes.

Interactive Associations

Mycorrhizae are mutualistic associations between fungi and vascular plants whereby both members of the association benefit. A fungus that grows on plant roots facilitates nutrient and water uptake for the plant, and the plant provides organic nutrients to the fungus. About 90 percent of higher

PhotoDisc

Mushrooms are some of the best-known representatives of the kingdom Fungi.

plants have mycorrhizal associates. The fungus will form one of two types of associations with the plant. *Endotrophic mycorrhizae* penetrate cortical root cells with specialized hyphae that are finely branched. Other fungi grow around the root and between the cortical cells but never penetrate the cells. More than 80 percent of fungal genera that form mychorrizae are in the phylum *Basidiomycota*.

Lichens are an association that appears to be a controlled parasitism of an alga partner by a fungal partner. Ninety percent of lichens have one of three genera of algae as the photosynthetic partner: *Trebouxia*, *Trentepohlia*, and *Nostoc*. The first two are *Chlorophyta* (green algae), and the latter is a cyanobacterium (blue-green bacteria, formerly thought to be blue-green algae). Of all fungal partners, 98 percent are members of the phylum *Ascomycota*. In this controlled parasitism, the fungus obtains minerals and water and develops a physical structure to house the algal partner. The algal partner provides photosynthetic products to the fungal partner. These organisms can live in extreme environments such as deserts or Arctic regions. Because they have no way to eliminate toxic materials, they are extremely sensitive to air pollution. Indeed, the condition of lichens is sometimes used as an indicator of air pollution.

Some fungi have trapping mechanisms that allow them to prey upon invertebrate organisms such as nematodes, rotifers, and copepods. These trapping mechanisms involve networks of adhesive hyphae, adhesive branches, adhesive nets, adhesive knobs, nonconstricting rings, and constricting rings.

Chytrids

The type of sexually produced spore determines the taxonomy of fungal phyla. *Chytridiomycota*, or chytrids, reproduce sexually by a variety of means, including isogamy, anisogamy, oogamy, contact between gametangia (structures that contain the gametes), and contact between vegetative structures. However, the chytrids are better defined by their asexually produced, motile, uniflagellated zoospores; in fact, the chytrids are the only phylum of fungi that produce such spores. There are about 790 species in this phylum.

Zygomycota

Zygomycota reproduce sexually by producing zygospores within a zygosporangium. These fungi have a mycelial growth form that forms crosswalls only at reproductive structures. The zygomycetes produce spores asexually within a sporangium. Sexual reproduction leads to the production of a zygospore within a zygosporangium.

Mycelial cultures of a single strain may mate (in homothallic species) or may require a different mycelial strain (in heterothallic species) in order to mate. In both cases, copulation of two multinucleated gametangia occurs. Two lateral branches grow toward each other, sometimes attracted by the hormone trisporic acid. When these branches touch, a wall is laid down near the tip of each branch, creating the multinucleated gametangia. The wall separating the two gametangia at the point of contact breaks down, the protoplasmic contents mix, and the nuclei pair up and fuse. As the nuclei pair, a wall surrounding the fused gametangia develops into the zygosporangium. This thick-walled structure is resistant to environmental abuse. At or just prior to germination, the nuclei within the zygospore undergo meiosis. A stalk grows out of the zygospore bearing a sporangium. Included in this phylum of about 1,060 species are *Rhizopus*, the black bread mold; *Pilobolus*, the "cap" throwing fungus; and *Entomophthora*, the fly fungus.

Ascomycota

The ascomycetes reproduce sexually by producing ascospores within an ascus. Ascomycetes have a mycelial growth form with incomplete crosswalls. The septal hole permits the migration of cellular contents from cell to cell. *Yeasts* are single-celled ascomycetes that normally do not produce mycelial forms. Asexually, the *Ascomycota* reproduce by budding, fission, or production of chlamydospores or conidiospores. The unicellular yeasts reproduce using fission and budding methods. The majority of ascomycetes reproduce asexually, using conidiospores. A cell that is going to generate a conidium grows directly from hyphae or at the end of a stalk. The conidiogenous cell produces a swelling at the tip, into which protoplasm and a nucleus migrate. The nucleus is produced by mitotic means and is haploid. After swelling is complete and migration finishes, a wall is formed, separating the conidiospore from the conidiogenous cell.

Sexual reproduction occurs by gametangial contact between the female structure (the ascogonium) and the male structure (the antheridium). Usually, opposite mating types are required for sexual reproduction to occur. When contact between the gametangia occurs, nuclei from the antheridium migrate into the ascogonium and pair up with nuclei in the ascogonium. Alternatively, conidia or microconidia may land on the ascogonium and fuse with it. In both cases, fusion of paired nuclei is delayed until development of the ascus. Instead, special hyphae grow out from the ascogonium and will eventually generate the ascus. These ascogenous hyphae possess two nuclei, one of each mating type, in each cell.

Frequently the development of the ascogenous hyphae and ascus is associated with the development of a fruiting body. When the fruiting body is at the appropriate developmental stage, a hooklike structure develops at the end of the ascogenous hyphae. At this time the nuclei fuse, producing the only diploid cell in the life cycle of these organisms. As the saclike ascus elongates, the diploid nucleus undergoes meiosis, producing four haploid nuclei. Usually one mitotic division then occurs, resulting in eight nuclei in the elongated sac. Eventually walls are formed around each nucleus, creating the ascospore. As noted above, many *Ascomycota*—but not the yeasts—produce a fruiting body, called the ascoma. The ascoma may take a variety of shapes, from a closed, ball-like structure (cleistothecium) to a pear-shaped structure with an opening at the top (perithecium) to a cup-shaped open structure (apothecium) or a stromatic structure containing cavities (ascostroma). In all cases, the asci with the ascospores are contained within these structures. The type of ascoma, the number of walls in the ascus, and the presence or absence of a fertile layer from which the asci arise are criteria used to distinguish among the about 32,300 species of *Ascomycota*.

Basidiomycota

Basidiomycota reproduce sexually by producing basidiospores on a basidium. Like the *Ascomycota*, the *Basidiomycota* fungi also have a mycelial growth form with incomplete crosswalls. However, the structure of these crosswalls is different in that there is a swelling surrounding the pore where the wall is incomplete. There is also a curved membrane on each side of the hole, together looking much like parentheses. This septal structure is called the dolipore septum and is a secondary characteristic of the *Basidiomycota*.

The mycelia of most *Basidiomycota* pass through three stages. The primary mycelium has cells with a single nucleus, all derived from the germinated basidiospore; it is said to be *homokaryotic*. Later in development, fusion of hyphae of opposite mating types occurs, establishing the secondary mycelium, in which each cell has two nuclei; the secondary mycelium is therefore *dikaryotic*. Clamp connections occur on the secondary mycelium to facilitate division of the two nuclei in limited space. *Clamp* *connections* are another secondary characteristic of the *Basidiomycota*. Tertiary mycelium develops in the specialized organized tissues of the fruiting bodies, the *basidioma*.

Asexual reproduction takes place by means of budding, fragmentation of mycelium, production of chlamydospores, or conidia. Chlamydospores are fragmented sections of mycelia that have rounded up and formed thick walls. Sexual reproduction in the *Basidiomycota* occurs primarily by fusion of genetically compatible hyphae, thus establishing the secondary mycelium. Fusion of these nuclei is delayed until the production of the basidium. Nuclei of the dikaryotic cell that is to become the basidium fuse to produce one diploid nucleus that immediately undergoes meiosis, resulting in four haploid nuclei. Depending on the type of basidiomycete fungus, the haploid nucleus and associated cytoplasm migrate into a swelling that develops at the tip of the basidium. When full-sized, a wall separates the basidiospore from the basidium. Eventually the basidiospore falls off or is shot off the basidium. Classification of the approximately 22,250 species of *Basidiomycota* depends on the presence or absence of a fruiting body, septation, and the number of cells in the basidium.

Fungi: Phyla and Characteristics

Group	*Species*	*Characteristics*
Ascomycota	32,000+	Members of this phylum produce sexual spores in a specialized cell called an ascus. Includes *Neospora* (powder mildew), *Morchella* (morels), and *Tuber* (truffles). Causes mildews, fruit rots, chestnut blight, Dutch elm disease.
Basidiomycota	22,000+	Members of this phylum produce sexual spores on a specialized cell called a basidium. Includes three classes: *Basidiomycetes* (mushrooms, stinkhorns, puffballs, bird's nest fungi), *Teliomycetes* (rusts), and *Ustomycetes* (smuts). Causes rusts and smuts; includes poisonous varieties of mushrooms such as *Amanita*.
Chytridiomycota	800+	Members of this phylum are mainly aquatic organisms with motile spores with a whiplike flagellum. Includes gut chytrids, which live in the rumina of herbivores. Includes *Allomyces*, *Batrachochytrium* (parasite of frogs), and *Coelomomyces* (parasite of various insect hosts). Causes corn spots, crown wart in alfalfa, black wart in potatoes.
Zygomycota	750+	Members of this phylum are recognized by their rapidly growing hyphae. Includes bread molds and fruit rots (*Rhizopus stolonifer*); *Glomus versiforme* is often involved in mycorrhizae ("fungus roots").
Deuteromycetes	15,000+	Also called "fungi imperfecti," an artificial group based on the members' purely asexual form of reproduction. Includes fungi in the genus *Penicillium*, involved in cheese making and in the antibiotic penicillin. Also cause rots, molds, diseases of grains, vegetables, and fruits. *Aspergillus flavus* produces the carcinogenic toxin found on peanuts, aflatoxin.
Lichens	17,000+	Symbiotic relationships of fungal (mycobiont) and algal (photobiont) partners, familiar on substrates such as rocks, wood, tree trunks. Most of the mycobionts are members of *Ascomycota* or *Basidiomycota*. Some species live more than a century. Important as environmental indicators, food for tundra animals, sources of dyes, potential medicinal properties.
Yeasts	600+	Not a formal taxon but an artificial group of unicellular fungi that grow by budding. Yeasts in genus *Saccharomyces* are used in food manufacturing (bread dough, alcohol fermentation); also cause disease, such as fungal infections (*Candida albicans*) and pneumonia (*Pneumocystis carini*). Most are members of *Ascomycota*; a quarter are from *Basidiomycota*.

Source: Data on species are from Peter H. Raven et al., *Biology of Plants*, 6th ed. (New York: W. H. Freeman/Worth, 1999).

Deuteromycota

Deuteromycota are fungi that reproduce only asexually, by production of conidiospores. The majority of these fungi are thought to be derived from the *Ascomycota* by evolutionary loss of sexual stages; either that, or the sexual stages have yet to be discovered. Because the sexual stages, also called the "perfect" stages, have been lost, these fungi are also referred to as the "imperfect fungi," or "fungi imperfecti." About fifteen thousand form-species are grouped into larger form-genera and form-classes, based on the morphological characteristics of their asexual reproductive structures. Because this is an artificial classification (not based on evolutionary relationships), no basis for conclusions about relatedness within groups can be implied or inferred.

Evolutionary History

Because of a lack of sufficient fossil evidence, phylogenetic relationships have been inferred based on morphological features associated with cell structure and sexually produced structures. With the advent of sequencing analysis of proteins and nucleic acids, observations of some relationships have been confirmed, and new relationships are being discovered.

Small subunit rDNA sequence analysis shows that the fungi are derived from a flagellated animal ancestor. These data show fungi to be a *monophyletic* group, with the *Chytridiomycota* and *Zygomycota* as the earliest branches within the group. The facts that all fungi utilize the AAA synthetic pathway for lysine and possess cell walls of chitin support this monophyletic view of all fungi. Sequence analysis supports a relationship between the *Ascomycota* and *Basidiomycota*, perhaps both being derived from yeasts. The evidence for the monophyletic evolution of the *Basidiomycota* is strong, based on sequence analysis and morphological features such as ballistospores, basidia, and clamp connections. Sequence analysis, however, appears to contradict morphologically based phylogeny groupings, which use structure and number of cells in the basidium and presence or absence of a fruiting body as key features. Within the *Ascomycota*, phylogeny appears to be monophyletic, but the evidence is not strong.

John C. Clausz

See also: Ascomycetes; *Basidiomycetes*; Basidiosporic fungi; Chytrids; Deuteromycetes; Lichens; Rusts; *Ustomycetes*; Yeasts; Zygomycetes.

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GARDEN PLANTS: FLOWERING

Categories: Angiosperms; economic botany and plant uses; gardening

The most popular flowering garden plants worldwide include roses, lilies, tulips, irises, and daffodils. These plants range in form from herbs to bushes to trees. Their leaves, flowers, and optimum growth needs differ greatly.

Flowering plants (*angiosperms*) are grown in gardens for their beauty and their fragrant aromas. They and their relatives can also be grown for food. Myriad flowering plant types are grown in the world's gardens. Most popular flowering garden plants are in the rose family (*Rosaceae*, about three thousand species) and the lily family (*Liliaceae*, about forty-five hundred species), which together make up a wide variety of herbs, bushes, and trees. Also quite popular are members of the iris family, *Iridaceae*, which includes crocuses. Lilies and irises belong to the order *Liliales* (about eight thousand species) of herbaceous flowering plants. Other well-known plants of this order are tulips, daffodils, and hyacinths.

Roses and Lilies

The most popular garden plants are roses and lilies. Rose is the common name for members of the family *Rosaceae*, a family of one hundred genera and three thousand species. Included are important fruit and ornamental species, including the familiar genus *Rosa* (true roses). *Rosaceae* and more than twenty other families belong to the order *Rosales*. *Rosaceae* grow as trees, shrubs, or perennial herbs. Within this family, food is produced by apple, pear, peach, plum, cherry, apricot, almond, and nectarine trees. Many berries, including raspberries, blackberries, and strawberries, are *Rosaceae*.

Since antiquity, the true rose has been among the most popular garden flowers in the world. Roses evolved from sweetbriers (wild roses). This genus of perennials, with about one hundred species, is mostly native to the north temperate zone. Experts recognize two main classes of the approximately thirteen thousand cultivated rose varieties (*cultivars*) which have arisen from hybridization of a few original species, mostly from Asia. Members of the original class, such as brier, damask, and moss roses, bloom once a year, in early summer. The others, called *perpetual roses*, bloom more than once a season. They include the tea roses, polyanthas, and rugosas. Tea roses smell like tea or fruit. Other roses have the distinctive rose smell or no smell at all. True rose flowers are white or various shades of yellow, orange, pink, or red. A perpetual rose bush can grow up to 6 feet (2 meters) tall. Polyantha bushes are low and bear flower clusters; shrub roses grow up to 15 feet (4.5 meters) tall. The leaves of rose plants have stipules (leaflike appendages) at stalk bases and are most often compound.

The name "lily" indicates any of forty-five hundred species of the family *Liliaceae*. This is one of the largest, most important plant families in the order *Liliales*. The herbaceous flowering plants have beautiful, showy flowers. True lilies, *Liliaceae* of the genus *Lilium* (one hundred species), are native to temperate areas of the Northern Hemisphere and are among the oldest of cultivated plants. Examples are Colchis, tiger, Madonna, and Easter lilies. Within the same family are onions, garlic, and asparagus. Also included in *Liliales* are tulips, daffodils, hyacinths, and amaryllis. Among the eight thousand *Liliales* species are herbs, climbing shrubs, succulents, and trees. Their thick, fleshy stems grow from underground storage organs, and all have narrow, upright leaves with parallel veins. Most grow worldwide but flourish only in temperate and subtropical areas. These perennials bloom once yearly and store food and water in scaly bulbs, corms, or rhizomes. Stems and leaves may be storage organs, too, and have thick bark to prevent water loss. Many plants in the group can carry out asexual reproduction via bulblets on parent bulbs or flower clusters (for example, garlic).

Tulips, Daffodils, and Irises

Tulips and irises share some characteristics. The *Liliaceae* genus *Tulipa* contains about one hundred tulip species. They are native to Asia and the eastern Mediterranean region, and thousands of tulip cultivars are popular garden flowers. A tulip plant produces two to three thick, blue-green leaves, clustered at its base.

Irises, also in the *Liliales* order, belong to the family *Iridaceae*, which includes some of the world's most popular garden flowers. Irises are indigenous to the north temperate zone, Asia, and the Mediterranean region. "Iris" is the common name for spring-flowering, bulbous herbs. The leaves of iris plants rise directly from the bulb or rootstock; they are very narrow, erect, and swordlike. Iris plants arise from rhizomes (stems underground) or bulbs and have large flowers. *Iris*, the Greek word for "rainbow," refers to the flowers' rainbowlike color combinations.

Garden Plants and Places of Original Cultivation

Plant	*Region*	*Plant*	*Region*
Acacia	Australia	Hydrangea	China
African violet	Africa	Impatiens	Africa
Azalea	Japan	Japanese iris	Japan
Bellflower	Europe	Lily of the valley	Europe
Bird of paradise	Africa	Lobelia	Africa
Black-eyed Susan	North America	Lupine	North America
Bleeding heart	Japan	Marigold	Mexico
Bottle brush	Australia	Michaelmas daisy	North America
California poppy	North America	Morning glory	South America
Calla lily	Africa	Nasturtium	South America
Camellia	China	Nemesia	Africa
Candytuft	Mediterranean	Oleander	Mediterranean
Carnation	Mediterranean	Pansy	Europe
Checkered lily	Europe	Pelargonium	Africa
China aster	China	Penstemon	North America
Chrysanthemum	China	Peony	China
Clarkia	North America	Petunia	South America
Clematis	China	Phlox	North America
Columbine	North America	Plumbago	Africa
Coreopsis	North America	Poinsettia	Mexico
Cosmos	Mexico	Polyanthus	Europe
Crocus	Europe	Portulaca	South America
Dahlia	Mexico	Rose	Europe
Day lily	China	Salpiglossis	South America
Forget-me-not	Europe	Scabious	Europe
Forsythia	China	Snapdragon	Mediterranean
Foxglove	Europe	Snowdrop	Europe
Frangipani	Mexico	Stock	Europe
Freesia	Africa	Strawflower	Australia
Fuchsia	South America	Sunflower	North America
Gardenia	China	Sweet alyssum	Mediterranean
Gladiolus	Africa	Sweet pea	Mediterranean
Gloxinia	South America	Verbena	South America
Grape hyacinth	Mediterranean	Wallflower	Europe
Hollyhock	China	Wisteria	Japan
Hyacinth	Mediterranean	Zinnia	Mexico

Source: Data are from Brian Capon, *Botany for Gardeners: An Introduction and Guide* (Portland, Oreg.: Timber Press, 1990), pp. 81-82.

"Iris" is the common name for spring-flowering, bulbous herbs. Irises are indigenous to the north temperate zone, the Mediterranean region, and Asia.

Another interesting and popular group of flowering garden plants is daffodils, of the genus *Narcissus*. They are sold as bulbs. Daffodils are so popular that they have been widely hybridized. A daffodil plant usually produces five to six lance-shaped leaves grouped about the base of its stem. Each plant has one large flower.

Blooming Habits: Roses and Lilies

Wild rose plants have regular, single flowers, with five petals. In most cultivars *double flowers*, having petals numbered in multiples of five, are produced. The flower also has a calyx with five lobes, many stamens, and one or more carpels. Rose sprouts have two seed leaves, so the plants are eudicots. Flowers of most cultivars bear few seeds, and the majority of them are sterile. The number of seeds is small because in double roses, flower parts that would otherwise produce seeds become extra petals. Therefore, most roses are grown from cuttings. All new rose varieties begin as seedlings, raised from fertile seeds.

Lily flowers grow one per stalk or in clusters. In contrast to roses, they have six petal-like segments, causing the flowers to resemble trumpets or cups. The flowers range from white to shades of almost all other colors except blue. Lily flowers all have three-chambered ovaries with nectaries between the chambers. They produce large, well-developed seeds which hold plenty of food-storage tissue and embryos. Plants of most species are 1 to 4 feet (0.3 to 1.3 meters) tall, though a few grow up to 8 feet (nearly 3 meters) tall. Lilies are usually raised from bulbs but can be grown from seed. Most species of these perennials bloom once, in July or August. However, flowering periods of some species begin in May or late autumn.

Blooming Habits: Tulips, Irises, and Daffodils

Tulip flowers can be single or double, and most, called "self-colored," grow in a huge range of solid colors, from pure white to many shades of yellow, red, brown, and purple. Some, called "broken tulips," have varicolored flowers caused by a harmless virus carried by aphids. The garden tulip, introduced into Western Europe from Turkey in the 1600's, is commercially cultivated most in the Netherlands and the United States, especially Michigan and Washington. Bell-shaped lilies are usually solitary. They have three petals and three sepals, six stamens, and a triple ovary that ends in a three-lobed stigma. A tulip fruit holds numerous seeds, but many of the four thousand tulip cultivars can be propagated only via their scaly bulbs.

Iris flowers are more asymmetric than those of roses, lilies, or tulips. They possess six petallike floral segments: three inner, erect *standards* forming an arch atop the flower and three outermost, drooping, often multicolored *falls*. A set of three petallike stigmas also cover the stamens. Iris colors include white, yellow, bronze, mauve, purple, and red. Best-known are rhizomatious bearded (German) irises, which have multicolored falls. These cultivars arose from European species. They have stems up to 3 feet (1 meter) tall and yearly bear at least three flowers per plant. The twentieth century saw the development dwarf bearded irises and fragrant cultivars. The best-known beardless, rhizomatous irises are Japanese and Siberian irises, which have clusters of blooms. English and Spanish irises grow from bulbs.

Daffodils, the best-known members of the genus *Narcissus*, are indigenous to northern Europe and have been widely cultivated there and in North America. Usually daffodil plants grow to heights of about 1.5 feet (about 0.5 meter). Each plant produces one large blossom on its centrally located stem. The blossom has a corolla split into six lobes and a centrally located trumpet, the *corona*. The corona is frilled at its edges, contains flower stamens, and leads to its pistil. The flowers were originally yellow; however, they have been hybridized into cultivars in which the trumpet and petals are often of contrasting yellows, whites, pinks, or oranges.

Rose and Lily Cultivation

Although found all over the world, roses grow best in mild climates, such as southern France and the U.S. Pacific coast. Roses' excellent growth in many different kinds of soil and climate is a result of the availability of myriad cultivars. A rose garden should be protected from cold wind and be exposed to sunlight for several hours a day. Deep, rich loam is best for roses, but most cultivars grow in sandy and gravelly soil. The soil must be well drained. Roses are planted in spring, about 2 feet (0.6 meter) apart. In the United States, about sixty-five million commercial rose plants are cultivated yearly. About 35 percent are grown for cut flowers, and the rest are used in gardens or landscaping. For the best growth, rose plants require severe pruning, which is adapted to the intended use of the flowers. Most varieties are grown by budding on understocks. Roses are susceptible to diseases such as rust and black-spot disease, so pests should be watched for and discouraged.

Lilies grow best in well-drained, deep, sandy loam, sheltered from winds and hot sunlight. Their bulbs are planted 6 or more inches (15 or more centimeters) underground, in late fall. This deep placement is used because they send out their roots well above the bulbs. As soon as blooms wilt, their seed pods should be removed. Lilies can be made to bloom early by putting the bulbs in pots and covering them with peat moss or soil. When kept at 50 degrees Fahrenheit for two weeks and then stored at 60 degrees Fahrenheit, they bloom in three months. Lilies are susceptible to a number of diseases. The most serious is mosaic, carried from plant to plant by aphids. Infected plants should be uprooted at once and burned to prevent an epidemic. A second severe disease of lilies is botrytis blight.

Tulip, Daffodil, and Iris Growth

Tulips are early bloomers, flowering in early spring; mid-season-bloomers; or late bloomers. Late bloomers are the largest group, with the widest range of growth habits and colors. Tulips flourish in any good soil but, like roses, do best in well-drained loam. The bulbs are planted in autumn at depths of 6 or more inches. These perennial plants flower annually for a few years, but eventually flowering diminishes. For best flower yields, after four to five years it is necessary to dig up bulbs after the flowers are gone and the foliage yellows. The bulbs should then be stored in a cool, dry place and replanted in autumn. Tulips are rarely attacked by garden pests.

Daffodil bulbs are planted in the fall, in loose soil, about 4 inches (10 centimeters) deep. The plants appear in mid-February. Their blossoms open in early April, announcing spring. Like tulips, the plants flower well, annually, for a few years and then diminish. For best flower yields, it is useful to store the bulbs every four to five years in the manner described above for tulips.

Irises bloom from March to July and may be planted in the spring before blooming or in the autumn. These perennials give the best flowers if plants are replanted every four to five years to eliminate the problem of overcrowding. Bearded irises do best in sunny areas where the soil is not too rich, but beardless ones prefer damp, rich soil. Iris diseases include crown rot, soft rot, and leaf spot. If the disease is serious, roots and soil may have to be treated. The worst iris insect enemy is the iris borer. Its larvae eat through leaves and roots, bringing on soft rot.

Sanford S. Singer

See also: Angiosperms; Bulbs and rhizomes; Flower structure; Flower types; Fruit crops; Hybridization.

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GARDEN PLANTS: SHRUBS

Categories: Angiosperms; economic botany and plant uses; gardening

Shrubs are perennial, woody plants that have multiple ecological uses and are economically important for a variety of landscape purposes. Like trees, the shrubs consist of both primary and secondary cambium (cells that ultimately form wood or bark), but unlike trees, shrubs typically have multiple stems and are somewhat shorter in height.

Native and nonnative shrubs have many uses, both in private gardens and as elements in commercial and civic landscaping. Shrubby willows and alders function as soil stabilizers, preventing erosion naturally along waterways. Other shrubs are natural windbreaks that reduce wind flow over open soils. Farmers value shrubby windbreaks that preserve barren farm soils during fall and winter months, when the land is barren and topsoil is especially liable to be blown away during winter storms. For much the same reason, homeowners may plant certain types of shrubs at strategic locations along the boundaries of the yard to reduce air flow.

Many shrubs are economically important as landscape ornamentals. They are prized for the beauty, variety, pattern, and color of their leaves, buds, flowers, or fruits. The color, shape, and texture of their leaves are all valued qualities for which shrubs are appreciated and used. Their shape, texture, pattern, and even the intricate contrast and pattern of their leafless twigs in winter can enhance the beauty and interest of a garden landscape.

Food Sources

In addition to their uses in gardens, many shrubs are important sources of foods for wildlife and for humans. Fruits of blackberries, blueberries, huckleberries, currents, gooseberries, plums, and hazelnuts are but a few of the foods obtained from shrubs. Many, such as blueberries and raspberries, are made into pies. Some currents and gooseberries are key components of jams and spreads. Still others, such as plums, cherries, and grapes, are eaten as fruits or used in the preparation of jams, jellies, pies, as cooking ingredients, or used for other baked goods. Some fruits are gathered only in the wild, but many others are cultivated. Cranberries, blueberries, and blackberries are cultivated varieties derived from hundreds of years of selecting and cultivating wild native shrubs. Fruits of plums, cherries, and especially the serviceberries, or Juneberries, are used to make fine and natural wines, and it may be that serviceberries were named because they provided the earliest fruits that could be made into wines for the Eucharist during church services.

Ecologically, shrubs are also important for wildlife. They provide food, shelter, and resting and nesting areas for a wide variety of birds. For example, at least forty-six species of birds feed on elderberry fruits.

Medicinal Uses

By 1812 Johann Jacob Paul Moldenhawer had shown that plant tissue was composed of independent cells, and in 1826 Henri Milne-Edwards determined that all animal tissues were formed from globules. From time immemorial, humans have enjoyed the medicinal advantages of many species of shrubs. An extract derived from the bark of willows, called salicin, is the active ingredient in one of the most important and useful of all household drugs: aspirin. The distilled liquid from the bark of witch hazel is sold as a skin ointment. A soothing ointment is made of the oil of teaberry. Tannic acid, used for tanning leather and for medicinal purposes, was for many years obtained from the fruits of native sumacs.

Barberries

The barberries (*Berberis*) are a worldwide group of deciduous shrubs best known for their thorns and bright red berries. They have yellow wood and simple alternate or whorled leaves clustered on short spurs. Barberries were very popular landscape ornamentals, but their reputation and use drastically decreased when they were found to be the alternate host for the black stem rust, a fungus that infects wheat. The use of hybrid varieties eliminates this ecological problem, and the barberries have once again become common as interesting and colorful ornamentals that provide good hedges, ground covers, and living barriers. The bright red leaves make them an attractive fall shrub, while the persistent, bright red berries attractively color a yardscape through the winter months. The berries are also an important wildlife food used by a variety of birds and small mammals through the winter months.

Burning Bushes and Dogwoods

The various species of burning bushes, or *Euonymous*, are attractive and bushy shrubs that offer good landscape contours and contrast, but they are probably best known for their gorgeous scarlet, fire-red, or fire-pink colors during the fall season. Dogwoods (*Cornus*) are shrubs or small trees that have opposite deciduous leaves and branching. A number of dogwood shrubs are useful and colorful as garden ornamentals. Chief among these are the silky dogwood (*Cornus amomum*) and red-osier dogwood (*Cornus stolonifera*), which grow in moist soil conditions. Red-osier dogwood is the more colorful of the two shrubs, with bright red branches that provide attractive year-round landscape color, especially in winter. Almost all of the dogwoods are valuable garden shrubs for wildlife, both as nesting cover and for their fruits.

Dwarf Trees as Evergreen Shrubs

Evergreen shrubs add beauty, texture, and year-round cover as ornamentals. Many species are noted for their broad leaves and showy flowers, others for the protective cover that they offer wildlife. Many dwarf varieties of trees have also become landscape shrubs that offer year-round color, variety, and cover. Another of their properties is their remarkably slow growth, usually only a few inches a year. Dwarf trees are used as ground covers, creeping along the ground and over stone walls and fences. Some of the many types include the cypress (*Chamaecyparis*), which provides dense and colorful foliage; junipers (*Juniperus*), which range from low growth forms to spreading forms and are able to tolerate urban and suburban conditions of low moisture and poor soils; dwarf pines (*Pinus*), whose long needles offer landscape and rock garden diversity; and yews (*Taxus*), which are commonly used for hedges and topiaries.

Of these, the prostrate or ground junipers are especially useful. These low-growing evergreen shrubs rarely reach a height greater than 3 feet but may spread in a circular mat several feet in diameter. The horizontal stems of ground juniper burrow into the soil surface to send up numerous upright-arching stems that form a dense ground cover. The sharp and prickly points of the leaves also make this shrub useful as a protective mat or hedge.

Fruiting Shrubs

In addition to cover and color, many species and varieties of shrubs offer fruits for humans and for wildlife. These include the blueberries (*Vaccinium*), which occur in ornamental forms and also in low, spreading varieties, and the currants and gooseberries (*Ribes*), which offer black, purple, red, and white berries, depending on variety or species, that can be harvested and made into jellies and jams or simply left on the shrub to attract wildlife. The blackberries and raspberries (*Rubus*) are a diverse group of fruiting shrubs famous for their fruits but less desirable as garden shrubs because of their tenacious ability to spread if left untended. However, the fruits are harvested for preserves, pies, wines, and as ingredients in breads and other baked goods. The tangled thickets or briar patches that they form can be useful both as living hedges and as wildlife cover for quail, songbirds, and a variety of mammals.

Hollies and Hydrangeas

The hollies (*Ilex*) and inkberries are reasonably hardy shrubs that offer year-round beauty, color, and texture as landscape ornamentals. They are best known for their lustrous, bright green leaves, intricate spiny leaf shapes, and bright red berries, and they are especially desirable as plants during the winter holidays, when holly sprigs and berries brighten both outdoor yards and indoor holiday festivities. Many species offer cover and seasonal nesting habitat for a variety of bird species. Another favorite shrub is the hydrangea (*Hydrangea*), with its large clusters of flowers; it is available in both a compact growth form and larger varieties. Hydrangeas are most often used as decorative shrubs for shady or semishady and moist corners of lots and buildings.

Rhododendrons and Azaleas

Taking their name from two Greek words, *rhodo* for "rose" and *dendron* for "tree," the rhododendrons and azaleas (*Rhododendron*) are best known for their bright and showy flowers, but these shrubs also offer glossy green leaves. The large and showy flowers of rhododendrons come in purple, pink, red, and white, while azalea flowers offer additional yellow, orange, and apricot shades. Many rhododendrons are huge shrubs that are especially valuable as wildlife cover and as nesting habitat for desired species, such as cardinals.

Roses

Roses (*Rosa*) have been cultivated for centuries and celebrated in poetry, songs, and artwork for an equally long time. They occur in an enormous number of species and varieties and in every shade of flower color except blue. Roses have been bred into many varieties, from miniatures to ground-covering polyanthas to bush roses and floribundas to tall hybrid teas, grandifloras, and climbers. "Old roses" and wild roses have returned to commercial markets in recent years. Prolific and relatively easy to grow in most climates, roses fill many landscape needs, from garden color to cut flowers and even living fences to protect property.

Spireas and Sumacs

Spireas (*Spirea*) are deciduous shrubs with small, alternate, toothed, or lobed leaves. They are popular deciduous shrubs because they are generally easy to grow and make useful hedges, mass plantings, and borders. They are also popular for their dainty clusters of spring flowers. Many varieties are desired for their long blooms from spring through most of summer, while others are sought for their fall colors or yellowish-green foliage. Some of the spirea varieties offer low, spreading ground covers, while others are compact decorative shrubs. The sumacs (*Rhus*) are shrubs or small trees that often grow in thickets. Although infrequently used in gardens, several species offer both rapid growth cover in poor soils and rich fall colors.

Dwight G. Smith

See also: Fruit: structure and types; Garden plants: flowering; Leaf arrangements; Leaf shapes.

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GAS EXCHANGE IN PLANTS

Categories: Photosynthesis and respiration; physiology

Gas exchange is the process whereby water vapor and oxygen leave and carbon dioxide enters plant leaves. The gaseous balance in plants is quite complex because plant cells carry on both respiration and photosynthesis.

All living organisms continually produce gases via metabolic and cellular activities, and the vast majority of living things are in one way or another in intimate contact with a gaseous medium. In most instances, therefore, there is ample opportunity for all organisms to exchange gases with the environment. The gaseous balance in plants is quite complex because plant cells carry on both *respiration* and *photosynthesis*. Plants respire in much the same way as animals; oxygen is used to oxidize carbohydrates, and carbon dioxide and water are produced as waste products. The photosynthetic process requires an input of carbon dioxide and water. These two *reactants* are used to produce carbohydrates, and oxygen is released as a waste product. Under normal conditions, photosynthetic rates are higher than respiration rates; thus, there is a net increase in oxygen production, accompanied by a net increase in the usage of carbon dioxide. On balance, therefore, plants use carbon dioxide and produce oxygen.

Stomata and Guard Cells

The gases move into and out of the plants through specialized openings located along the lower surface of the leaf. These openings, called *stomata*, are of optimum size, shape, and distribution for the efficient diffusion of gases. Each stoma (or stomate) is surrounded by two specialized structures called *guard cells*. These two cells are attached together at each end of both cells. The lateral edges of the two cells are not attached to each other, but, when flaccid, the sides of the guard cells do touch each other and effectively close the stomate. Specialized structural components prevent the guard cells from increasing in diameter as expansion occurs. Hence, when guard cells take up water, expansion takes place only along the longitudinal axis. Because the ends of the cells are connected to each other, the expanding of the cells forces the sides apart and results in the opening of the stomate.

Role of Water

The opening of stomata is dependent on how well hydrated the plant is. The water initially comes from the soil. The water enters the root by *osmotic* processes, then moves across the root and into the *xylem* tissues, which transport it up the stem to the leaves. From the xylem in the leaves, the water moves into the *palisade* and spongy *parenchyma cells*, which make up the bulk of the leaf tissue. The water then moves into the subsidiary cells that immediately surround the guard cells.

When the leaf is exposed to light, the process of photosynthesis begins. As the photosynthetic reactions proceed in the guard cells, the residual carbon dioxide is converted to carbohydrates. The disappearance of carbon dioxide from the cytosol of the guard cell results in an increase in the cellular pH. As the pH rises, the activity of the enzymes that convert starch and sugars to organic acids increases. The higher concentration of organic acids results in a higher concentration of hydrogen ions. The hydrogen ions of the guard cells are then exchanged for potassium ions in the subsidiary cells. This increased concentration of potassium, combined with the higher levels of organic acids, lowers the osmotic potential of the guard cells, and, since water moves from regions of high osmotic potential to regions of lower osmotic potential, water will move from the subsidiary cells into the guard cells. This movement of water increases the *turgor pressure* (inner pressure) of the guard cells and causes them to swell. Thus, the stomata open.

Oxygen Out, Carbon Dioxide In

Once the stomata open, the intercellular free space around both the palisade and spongy parenchymas is put into continuous contact with the outside atmosphere. As the water within the parenchyma cells moves across the cellular membranes, it evaporates into the free space and diffuses through the stomata into the atmosphere. Oxygen produced during photosynthesis exits the plant in much the same manner as the water vapor.

Carbon dioxide, however, follows the reverse path. It enters through and across cell membranes into the parenchyma tissues. In each case, the gas involved moves down a concentration or pressure gradient. The pressure of water vapor and oxygen is higher inside the leaf's free space than in the atmosphere, whereas the partial pressure of carbon dioxide is greater in the atmosphere than within the free space. Thus, the impetus is for the former two gases to move out of the plant and for the latter to enter it.

This exchange will take place as long as the stomata remain open and the pressure gradient is in the right direction. As a general rule, stomata close in the dark. Without an input of solar energy, the light-mediated reactions of photosynthesis stop. In the absence of these reactions, the carbon dioxide level increases, thus decreasing the pH. The lower pH activates the enzymatic conversion of organic acids to sugars and starch. This causes the potassium ions to move from the guard cells into the subsidiary cells. As a result, the osmotic potential of the guard cells is raised, the water moves out, the cells become flaccid, and the stomata close.

External Influences

Environmental conditions can affect stomatal openings. Drought conditions, which induce water stress, can affect gas exchange because the lack of water moving through the plant causes the guard cells to lose turgor and close the stomata. When the temperature becomes too warm, stomata also tend to close. In some instances, the higher temperature causes water to leave the leaf more rapidly, which leads to water stress.

In other cases, the increase in temperature causes an increase in cellular respiration that, in turn, increases carbon dioxide levels. Internal high carbon dioxide concentrations both reverse the carbon dioxide pressure gradient and cause the stomata to close.

The percentage of relative humidity can drastically affect the rate of water evaporating from the leaf surface. As the humidity increases, the higher water content of the air decreases the rate of water loss from the leaf because the water pressure gradient no longer favors evaporation from the leaf surface. The amount of solar radiation can also influence gas exchange. As the amount of light increases, the stomata open faster and wider, resulting in a more rapid rate of gas exchange. Wind currents will also increase gas exchange rates: As the wind blows across the leaf, it carries water vapor away and, in a sense, reduces the humidity at the leaf surface. Because of this lower humidity, the water evaporates from the leaf surface more rapidly.

Ecological Impact

The exchange of gases between living plants and the atmosphere is critical to the survival of all living organisms. Without the release of the oxygen produced during photosynthesis, the atmosphere would contain very little of this necessary gas. Furthermore, the vast majority of organisms on earth depend on the organic materials supplied by plants. The carbon dioxide taken from the atmosphere is photosynthetically fixed into the more complex carbon molecules that eventually serve as food not only for the plants but also for all those organisms that consume plants. The amount of carbon dioxide fixed in this fashion is tremendous: It is estimated that an average of approximately 191 million metric tons of carbon dioxide is fixed daily.

The flux of oxygen out of and carbon dioxide into the plant is possible only because of the opening of the stomata, which in turn is dependent on the flow of water through the plant. Studies have shown that for every kilogram of grain (such as corn) produced, as much as 600 kilograms of water will transpire through the stomata in a process called *transpiration*. This represents tremendous water loss and raises the question: What is the selective advantage of transpiration that outweighs its wastefulness?

The most logical explanation is that water loss by transpiration is the price plants pay to absorb carbon dioxide, essential to the life of the plant. There is the additional possibility that transpiration may serve some purpose beyond opening the stomata, such as mineral transport. Plant cell growth appears to be partially dependent on the existence of turgor pressure within the cell. Hence, the transpirational flow of water through the plant could supply the turgidity necessary for plant cell growth. Transpiration may also serve the same purpose in plants that perspiration does in humans—that is, to cool the leaf surface through water evaporation.

Gas exchange and transpiration in plants are very dynamic and interrelated processes. A thorough knowledge of both processes and of the interaction between them could one day lead to increasing maximum crop production while decreasing the amount of water required for the process.

D. R. Gossett

See also: Active transport; C_4 and CAM photosynthesis; Calvin cycle; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Photosynthesis; Respiration; Vesicle-mediated transport; Water and solute movement in plants.

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GENE FLOW

Categories: Ecology; genetics

Gene flow represents a recurrent exchange of genes between populations. This exchange results when immigrants from one population interbreed with members of another.

Charles Darwin published *On the Origin of Species by Means of Natural Selection* in 1859. Since then, scientists have modified and added new concepts to the theory of evolution by natural selection. One of those concepts, which was only dimly understood in Darwin's lifetime, is the importance of genetics in evolution, especially the concepts of migration and gene flow.

Genes

Genes are elements within the cells of a living organism that control the transmission of hereditary characteristics by specifying the structure of a particular protein or by controlling the function of other genetic material. Within any species, the exchange of genes via reproduction is constant among its members, ensuring genetic similarity. If a new gene or combination of genes appears in the population, it is rapidly dispersed among all members of the population through inbreeding. New *alleles* (forms of a gene) may be introduced into the *gene pool* of a breeding population (thus contributing to the evolution of that species) in two ways: *mutation* and *migration*. Gene flow is integral to both processes.

A mutation occurs when the DNA code of a gene becomes modified so that the product of the gene will also be changed. Mutations occur constantly in every generation of every species. Most of them, however, are either minor or detrimental to the survival of the individual and thus are of little consequence. A very few mutations may prove valuable to the survival of a species and are spread to all of its members by migration and gene flow.

Separation and Migration

In nature, gene flow occurs on a more or less regular basis between *demes*, geographically isolated populations, races, and even closely related species. Gene flow is more common among the adjacent demes of one species. The amount of migration between such demes is high, thus ensuring that their gene pools will be similar. This sort of gene flow contributes little to the evolutionary process, as it does little to alter gene frequencies or to contribute to variation within the species.

Much more significant for the evolutionary process is gene flow between two populations of a species that have not interbred for a prolonged period of time. Populations of a species separated by geographical barriers (as a result, for example, of seed dispersal to a distant locale) often develop very dissimilar gene combinations through the process of natural selection. In isolated populations, dissimilar alleles become fixed or are present in much different frequencies. When circumstances do permit gene flow to occur between populations, it results in the breakdown of gene complexes and the alteration of allele frequencies, thereby reducing genetic differences in both. The degree of this homogenization process depends on the continuation of interbreeding among members of the two populations over extended periods of time.

Hybridization

The migration of a few individuals from one breeding population to another may, in some instances, also be a significant source of genetic variation in the host population. Such migration becomes more important in the evolutionary process in direct proportion to the differences in gene frequencies—for example, the differences between distinct species. Biologists call interbreeding between members of separate species *hybridization*. Hybridization usually does not lead to gene exchange or gene flow, because hybrids are not often well adapted for survival and because most are sterile. Nevertheless, hybrids are occasionally able to breed (and produce fertile offspring) with members of one or sometimes both the parent species, resulting in the exchange of a few genes or blocks of genes between two distinct species. Biologists refer to this process as *introgressive hybridization*. Usually, few genes are exchanged between species in this process, and it might be more properly referred to as "gene trickle" rather than gene flow.

Introgressive hybridization may, however, add new genes and new gene combinations, or even whole chromosomes, to the genetic architecture of some species. It may thus play a role in the evolutionary process, especially in plants. *Introgression* requires the production of hybrids, a rare occurrence among highly differentiated animal species but quite common among closely related plant species. Areas where hybridization takes place are known as *contact zones* or *hybrid zones*. These zones exist where populations overlap. In some cases of hybridization, the line between what constitutes different species and what constitutes different populations of the same species becomes difficult to draw. The significance of introgression and hybrid zones in the evolutionary process remains an area of some contention among life scientists.

Speciation

Biologists often explain, at least in part, the poorly understood phenomenon of *speciation* through migration and gene flow—or rather, by a lack thereof. If some members of a species become geographically isolated from the rest of the species, migration and gene flow cease. Such geographic isolation can occur, for example, when populations are separated by water (as occurs on different islands or other landmasses) or valleys (different hillsides). The isolated population will not share in any mutations, favorable or unfavorable, nor will any mutations that occur among its own members be transmitted to the general population of the species. Over long periods of time, this genetic isolation will result in the isolated population becoming so genetically different from the parent species that its members can no longer produce fertile progeny should one of them breed with a member of the parent population. The isolated members will have become a new species, and the differences between them and the parent species will continue to grow as time passes. Scientists, beginning with Darwin, have demonstrated that this sort of speciation has occurred on the various islands of the world's oceans and seas.

Paul Madden

See also: Adaptive radiation; Coevolution; Community-ecosystem interactions; Evolution: convergent and divergent; Genetic drift; Genetics: mutations; Hybrid zones; Hybridization; Population genetics; Reproductive isolating mechanisms; Species and speciation.

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GENE REGULATION

Categories: Cellular biology; genetics

Genetic regulation is the manner in which a cell carries out transcription of its DNA (by copying it to messenger RNA) and the production of corresponding protein, called translation.

When a gene is expressed, one strand of that gene's double helical deoxyribonucleic acid (DNA) is copied, in the process of *transcription*, by an enzyme called RNA (ribonucleic acid) polymerase to make a *messenger RNA* (mRNA). The mRNA then associates with a *ribosome* (formed by specific ribosomal RNAs and proteins), where the nucleic acid base sequence is read, to produce the corresponding protein in a process called *translation*. A section of three nucleotides, called a *codon*, codes for one amino acid. Small RNA molecules called *transfer RNAs* (tRNAs) carry specific amino acids to the ribosome during translation. That amino acid is added to the growing polypeptide chain when the anticodon part of the tRNA pairs with a codon of the mRNA being translated.

Prokaryotic vs. Eukaryotic Regulation

Prokaryotes (*Bacteria* and *Archaea*) and eukaryotes (all other life-forms, including plants and animals) carry out transcription and translation in very similar ways, but there are some differences. The RNA polymerases and ribosomes differ between the two types of cell. In a prokaryote, such as a bacterium, translation of an mRNA can begin as soon as the first part of the mRNA molecule has been made from the DNA template. This is said to be "coupled" transcription and translation. In the eukaryotic cell, mRNA is transcribed in the nucleus and crosses the nuclear envelope to go to the cytoplasm, where the mRNA is translated into proteins on ribosomes.

Promoters

Transcription begins at a *promoter*, which is a DNA sequence at the start of a gene that tells the RNA polymerase where to start transcribing the DNA to make mRNA. The promoter includes the site where transcription begins (the initiation site) as well as sequences upstream, which are not transcribed. In eukaryotes, RNA polymerase II recognizes a DNA sequence called the TATA box (because it contains many thymine (T) and adenine (A) bases) that is about thirty nucleotides upstream of the initiation site. Another element often found in promoters is the CAAT box (which includes cytosine (C) bases).

Other regulatory elements include *enhancer* sequences, which can be in either orientation in the chromosome and far from the coding region of the gene. Enhancers may be involved in regulating the specificity of expression of a gene in a particular tissue or organ. *Silencer sequences* are structurally similar to enhancers but function to decrease gene expression. Other proteins, called *transcription factors*, aid the RNA polymerase in locating and binding to the promoter. The DNA-binding domains of eukaryotic transcription factors may have one of several types of structural motifs, such as a helix-turn-helix structure, a zinc finger (a cysteine- and histidine-rich region of the protein that complexes zinc), or a leucine zipper. Once the polymerase binds, it separates the two strands of DNA at the initiation site, and transcription begins. Transcription ends at a termination site on the DNA. In eukaryotes, a common termination sequence is AATAAA.

Other Regulatory Elements

Genes with related functions often have similar regulatory elements. A number of environmentally induced genes in plants contain the G-box with the sequence 5'CCACGTGG3'. Genes that respond to light, ultraviolet radiation, cold, and drought have the G-box and at least one additional regulatory element. For example, genes that respond to the hormone abscisic acid also have an abscisic acid-responsive element.

Role of Chromatin

The chromosomes of eukaryotes consist of unique, single-copy genes among a complex pattern of repetitive DNAs. In addition, there are DNAs in organelles outside the nucleus, such as mitochondria and chloroplasts. Each eukaryotic chromosome contains a single long DNA molecule that is coiled, folded, and compacted by its interaction with chromosomal proteins called *histones*. This complex of DNA with chromosomal proteins and chromosomal RNAs is *chromatin*. The DNA of higher eukaryotes appears to be organized into looped domains of chromatin by attachment to a nuclear scaffold. The loops are anchored at matrix-attachment regions that function in the structural organization of the DNA and may increase transcription of certain genes by promoting the formation of a less-condensed chromatin.

Transcription and mRNA Processing in Eukaryotes

In the eukaryote, as mRNA makes its way from the nucleus to the ribosomes in the cytoplasm, the mRNA molecule is modified (RNA processing). Both ends of the mRNA are altered. The 5′ end (the end that is first formed during transcription) is capped by the addition of a modified guanine (G) residue (7-methylguanosine). The 5′ cap protects the mRNA from degradation by nucleases and serves as a signal for the attachment of small ribosomal subunits to the mRNA. While still in the nucleus, the 3′ end of the mRNA is also modified. An enzyme adds thirty to two hundred adenine nucleotides (called a poly-A tail). The poly-A tail inhibits mRNA degradation and may aid in mRNA transport to the cytoplasm.

In addition, many eukaryotic mRNAs are spliced in a cut-and-paste process in which a large part of the RNA molecule initially synthesized is removed. The parts of the DNA that code for the RNA that will be discarded are the intervening sequences, or introns. The DNA that codes for the parts of the RNA that will be translated are exons.

Susan J. Karcher

See also: Bacteria; DNA in plants; DNA replication; Eukaryotic cells; Genetic code; Genetics: mutations; Nucleic acids; Nucleus; Plant cells: molecular level; Prokaryotes; Ribosomes.

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GENETIC CODE

Categories: Genetics; reproduction

The genetic code defines each amino acid in a protein, or polypeptide, in terms of a specific sequence of three nucleotides, called codons, in the DNA. The genetic code is therefore the key to converting the information contained in genes into proteins.

The genetic code defines each amino acid in a protein, or *polypeptide*, in terms of a specific sequence of three *nucleotides*, called codons, in the deoxyribonucleic acid (DNA). Therefore, the genetic code is called a *triplet code*. The four different nucleotides in DNA can form sixty-four different triplet codons. Because there are only twenty amino acids found in proteins, some amino acids are encoded by more than one codon. Therefore, the genetic code is said to be redundant, or *degenerate*. Three of the triplet codons do not encode any amino acids. These are *stop codons*, which identify the end of the message (similar to the period at the end of a sentence) encoded in genes. The genetic code is nearly universal; that is, specific codons code for the same amino acids in nearly all organisms. However, a few exceptions have been found, primarily in *mitochondrial DNA* (mtDNA), but also in a few protozoa and a single-celled algae, such as *Acetabularia*. (DNA is found in three places in eukaryotic cells: the nucleus, plastids, and mitochondria.)

Role of RNA

There are two distinct steps in the conversion of DNA sequences into protein sequences: *transcription* and *translation*. Transcription is the process by which the nucleotide sequence of a gene (in the DNA of a chromosome) is used to make a complementary copy of RNA (*ribonucleic acid*). DNA is a double-stranded molecule, and genes are arranged along DNA on each strand. Wherever there is a gene on one strand, called the *coding strand*, the other strand opposite the gene contains a nucleotide sequence that is complementary. The opposite strand is called the *non-coding strand*. When transcription of a gene occurs, it is the coding strand that is transcribed into a complementary stand of RNA. The transcribed RNA is complementary in the sense that for each adenine (A) in the DNA, a uracil (U) is incorporated into the RNA. Likewise, for each uracil, guanine (G), and cytosine (C) in the DNA, an adenine, cytosine, and guanine are incorporated into the RNA, respectively. Thus, for the codon AGT in the DNA, it becomes UCA in the RNA.

In *prokaryotes* (bacteria), the RNA resulting from transcription is called *messenger RNA* (mRNA), and it is immediately ready for the next step, translation. In the subsequent translation process, the mRNA is translated into a protein sequence by a *ribosome*. Ribosomes are macromolecular assemblies composed of various proteins and a second type of RNA, *ribosomal RNA* (rRNA). Ribosomes bind to mRNA molecules near the 5′ end and scan along the nucleotides until they reach an *initiation* or *start codon*, which indicates where translation should begin and establishes the *reading frame*. The start codon is always AUG and is the first translated codon in all mRNAs. Translation ends when a stop codon is reached. Most organisms have three stop codons (UAA, UGA, and UAG), and each gene ends with one of these. A stop codon does not code for an amino acid but simply identifies the end of the gene. Because nucleotide bases are read three at a time along a continuous chain of nucleotides, shifting the reading frame by inserting or deleting a single nucleotide within a gene can dramatically alter the amino acid sequence of the protein it can produce.

Although ribosomes are essential for translating mRNAs, they are not directly responsible for interpreting the codons. *Transfer RNA* (tRNA) molecules are single-stranded RNA molecules that exhibit extensive intramolecular base-pairing such that the tRNA has a two-dimensional structure with a stem and three loops resembling a three-leaf clover. The middle loop contains a region, composed of three nucleotides, called the *anticodon*, which is complementary to a specific codon. The tRNA molecules directly decode the mRNA sequence or translate it into a correct amino acid sequence by their ability to bind to the right codon. Each tRNA carries a specific amino acid to the ribosome where protein synthesis occurs. The binding of amino acids to tRNAs occurs at a place on the tRNA called the *amino acid attachment site*. Amino acids are added to tRNAs by special enzymes called *aminoacyl-tRNA synthetases*. Each tRNA has a special region on the stem below the amino acid attachment site whose nucleotide sequence determines which amino acid needs to be attached to the tRNA. This code is often called the second genetic code, and geneticists have discovered that if the nucleotide region is changed in this region, the wrong amino acid gets attached.

There are at least one type of tRNA for each of the twenty amino acids. It is the pairing of the codons of the mRNA molecules and anticodons of tRNA molecules that determines the order of the amino acid sequence in the polypeptide chain. The third base of the anticodon does not always properly recognize the third base of the mRNA codon. The third base is called the *wobble* position because nonstandard base pairing can occur there. This phenomenon, together with the degeneracy of the genetic code means that cells do not have to have sixty-one different tRNA types (one for each codon that specifies an amino acid). For example, only two tRNAs are needed to recognize four different codons for the amino acid glycine. Consequently, most organisms have about forty-five different tRNA types.

Polypeptide Sorting

A typical plant cell contains thousands of different kinds of proteins. For the cell to function properly, each of its numerous proteins must be localized to the correct cellular membrane, or cellular compartment. The process of protein sorting, or protein targeting, is critical to the organization and functioning of plant cells. Protein sorting relies upon the presence of special *signal sequences* at one end of the protein molecule. These signal sequences direct proteins to various sites. For example, some proteins synthesized on ribosomes in the cytoplasm are targeted to organelles, such as the mitochondria or chloroplasts. Other proteins, such as those found in the plant cell wall, are targeted to the cytoplasmic membrane for transport out of the cell to the cell wall. The signal sequences are frequently removed once the protein has reached its intended destination.

Lisa M. Sardinia

See also: DNA in plants; DNA replication; Endomembrane system and Golgi complex; Gene regulation; Genetics: mutations; Nucleolus; Nucleus; Proteins and amino acids; Ribosomes; RNA.

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GENETIC DRIFT

Categories: Ecology; genetics; reproduction and life cycles

Genetic drift refers to random changes in the genetic composition of a population. It is one of the evolutionary forces that cause biological evolution, the others being selection, mutation, and migration, or gene flow.

Drift occurs because the genetic variants, or *alleles*, present in a population are a random sample of the alleles that adults in the previous generation would have been predicted to pass on, where predictions are based on expected migration rates, expected mutation rates, and the direct effects of alleles on fitness. If this sample is small, then the genetic composition of the offspring population may deviate substantially from expectation, just by chance. This deviation is called genetic drift. Drift becomes increasingly important as population size decreases. The key feature of drift that distinguishes it from the other evolutionary forces is the unpredictable direction of evolutionary change.

Anything that generates *fitness variation* among individuals (that is, variation in the ability of individuals to survive and reproduce) will increase the magnitude of drift for all genes that do not themselves cause the fitness variation. Because of their indeterminate growth, plants often vary greatly in reproductive potential because of local environmental variation, and this magnifies genetic drift. For example, the magnitude of drift in most annual plants is more than doubled by size variation among adults. This makes sense if one considers that larger individuals contribute a larger number of offspring to the next generation, so any alleles they carry will tend to be overrepresented.

Fitness variation caused by selection will also increase the magnitude of drift at any gene not directly acted upon by the selection. If an individual has high fitness because it possesses one or more favorable alleles, then all other alleles it possesses will benefit. This is called *genetic hitchhiking*. This is a potent source of evolution because the direction of change at a hitchhiking gene will remain the same for multiple generations. However, it is not possible to predict in advance what that direction will be because where and when a favorable mutation will occur cannot be predicted.

The opportunities for drift to occur are greatly influenced by *gene flow*. Most terrestrial plants are characterized by highly localized dispersal. Thus, even in large, continuous populations, the pool of potential mates for an individual, and the pool of seeds that compete for establishment at a site, are all drawn from a small number of nearby individuals known as the *neighborhood*. If the neighborhood is sufficiently small, genetic drift will have a significant impact on its genetic composition.

For these and other reasons, population size alone is not sufficient to predict the magnitude of drift. The *effective size* of a population, N_e, is a number that is directly related to the magnitude of drift through a simple equation. Thus, N_e incorporates all characteristics of a population that influence drift.

Loss of Variability

The long-term consequence of drift is a loss of genetic variation. As alleles increase and decrease in frequency at random, some will be lost. In the absence of mutation and migration, such losses are permanent. Eventually, only one allele remains at each gene, which is said to be fixed. Thus, all else being equal, smaller populations are expected to harbor less genetic variation than larger populations.

An important way in which different plant populations are not equal is in their reproductive systems. With self-fertilization (selfing), or asexual reproduction, genetic hitchhiking becomes very important. In the extreme cases of 100 percent selfing or 100 percent asexual reproduction, hitchhiking will determine the fates of most alleles. Thus, as a new mutation spreads or is eliminated by selection, so too will most or all of the other alleles carried by the individual in which the mutation first arose. This is called a *selective sweep*, and the result is a significant reduction in genetic variation. Which alleles will be swept to fixation or elimination cannot be predicted in advance, so the loss of variation reflects a small N_e. Consistent with this expectation, most populations of flowering plants that reproduce partly or entirely by selfing contain significantly less genetic variation than populations of related species that do not self-fertilize.

Extinction

Mutations that decrease fitness greatly outnumber mutations that increase fitness. In a large population in which drift is weak, selection prevents most such mutations from becoming common. In very small populations, however, alleles that decrease fitness can drift to fixation, causing a decrease in average fitness. This is one manifestation of a phenomenon called *inbreeding depression*. In populations with very small N_e, this inbreeding depression can be significant enough to threaten the population with extinction. If a population remains small for many generations, mean fitness will continue to decline as new mutations become fixed by drift. When fitness declines to the point where offspring are no longer overproduced, population size will decrease further. Drift then becomes stronger, mutations are fixed faster, and the population heads down an accelerating trajectory toward extinction. This is called *mutational meltdown*.

Creative Potential

By itself, drift cannot lead to adaptation. However, drift can enhance the ability of selection to do so. Because of diploidy and sexual recombination, some types of mutations, either singly or in combinations, will increase fitness when common but not when rare. Genetic drift can cause such genetic variants to become sufficiently common for selection to promote their fixation. A likely example is the fixation of new structural arrangements of chromosomes that occurred frequently during the diversification of flowering plants. New chromosome arrangements are usually selected against when they are rare because they disrupt meiosis and reduce fertility. The initial spread of such a mutation can therefore only be caused by strong genetic drift, either in an isolated population of small effective size or in a larger population divided into small neighborhoods.

John S. Heywood

See also: Endangered species; Gene flow; Genetics: mutations; Population genetics; Selection.

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GENETIC EQUILIBRIUM: LINKAGE

Categories: Cellular biology; genetics

Genetic equilibrium is the tendency for genes located close together on the same chromosome to be inherited together. The farther apart the genes, the less likely it is that they will be passed along together.

The genetic complement of any organism is contained on one or more types of *chromosomes*. Whether there are only a few chromosomes or many (such as in a diploid organism), each type occurs as a set of two, called *homologs*. Each gene at a particular *locus*, or site, along the chromosome occurs twice in the same cell (except for some loci which only occur on one of the two sex chromosomes), one copy of each homolog. The particular information at each locus may be different because genes can exist in several forms.

An alternative form of a particular gene is called an *allele*. For example, one of the genes for flower color in pea plans can exist as a white allele or a purple allele. A given pea plant could have a white allele on one homologous chromosome and a purple allele on the other. Each homologous chromosome, therefore, contains an allele at a locus which may or may not be the same as the allele on its homolog.

During reproduction, this chromosomal material is copied, thereby duplicating the individual genes which lie along the chromosome. During *mitosis*, a copy of each chromosome is distributed to each of the two new nuclei. In *meiosis*, however, during gamete production, the chromosome copies are separated so that only a single chromosome from each pair of homologous chromosomes is distributed to each of four new nuclei. Before this happens, however, the homologs and their duplicates, called *sister chromatids*, become aligned. The arms of sister chromatids undergo crossover near the beginning of the first part of meiosis, which results in the exchange of homologous regions of these chromosomes.

The result of this *crossing over* is that alleles that were once on one homolog are now on the other. In mitosis, genes on the same chromosome exhibit linkage and tend to remain together and be inherited by the daughter cell together; in meiosis, these linked genes can become recombined in new associations so that linkage is partial. Individuals with chromosomes exhibiting these new combinations of alleles are called *recombinants*.

Discovery of Linkage

Mendelian genetics (named for Gregor Mendel) predicts a 3:1 phenotypic ratio in a monohybrid cross (a cross involving only one gene having two alleles, one dominant and one recessive) and a 9:3:3:1 phenotypic ratio in a dihybrid cross (a cross involving two genes on different chromosomes, each having two alleles, one dominant and one recessive). Early in the twentieth century, geneticists began to notice that not all crosses produced offspring in the proportions predicted by Mendel's *law of independent assortment*. Cytologists also discovered that occasionally homologous chromosomes did not look exactly alike. Geneticists used these differences in chromosomes as cytological markers and associated them with genetic markers or alleles with specific effects.

In 1911 T. H. Morgan concluded that during segregation of alleles at meiosis, certain genes tend to remain together because they lie near each other on the same chromosome. The closer genes are located to each other on the chromosome, the greater their tendency to remain linked.

In 1909 *chiasmata* had been described. Chiasmata represent the locations of exchanges (crossover) between maternal and paternal homologous chromosomes. Morgan hypothesized that partial linkage occurs when two genes on the same chromosome are separated physically from each other by crossover during meiosis. Crossover provides new combinations of genes, genes which did not exhibit the linkage relationship in the parents but which were recombined. In these kinds of crosses, the parental phenotypic classes are most frequent in the offspring, while the recombinant classes occur much less frequently.

Genetic recombination results from physical exchange between homologous chromosomes that have become tightly aligned during meiotic prophase. A chiasma is the site of crossing over and is where homologs have lined up touching each other where they are homologous. Crossing over itself is the exchange of parts of nonsister chromatids of homologous chromosomes by symmetrical breakage and crosswise rejoining. Two papers providing convincing evidence of this were published within weeks of each other in 1930.

Harriet Creighton and Barbara McClintock worked with corn (*Zea mays*). They studied individuals in which the two copies of chromosome 9 had a strikingly different appearance. They studied two loci on chromosome 9, one affecting seed color (colored and colorless, dominant and recessive, respectively) and the other affecting endosperm composition (waxy or starchy, dominant and recessive, respectively). One homolog was dominant for both traits (colored and waxy) and lacked the knob and the extension. Plants with these two homologs of chromosome 9 had colored, waxy seeds. Recombinant offspring would have either colored and starchy seeds or colorless and waxy seeds and their copies of chromosome extension but no knob. Offspring that were like the parents showed no change in chromosome structure. This provided visual evidence that crossover had occurred.

Genetic Maps

The frequency of crossover can be used to construct a *genetic map*. The more closely linked genes are, the less frequently crossing over will take place between them. The recombinants will occur much less frequently than when linked genes are more widely separated.

With widely separated genes, the chances of double crossovers increases, so that the recombination frequency may actually underestimate the crossover frequency and, hence, the *map distance*. The map distance is a relative distance based on the percent of recombination and is not a precise physical distance. The presence of a chiasma in one region often prevents the occurrence of a second chiasma nearby. This phenomenon is called *interference*.

In many large, randomly mating natural populations, the genotype frequencies at each locus will typically be found at a mathematically determined *equilibrium*. In a single generation of random mating, unlinked loci separately attain equilibrium of genotype frequencies. This is not true of linked loci. If loci are unlinked, equilibrium occurs very rapidly, but if the loci are on the same chromosome, the speed of approach to equilibrium is proportional to the map distance between them.

Once equilibrium is attained, repulsion and coupling gamete frequencies do not depend on the degree of linkage. Another way of saying this is that the characters produced by alleles at linked loci show no particular association in an equilibrium population. When characters happen to be associated in a population, the association may form because alleles at separate loci that are in genetic disequilibrium result from recent population immigrations. They may also be the result of selection for certain allelic combinations. Like dominance, linkage can be confirmed only in controlled breeding experiments.

Mutations

Mutations are the ultimate source of variation. In populations, mutant alleles may accumulate over time because they are recessive to the normal allele. Recessive lethal alleles, as well as beneficial alleles, persist in populations because recessive alleles are hidden when in the heterozygous state (that is, in individuals who have one normal, dominant allele and one mutant, recessive allele). It is only when the mutant becomes widely distributed in the population that they are revealed.

With ten loci and four alleles at each locus, ten billion different possible genotypes will occur with equal frequency if all the alleles occur with equal frequency and segregate independently. This describes a state of linkage equilibrium. In a natural population, however, these conditions are rarely met. The probability is that some genotypes will be more common than others, even if the allele frequencies are all the same.

Diploid organisms typically have tens of thousands of gene loci. Because they have only a small number of chromosomes, usually less than forty, many loci lie on the same chromosome. The genotypes are highly biased toward already existing combinations. This does not alter the theoretical possibilities of particular genotypes, only the probability of their occurrence. It does ensure that variation is present in the population for adaptability to changing conditions, while maintaining large numbers of individuals that are adapted to existing conditions.

Functions of Linkage

Linked genes may control very different functions. For example, enzymes vary depending on climate. Northern species may possess an enzyme which functions at a lower temperature than the variant of the southern species. Linked to the gene which controls this highly adaptive allele may be an allele of another gene whose adaptive value is lower or neutral. This less adapted allele hitchhikes on the chromosome with the adaptive allele.

Linkage disequilibrium is decreased by recombination. The maintenance of favorable allelic combinations in linkage disequilibrium is enhanced by reducing recombination between the loci involved. This is achieved by inversions and translocations that include the loci involved. The genes included in these in the translocated or inverted region are sometimes called supergenes, because of their strong tendency to be inherited as a large unit of many genes. Inversions and translocation do not completely inhibit crossover in the regions involved, but they do reduce it. They also reduce the occurrence of recombinant chromosomes, because if a crossover does occur in one of these regions, most of their resulting recombinant chromosomes are either lethal or cause varying levels of sterility. Whenever linkage disequilibrium is favored by natural selection, chromosomal rearrangements increasing linkage among loci will also be favored by natural selection.

Judith O. Rebach, updated by Bryan Ness

See also: Chromosomes; DNA in plants; DNA replication; Genetics: Mendelian; Genetics: mutations; Genetics: post-Mendelian; Mitosis and meiosis; RNA.

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GENETICALLY MODIFIED BACTERIA

Categories: Bacteria; biotechnology; economic botany and plant uses; genetics

Bacteria may be genetically modified through the introduction of recombinant DNA molecules into their cells. Such bacteria may be used to produce human insulin or introduce disease-resistant genes into plants, as well as numerous other applications.

The ability to genetically engineer bacteria is the outcome of several independent discoveries. In 1944 Oswald Avery and his coworkers demonstrated gene transfer among bacteria using purified DNA (deoxyribonucleic acid), a process called *transformation*. In the 1960's the discovery of *restriction enzymes* permitted the creation of hybrid molecules of DNA. Such enzymes cut DNA molecules at specific sites, allowing fragments from different sources to be joined within the same piece of genetic machinery.

Restriction enzymes are not specific in choosing their target species. Therefore, DNA from any source, when treated with the same restriction enzyme, will generate identical cuts. The treated DNA molecules are allowed to bind with one another, while a second set of enzymes called *ligases* are used to fuse the fragments together. The recombinant molecules may then be introduced into bacteria cells through transformation. In this manner, the cell has acquired whatever genetic information is found in the DNA. Descendants of the transformed cells will be genetically identical, forming *clones* of the original.

Bacterial Plasmids

The most common forms of genetically altered DNA are bacterial *plasmids*, small circular molecules separate from the cell chromosome. Plasmids may be altered to serve as appropriate *vectors* (carriers of genetic material) for genetic engineering, usually containing an *antibiotic* resistance gene for selection of only those cells that have incorporated the DNA. Once the cell has incorporated the plasmid, it acquires the ability to produce any gene product encoded on the molecule.

The first such genetically altered bacteria used for medical purposes, *Escherichia coli*, contained the gene for the production of human insulin. Prior to creation of the insulin-producing bacterium, diabetics were dependent upon insulin purified from animals. In addition to being relatively expensive, insulin obtained from animals produced allergic reactions among some individuals. Insulin obtained from genetically altered bacteria is identical to that of human insulin. Subsequent experiments also engineered bacteria able to produce a variety of human proteins, including human growth hormone, interferon, and granulocyte colony-stimulating factor.

Use in Plants

Genetically modified bacteria may also serve as vectors for the introduction of genes into plants. The bacterium *Agrobacterium tumefaciens*, the cause of the plant disease called crown gall, contains a plasmid called *Ti*. Following infection of the plant cell by the bacterium, the plasmid is integrated into the host chromosome, becoming part of the plant's genetic material. Any genes that were part of the plasmid are integrated as well. Desired genes can be introduced into the plasmid, promoting pest or disease resistance.

In April of 1987 scientists in California sprayed strawberry plants with genetically altered bacteria to improve the plants' freeze resistance, marking the first deliberate release of genetically altered organisms in the United States to be sanctioned by the Environmental Protection Agency (EPA). The release of the bacteria climaxed more than a decade of public debate over what would happen when the first products of biotechnology became commercially available. Fears centered on the creation of bacteria that might radically alter the environment through elaboration of gene products not normally found in such cells. Some feared that so-called super bacteria might be created with unusual resistance to conventional medical treatment. Despite these concerns, approval for further releases of genetically altered bacteria soon followed, and the restrictions on release were greatly relaxed. By 2002, permits for field tests of hundreds of genetically altered plants and microorganisms had been granted.

Richard Adler

See also: Biotechnology; DNA: recombinant technology; Genetically modified foods; Plant biotechnology.

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GENETICALLY MODIFIED FOODS

Categories: Agriculture; biotechnology; economic botany and plant uses; food; genetics

Foods derived from living organisms that have been modified using gene-transfer technology are known as genetically modified foods. Many of these foods are plant crops.

Applications of genetic engineering in agriculture and the food industry could increase world food supplies, reduce environmental problems associated with food production, and enhance the nutritional values of certain foods. However, these benefits are countered by food-safety concerns, the potential for ecosystem disruption, and fears of unforeseen consequences resulting from altering natural selection. Humans rely on plants and animals as food sources and have long used microbes to produce foods such as cheese, bread, and fermented beverages. Conventional techniques such as cross-hybridization, production of mutants, and selective breeding have resulted in new varieties of crop plants or improved livestock with altered genetics. However, these methods are relatively slow and labor-intensive, are generally limited to intraspecies crosses, and involve a great deal of trial and error.

Genetically Modified Crop Plants Unregulated by the U.S. Department of Agriculture

Crop	*Patent Holder*	*Genetically Engineered Trait(s)*
Canola	AgrEvo	herbicide tolerance
Corn	AgrEvo	herbicide tolerance
	Ciba-Geigy	insect resistance
	DeKalb	herbicide tolerance; insect resistance
	Monsanto	herbicide tolerance; insect resistance
	Northrup King	insect resistance
Cotton	Calgene	herbicide tolerance; insect resistance
	DuPont	herbicide tolerance
	Monsanto	herbicide tolerance; insect resistance
Papaya	Cornell	virus resistance
Potato	Monsanto	insect resistance
Squash	Asgrow	virus resistance
	Upjohn	virus resistance
Soybean	AgrEvo	herbicide tolerance
	DuPont	altered oil profile
	Monsanto	herbicide tolerance
Tomato	Agritope	altered fruit ripening
	Calgene	altered fruit ripening
	Monsanto	altered fruit ripening
	Zeneca	altered chemical content in fruit

Source: U.S. Department of Agriculture Animal and Plant Health Inspection Service (APHIS).

Transgenic Technology

Recombinant DNA techniques, which manipulate cells' deoxyribonucleic acid (DNA), developed in the 1970's enable researchers rapidly to make specific, predetermined genetic changes. Because the technology also allows for the transfer of genes across species and kingdom barriers, an infinite number of novel genetic combinations are possible. The first animals and plants containing genetic material from other organisms (*transgenics*) were developed in the early 1980's. By 1985 the first field trials of plants engineered to be pest-resistant were conducted. In 1990 the U.S. Food and Drug Administration (FDA) approved chymosin as the first substance produced by modified organisms to be used in the food industry for dairy products such as cheese. That same year the first transgenic cow was developed to produce human milk proteins for infant formula. The well-publicized Flavr Savr tomato, modified to delay ripening and rotting, obtained FDA approval in 1994.

Goals and Uses

By the mid-1990's, more than one thousand genetically modified crop plants were approved for field trials. The goals for altering food crop plants by genetic engineering fall into three main categories: to create plants that can adapt to specific environmental conditions to make better use of agricultural land, increase yields, or reduce losses; to increase nutritional value or flavor; and to alter harvesting, transport, storage, or processing properties for the food industry. Many genetically modified crops are sources of ingredients for processed foods and animal feed.

Herbicide-resistant plants, such as the Roundup Ready soybean, can be grown in the presence of glyphosphate, an *herbicide* that normally destroys all plants with which it comes in contact. Beans from these plants were approved for food-industry use in several countries, but there has been widespread protest by activists such as Jeremy Rifkin and environmental organizations such as Greenpeace. Frost-resistant fruit containing a fish antifreeze gene, insect-resistant plants with a bacterial gene that encodes for a pesticidal protein (*Bacillus thuringiensis*), and a viral disease-resistant squash are examples of other genetically modified food crops that have undergone field trials.

Scientists have also created plants that produce healthier unsaturated fats and oils rather than saturated ones. Genetic engineering has yielded coffee plants whose beans are caffeine-free without processing and tomatoes with altered pulp content for improved canned products. Genetically modified microbes are used for the production of food additives such as amino acid supplements, sweeteners, flavors, vitamins, and thickening agents. In some cases, these substances had to be obtained from slaughtered animals. Altered organisms are also used for improving fermentation processes in the food industry.

Food and Environmental Issues

Food safety and quality are at the center of the genetically engineered food controversy. Concerns include the possible introduction of new toxins or allergens into the diet and changes in the nutrient composition of foods. Proponents argue that food sources could be designed to have enhanced nutritional value.

A large percentage of crops worldwide are lost each year to drought, temperature extremes, and pests. Plants have already been engineered to exhibit frost, insect, disease, and drought resistance. Such alterations would increase yields and allow food to be grown in areas that are currently too dry

Seeds of Dissent

Creation of transgenic crops has been alleged to create the risk of new allergenic proteins. Despite these risks, as of 2001, both giant agribusiness and the United States Department of Agriculture resisted informational labeling of genetically modified (GM) food products, arguing that GM foods are as safe as conventional foods and that there is no evidence they cause allergic reactions. Because GM products are often mixed with conventional products, unlabeled foods make it hard to trace individuals' allergic reactions. Similarly, people with culturally based dietary restrictions do not know whether produce they eat contains proteins derived from beef, pork, fish, or other animals.

Other potential risks of transgenic crops include increases in toxins and decreases in nutritional value. Accidental crossbreeding with wild species of plants has caused critics of "genetic pollution" to raise the specter of a steady stream of animal and microbial genes entering the gene pools of plants in wild ecosystems.

Additionally, herbicide-resistant weeds remind activists that soybeans dubbed Roundup Ready Soybeans have been bred to tolerate glyphosphate, enabling that herbicide's wider use. Development of pesticide resistance among insects was feared when U.S.-grown transgenic corn was shipped, unlabeled, to Europe in 1996. Situations like this could lead to increased application of chemicals already in use by farmers or a switch to different, more toxic chemicals.

These and other controversies and fears have caused many European nations and Japan to prohibit agricultural production of GM crops. Some nations have banned imports of all GM products.

or infertile, positively impacting the world food supply.

Environmental problems such as deforestation, erosion, pollution, and loss of biodiversity have all resulted, in part, from conventional agricultural practices. Use of genetically modified crops could allow better use of existing farmland and lead to a decreased reliance on pesticides and fertilizers. Critics fear the creation of "superweeds"—either the engineered plants or new plant varieties formed by the transfer of recombinant genes conferring various types of resistance to wild species. These weeds, in turn, would compete with valuable plants and have the potential to destroy ecosystems and farmland unless stronger poisons were used for eradication. The transfer of genetic material to wild relatives (*outcrossing*, or "genetic pollution") might also lead to the development of new plant diseases. As with any new technology, there may be other unpredictable environmental consequences.

Diane White Husic

See also: Biotechnology; DNA: recombinant technology; Genetically modified bacteria; Plant biotechnology.

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GENETICS: MENDELIAN

Categories: Disciplines; genetics; history of plant science

Mendelian genetics is the classical mechanistic explanation of heredity in sexually reproducing organisms. It explains how genetic information is passed from one generation to another.

In 1866 the Augustinian monk Gregor Mendel (1822-1884) published a paper titled "Versuch über Pflanzenhybriden" (*Experiments in Plant-Hybridisation*, 1910), describing the heredity of mutant characteristics of garden peas. Mendel founded the modern science of genetics with these experiments, because they led him to propose the existence of hereditary factors, now called *genes*, and rules describing their inheritance, now referred to as *Mendel's laws*. The importance of Mendel's work was not recognized until 1900, sixteen years after his death, when the movements of *chromosomes* during cell division were carefully studied. Since then, Mendel's laws have been shown to hold true throughout nature. The biochemical nature of genes has been discovered, the genetic code has been broken, and genetics has assumed a central role in modern biology, medicine, and agriculture.

Mendel's Experiments

Mendel was not the only researcher interested in genetics, or inheritance, as it was called in his day. The prevailing theories of his time, though, differed considerably from his final conclusions. It was believed by most biologists that inheritance involved the blending of some sort of element from each parent. The result is offspring that are intermediate between the parents. This process, as understood, was analogous to blending two colors of paint. Experiments by others made it difficult to challenge this theory, because they often studied numerous complex traits simultaneously, only analyzed offspring from a single generation, and worked with small numbers of organisms.

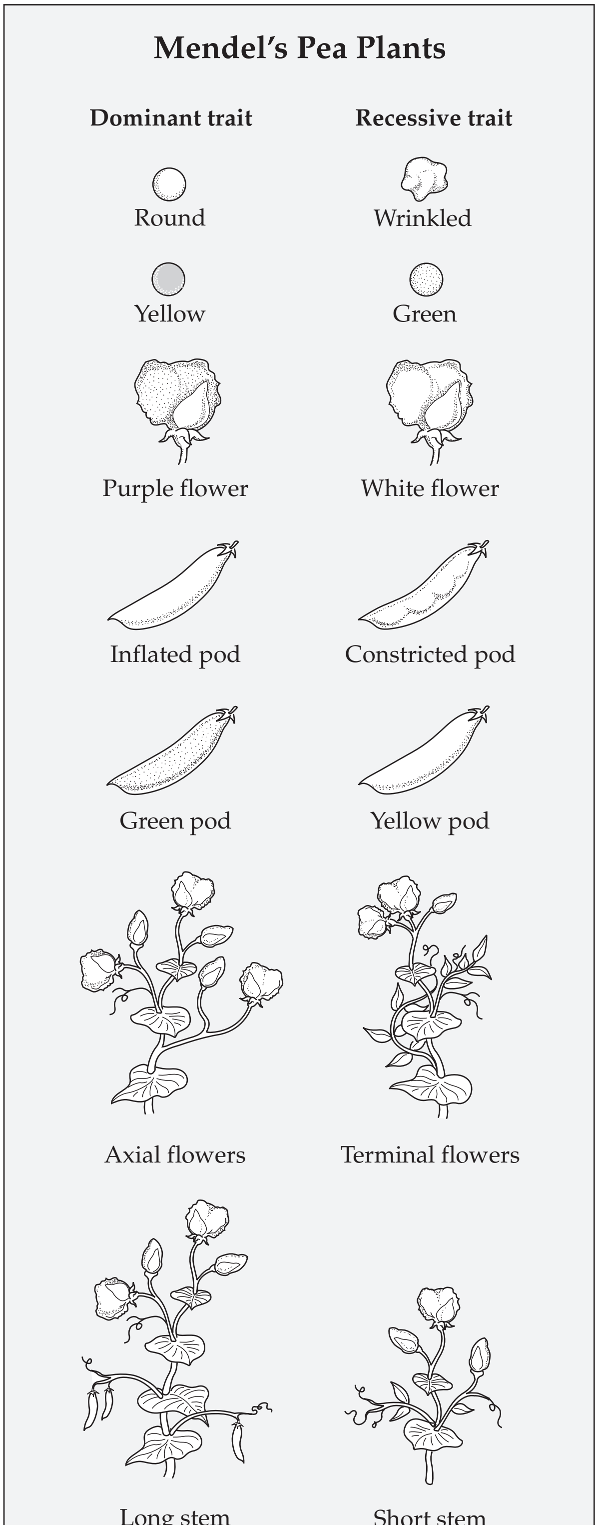
One of the reasons for Mendel's success was that he simplified the problem of heredity by analyzing a few simple, easily distinguishable, hereditary differences among a species that was easy to breed. He also initially studied one trait at a time and followed the inheritance of each trait for several generations, using large enough numbers to solidify his conclusions.

He began by selecting strains of garden peas that differed by a single trait from normal strains, such as wrinkled versus smooth, green peas versus yellow, and tall plants versus short. Once each strain bred true for a mutant variation, he crossed it with a different strain to see which trait was passed on to the offspring. Mendel observed that all the hybrid offspring of each individual cross resembled one of the parent types and not the other, rather than a mixture of the two types or an intermediate form (the conventional "mixed-paint" theory). Crosses between tall and short parent strains, for example, produced hybrids that were tall only. Mendel defined this phenomenon as *dominance* of one trait over the alternate trait, which he called the *recessive* trait.

Mendel then discovered that crossing two hybrids resulted in the reappearance of the recessive trait but only in one-fourth of the offspring. A cross between two tall hybrids, for example, produced about three-fourths tall plants and one-fourth short plants. Mendel proposed that hereditary factors (now called genes) existed for each of the traits with which he was working. He also proposed that hereditary factors exist in pairs, such that each individual inherits one from the pair carried by each parent. Mendel hypothesized that the pairs of factors would be separated, and one would be randomly included in each *gamete* (male or female germ cell—pollen or ovule, in the case of plants).

Testing the Theory

Mendel tested this theory with further crosses. (Because Mendel did not know of the existence of genes, he did not have a clear way to refer to the ge-



Electronic Illustrators Group

Mendel evaluated the transmission of seven paired traits in his studies of garden peas.

netic factors responsible for his results. The word "gene" is used in this discussion for convenience.)

He predicted, for example, that the original tall parent had two tall genes for height (symbolized as *TT*), and the original short parent had two short genes for height (*tt*). The hybrid would inherit one of each (*Tt*), but because the tall gene is dominant, the hybrid's appearance would be tall. Mendel predicted that crossing a *Tt* hybrid with one of the short (*tt*) plants should produce half tall (*Tt*) offspring and half short ones (*tt*). That is exactly what Mendel observed. He was also able to predict the outcomes of other crosses involving different traits. Mendel concluded that his theory worked: Paired hereditary factors must exist, and only one of the two, chosen at random, could be passed on to each offspring by each parent. Mendel labeled this phenomenon *segregation*, meaning that the parent's two hereditary factors are physically segregated into different cells during the production of gametes. This principle of segregation is now called Mendel's first law of inheritance.

Mendel's second law of inheritance describes the principle of *independent assortment*, which states that different hereditary factors segregate independently of one another. Mendel observed, for example, that if he crossed a tall and purple parent (*TT-PP*) with a short and white one (*tt-pp*), the hybrid offspring were tall and purple, as these genes are dominant. Then, when he crossed the tall and purple hybrid (*Tt-Pp*) with another, identical hybrid, the progeny showed an "assortment" of the two traits (tall and purple, tall and white, short and purple, short and white) in a 9:3:3:1 ratio, respectively. This is the ratio expected if each trait's genes segregate independently. Stated another way, whether a parent passes on a tall or short factor does not influence whether that parent also passes on the purple or white factor.

These two laws of heredity summarize Mendel's discovery of discrete genetic factors and their patterns of inheritance: Mendel had proposed that discrete genetic factors exist, had explained how they are passed on, and had supported his theories with experimental evidence. Mendel's discovery, however, was virtually ignored. He died in 1884 without receiving recognition for his work. Mendel's laws were independently rediscovered in the year 1900, and then their fundamental importance and general applicability were widely recognized.

Results of Mendel's Pea-Plant Experiments

Parental characteristics	*First generation*	*Second generation*	*Second generation ratio*
Round × wrinkled seeds	All round	5,474 round : 1,850 wrinkled	2.96 : 1
Yellow × green seeds	All yellow	6,022 yellow : 2,001 green	3.01 : 1
Gray × white seedcoats	All gray	705 gray : 224 white	3.15 : 1
Inflated × pinched pods	All inflated	882 inflated : 299 pinched	2.95 : 1
Green × yellow pods	All green	428 green : 152 yellow	2.82 : 1
Axial × terminal flowers	All axial	651 axial : 207 terminal	3.14 : 1
Long × short stems	All long	787 long : 277 short	2.84 : 1

Morgan's Contributions

Microscopic bodies in the nuclei of cells, called chromosomes, had been discovered by the end of the nineteenth century, and in 1901 it was proposed that chromosomes are the physical structures that contain Mendel's hereditary factors, or genes. Chromosomes were a likely structure for the location of genes because chromosomes occur in pairs, duplicate when the cell divides, and segregate into sperm and egg cells such that only one of the two chromosomes in each pair is passed on to any single offspring by each parent. The chromosomal theory of heredity made it easier for biologists to think of genes as physical objects of analysis, and studies of Mendelian patterns of inheritance and their chromosomal basis progressed rapidly.

A geneticist named Thomas Hunt Morgan at Columbia University made several key discoveries using fruit flies between 1910 and 1920. He and his colleagues discovered mutations in flies that showed different patterns of inheritance in males and females, which led to association of these genes with the sex-determining X and Y chromosomes. Traits affected by genes on these chromosomes show a sex-linked pattern of inheritance in which recessive traits appear more often in males than in females. Human sex-linked traits, for example, include hemophilia, color-blindness, and baldness.

Fruit flies have three pairs of chromosomes besides the sex chromosomes, and Morgan's laboratory team showed that traits could be grouped together in "linkage groups" corresponding to their four pairs of chromosomes. They realized that Mendel's second law describing the principle of independent assortment corresponded to the assortment of chromosomes being passed from parent to offspring. Any genes on different chromosomes would be passed on independently, while genes linked together on the same chromosome would be passed on together as a unit. The discovery of linkage groups supported the idea that chromosomes were made up of collections of a large number of genes linked together.

Sturtevant's Contributions

Morgan's laboratory group, however, also observed occasional exceptions to this pattern of linkage, when offspring showed unexpected new combinations of linked genes that did not exist in either parent. Alfred H. Sturtevant, a student in Morgan's laboratory, proposed that the paired chromosomes carrying different forms of the same genes (one carrying recessive forms, for example, *a-b-c*, versus the other, carrying dominant forms *A-B-C*) could undergo a reciprocal exchange of part of the chromosome. One chromosome pair could exchange, for example, *C* for *c*, resulting in new *a-b-C* and *A-B-c* combinations of the linked genes.

Sturtevant also discovered that such recombination events occur with different frequencies between different genes. Only 1 percent of the *A* and *B* genes might be switched in each cross, for example, but 20 percent of the *A* and *C* genes might recombine in the same cross. Sturtevant proposed that the genes are linked together in a linear sequence and that the frequency of recombination between them is a function of the physical distance separating them on the chromosome. Two genes that are far apart should recombine more frequently than two genes close together, since there would be a greater opportunity for the breakage and the exchange of different chromosomal material to occur between them.

Sturtevant proposed that differences in the frequency of recombination among linked genes on the same chromosome could be used to "map" the genes in a linear sequence that would reveal their order and relative positions on the chromosome. This principle turned out to be universal, and it allows genes to be mapped to specific locations on each chromosome in all organisms that can be systematically bred. Mendel's genes had, by the 1920's, been associated with chromosomes, and individual genes on each chromosome could be ordered and mapped using recombination analysis.

Mid-Twentieth Century Developments

The following two decades were marked by two important parallel developments in genetics. The first was a mathematical and experimental synthesis of Mendel's genetic theory with Charles Darwin's theory of natural selection. It was shown that the genetic mechanism described by Mendel provided the hereditary mechanism required for Darwin's theory of natural selection. The revision of Darwin's work that resulted is often referred to as the neo-Darwinian synthesis.

The second development was progress in identifying the biochemical nature of genes, primarily by the extension of genetic analysis to bacteria and viruses. These studies led to the identification of *deoxyribonucleic acid* (DNA) as the hereditary molecule and to the identification of its biochemical structure by James Watson and Francis Crick in 1953. Once the biochemical structure of genes was identified, an understanding of how DNA replicates and carries a genetic code that directs the synthesis of proteins followed rapidly.

One more revolutionary breakthrough that set the stage for the current era of genetics was the rapid development of *recombinant DNA technology* in the 1970's and its refinement and broad application in the 1980's. Recombinant DNA technology is a collection of methods that allows DNA sequences of one organism to be recombined with those of another. The application of these techniques is commonly referred to as "genetic engineering." The fact that the chemical structure of DNA and the genetic code for protein synthesis are virtually the same for all organisms makes recombinant DNA a powerful technology. Recombinant DNA techniques, together with an understanding of the genetic code and the ability to identify and map specific genes, have opened up a new era of biological investigation and applications to medicine and agriculture.

Bernard Possidente, Jr., updated by Bryan Ness

See also: Chromosomes; DNA: historical overview; DNA in plants; DNA: recombinant technology; DNA replication; Genetic equilibrium: linkage; Genetics: mutations; Genetics: post-Mendelian; Mitosis and meiosis.

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GENETICS: MUTATIONS

Categories: Cellular biology; evolution; genetics

A mutation is a heritable, sudden change in the structure of a gene, which has no relation to the individual's ancestry. The change can occur spontaneously or can be the result of exposure to ultraviolet radiation or chemicals.

In 1901 Hugo de Vries coined the term *mutation* to describe changes in the hereditary material of evening primrose (*Oenothera*). "Mutation" is a derivative of the Latin verb *mutare*, meaning "to move or change." The word was first used to describe spontaneous, heritable changes in the phenotype of an organism.

In the modern era of genomics, mutations can be defined as changes in DNA (deoxyribonucleic acid) sequences, that is, changes in the structure of a gene. The changes can occur spontaneously or can be induced via ionizing radiation (ultraviolet radiation) or chemicals, such as aflatoxin B_1 and ethylmethane sulfonate. A common cause of spontaneous mutations is *deamination*, in which the amino group on the number 2 carbon of cytosine (C) is removed, converting C to uracil (U) in DNA. Another cause is copying errors during DNA replication: slippage or shifting of the translational reading frame. Spontaneous mutations also may be caused by *depurination*, in which the bond between deoxyribose sugar and a purine base, adenine (A) or guanine (G), is hydrolyzed, or by *depyrimidination*, the hydrolization of the bond between deoxyribose sugar and a pyrimidine base, either C or thymine (T). Depyrimidination is less common than depurination. The sites where a base is missing are called apurinic sites (when a purine base is missing) or apyrimidinic sites (when a pyrimidine base is missing) or simply *AP sites*.

An individual with a mutation is called a *mutant*. When a mutation occurs in the reproductive tissue of an individual plant, it can be transmitted to the next generation. When a mutation occurs in the somatic tissue, it will be limited only to that generation and affects only the cells in which it occurs.

Heredity vs. Genetic Combinations

Mutation is the only process that creates new genetic variation that results from a change or changes in the structure of a gene or genes. Genetic variability also can arise from new genetic combinations produced through the processes of crossing over, gene segregation, and chromosome assortment. In the case of recombination, all the genes are already present in an individual, and new variation simply results from the shuffling of those genes during gamete formation; there are no structural changes in genes.

Sites and Types of Mutation

Gene mutation involves a change in a single base pair or a deletion of a few base pairs. It usually affects the function of a single gene. The substitution of one base (or nucleotide) for another base (or nucleotide) is called a *point mutation* or a *substitution mutation*. The replacement of a pyrimidine (cytosine and thymine) with another pyrimidine or the replacement of a purine (adenine and guanine) with another purine is termed *transition*. The replacement of a pyrimidine with a purine or the replacement of a purine with a pyrimidine is termed *transversion*.

Base pair or nucleotide changes can produce one of the following types of mutation:

- *Missense mutation*, which results in a protein in which one amino acid is substituted for another amino acid.
- *Nonsense mutation*, in which a stop codon is substituted for an amino acid codon, which results in premature termination of a protein.
- *Frameshift mutation*, which causes a change in the reading frame. These mutations can introduce a different amino acid into the protein and have a much larger effect on protein structure. Small deletions also have effects similar to those of frameshift mutations. A nonfunctional protein

may be produced, unless the frameshift is near the terminal end of a gene.

- *Chromosomal mutations* or *abnormalities*, which involve deletions or insertions of several contiguous genes, inversion of genes on a chromosome, or the exchange of large segments of DNA between nonhomologous chromosomes.

Effects of Mutations

Gene flow is the exchange of genes between different populations of the same species, produced by migrants and commonly resulting in changes in gene frequencies at many loci (locations) in the recipient gene pool. The effect of a mutation carried into a new population will depend upon the number of migrants that were mutants and the size of the recipient population.

Genetic drift is the random fluctuations of gene frequencies as a result of sampling errors. Drift occurs in all populations, but its effects are most striking in small populations. Due to periodic reductions in population size, genetic drift can affect gene frequencies. A large population may contract and expand again with an altered gene pool (called the *bottleneck effect*). A consequence of genetic drift is reduced variability. A mutation has a better chance of spreading faster in a smaller population than in a larger population.

The "founder effect" is a term first coined by Ernest Mayr in 1942, who referred to small groups of migrants that succeed in establishing populations in a new place as "founders." Two founders could carry only four alleles at each gene locus. If a rare (mutant) allele were included among them, its frequency would be considerably higher (0.25) than it was in the parental population.

Nonrandom mating, also called *assortative mating*, occurs when male and female plants are not crossed at random. If the two parents of each pair tend to be more (or less) alike than is to be expected by chance, then positive (or negative) assortative mating occurs. Positive assortative mating promotes *homozygosity*, whereas negative assortative mating tends to promote *heterozygosity*. Mating of similar homozygotes would increase their frequency at the expense of heterozygotes. A mutation should spread more quickly under assortative mating than under nonassortative mating.

Inbreeding is defined as the coming together, at fertilization, of two alleles that are identical by descent. This is the result of mating between closely related plants. A mutation has a better chance of establishing under mating systems in which close relatives are involved than under those where inbreeding is prevented. Assortative mating represents the mating of individuals with similar *phenotypes*, whereas inbreeding represents the mating of individuals of similar *genotypes*.

Autogamy, or self-fertilization, is the strictest form of inbreeding. A mutation would spread more quickly under self-pollination than under cross-pollination.

If a mutation occurs at a homozygous locus (*aa* × *Aa*, or *AA* × *Aa*), the result would be greater diversity. If a mutation occurs at a heterozygous locus (*Aa* × *AA* or *aa*), it would result in more uniformity. Depending on the size of the population, gene frequency will change.

Manjit S. Kang

See also: Genetic drift; Nonrandom mating; Population genetics.

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GENETICS: POST-MENDELIAN

Categories: Disciplines; genetics; history of plant science

Thirty years after the work of Gregor Mendel in the nineteenth century, several rediscoveries of his work in genetics brought his theories to the fore. At about the same time, the discovery of chromosomes, coupled with the earlier knowledge, took genetics in a new direction.

Gregor Mendel (1822-1884) is often considered the founder of the science of genetics. Though his experiments with pea plants became the basis for understanding genetics in all plants and animals, he died unknown. In 1900 three simultaneous "rediscoveries" of Mendel's studies put his name at the forefront of biology. With the reintroduction to the world of Mendel's genetic laws, biologists began to look more closely at genetic phenomena. These researchers used Mendel's laws as the basis for more in-depth studies of genetics, which led to the modern understanding of genes, chromosomes, and their inheritance.

Rediscovery of Mendel

In 1900, working independently of one another, biologists Erich Tschermak, Hugo de Vries, and Karl Erich Correns each published data that reasserted Mendel's historic principles of heredity. Each scientist came to this rediscovery from a slightly different perspective.

Tschermak, an Austrian botanist, coincidentally started pea plant breeding experiments in 1898. He performed these experiments for two years before he accidentally discovered a reference to Mendel's work from thirty years earlier. When he read Mendel's papers, Tschermak found that he had duplicated many of Mendel's breeding experiments, and, embarrassingly, his own work was not as thorough. The Austrian published his own findings and gave credit to Mendel for performing the original breeding work. Tschermak is known for applying the genetic principles he helped rediscover to developing wheat-rye hybrids and a disease-resistant oat hybrid.

Hugo de Vries, whose primary concern was understanding how evolution worked, was a professor at the University of Amsterdam. De Vries wanted to find a genetic basis for Charles Darwin's theory of natural selection to understand how species could change over time. De Vries studied the evening primrose and found that, after cultivating the plant for years, several varieties arose through abrupt, unexplained genetic changes. Based on these changes, he came up with a theory of *mutation* in which he hypothesized that rapid alterations in organisms could explain how evolution could quickly produce new species. For eight years, starting in 1892, de Vries conducted breeding experiments that led him to the same laws of heredity that Mendel had discovered. When he reported his own work, de Vries was very careful to attribute his concepts to Mendel.

Karl Correns was a German botanist at the University of Tübingen in the 1890's. By coincidence, Correns conducted breeding experiments with peas that reproduced Mendel's experiments. In a survey of the literature, Correns found Mendel's papers, published many years earlier. Much of Correns's life work was spent in developing additional evidence to support Mendel's hypotheses. Correns was the first researcher to suggest that if certain genes were physically close to each other, they might be "coupled" in some way and be consistently inherited in offspring. His concept explained why some traits did not seem to follow Mendel's *law of independent assortment*, which stated that all traits separated independently of one another when inherited by offspring.

Chromosomes

Chromosomes were not discovered until the end of the nineteenth century, so Mendel was never able to suggest any physical basis for his genetic theories. It was not until the science of cytology (the study of cells) was founded that scientists started to

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examine cells and their replication more closely. They discovered that *somatic cells* (that is, nonreproductive cells) consistently went through a pattern of division in which chromosomes were duplicated and separated between two new *daughter cells*.

Walter Sutton and Theodore Boveri, working with grasshopper cells, were the first scientists to notice that chromosomes in somatic cells occur in pairs. Sutton and Boveri suggested a connection between the pairs of chromosomes and Mendelian genetics. They believed that chromosomes carried the units of inheritance and that the way chromosomes divided accounted for how Mendel's laws functioned. Their work formed the basis for the *chromosomal theory of inheritance*.

The chromosomal theory of inheritance suggested that Mendel's genes reside on chromosomes and that when plants and animals reproduce, half their genetic material comes from each parent, forming sets of chromosomes. For example, barley has fourteen chromosomes in each somatic cell. Seven of those chromosomes are contributed from the "mother" plant and seven from the "father" plant, to make a total of fourteen chromosomes in the offspring. Therefore, half of the genes from all organisms come from each parent to determine the progeny's genetic makeup.

Each chromosome is essentially one long, linear strand of deoxyribonucleic acid (DNA), wrapped up and compacted for easy duplication and transport by the cell. There are two copies of each chromosome (called homologous pairs or homologs) in every somatic cell of an organism, each with the same physical appearance.

Such a cell with two copies of each chromosome type is called a *diploid* cell. Reproductive cells, known as *gametes*, have half the number of chromosomes and are known as *haploid* cells. It is these haploid cells from each parent that comprise the new diploid cells of the offspring. Half the chromosomes in each diploid cell come from each parental haploid cell.

Copies of the same gene on each chromosome pair are found at the same location (called a *locus*) and control traits of the organism. The copies of the same gene at a locus are called *alleles*. For example, one copy of chromosome #1 might be from the male parent and have a *dominant allele* (symbolized by *A*), and the other copy of chromosome #1 might be from the female parent and have a *recessive allele* (symbolized by *a*). These two alleles together (*Aa*), each on a separate chromosome, would constitute the *genotype*, and the expression of these alleles produces the *phenotype* (physical traits of an organism).

Linkage

In 1905 William Bateson and Reginald Punnet were the first to show clear evidence that Correns's theory of "genetic coupling" was correct. They crossed sweet peas having purple flowers and long pollen grains with sweet peas having red flowers and round pollen grains. According to Mendel's rules, the offspring in the second sweet pea generation should have *segregated* (genetically separated) into four phenotype combinations (purple/long, purple/short, red/long, and red/short) in a ratio of 9:3:3:1, because the two genes controlling these traits should have separated independently of each other. Bateson and Punnet did not obtain a 9:3:3:1 ratio. Instead, the parental traits stayed together in the offspring more often than expected, and more offspring looked like the parents than expected: purple/long or red/short. Bateson and Punnet called this phenomenon *linkage*, and any genetic traits that followed this pattern were said to be linked to each other.

In 1910 American geneticist Thomas Hunt Morgan explained the physical basis for linkage. Through his experiments with fruit flies, Morgan found that alleles for different traits only followed Mendel's law of independent assortment if they were on different chromosomes or if they were very far apart when they were on the same chromosome. If the genes for two traits were on the same chromosome, they were often passed down to the next generation jointly and stayed together consistently from generation to generation. Morgan further found that the physically closer that two alleles were to each other on a chromosome, the more closely "linked" they were to each other, staying together in offspring a greater percentage of the time.

Incomplete Dominance

Linkage was one of the first phenomena to break the Mendelian laws, but there were many additional conditions that Mendel would have puzzled over, such as *incomplete dominance*. Usually in a heterozygous organism (one with a dominant allele and a recessive allele at the same locus), the phenotype is controlled by the dominant allele, and the trait from the recessive allele will be masked. When incomplete dominance occurs, the dominant trait is weakened, and the heterozygotes look as though they have a trait partway between the recessive and dominant traits. For example, if a red-flowered snapdragon, *RR*, is crossed with a white-flowered snapdragon, *rr*, all the first-generation offspring are heterozygous, *Rr*. If the trait were dominant, then all the flowers in the offspring would be red. However, the trait displays incomplete dominance, and all the flowers are pink.

Multiple Alleles

Although an individual can have only up to two alleles at a locus, more than two alleles can exist in a population. For example, some populations of red clover are estimated to have hundreds of alleles at a locus for self-sterility. As a result, most individuals have alleles that are different from those of other members of the population, thus preventing self-pollination and making out-crossing with other plants successful. Some plants can also have more than two alleles at a locus if they are *polyploid*.

A polyploid plant has more than two homologous chromosomes of each type. The most common type of polyploid is a tetraploid, which has four homologous chromosomes of each type. With four chromosomes of each type, a locus has four alleles instead of just two. Other levels of polyploidy exist in plants, even as much as cases with ten, twenty, or more homologous chromosomes of each type.

Gene Interactions

Gene interactions occur when two or more different loci (gene locations) affect the outcome of a single trait. The most common type of gene interaction is known as *epistasis*. Epistasis describes a situation where an allele at one locus masks the phenotypic effects of a different locus. The gene being masked is called the *hypostatic* gene, while the gene doing the masking is called the *epistatic* gene.

Bateson and Punnet discovered this phenomenon during their sweet pea breeding experiments.

They crossed purple-flowered plants with white-flowered plants. In the first generation, they got all purple-flowered offspring—so they concluded that purple was the dominant gene. In the next generation, they did not get a 3:1 ratio of purple-flowered to white-flowered plants, as would be expected if purple was dominant. They got a ratio of 9:7 purple to white-flowered plants. It turned out that there were two different loci involved in the control of petal color: at the first locus *C* (purple) was dominant to *c* (white), and at the second locus *P* (purple) was dominant to *p* (white). When either locus was homozygous recessive, either *cc* or *pp*, the flowers were white, regardless of the genotype of the other locus. The recessive alleles were epistatically affecting (or masking) the dominant alleles.

Polygenic Inheritance

Certain traits are too complex to be controlled by a single locus. These traits are controlled by a complex of two or more loci, a phenomenon known as *polygenic inheritance*. In humans, multiple loci control height, intelligence, and skin coloration. These multiple genes lead to *continuous variation*, meaning that one observes a wide range of phenotypic variation. The first experiment demonstrating continuous variation was conducted by Swedish scientist Herman Nilsson-Ehle in 1910. He studied the inheritance of the red pigment on the hulls of wheat. He found that red-hulled wheat crossed with white-hulled wheat for several generations gave him plants ranging in pigment from white, light-pink, and pink to medium, basic, and dark-red. Nilsson-Ehle found that three loci control this color variation in the wheat.

Pleiotropy

Pleiotropy also breaks Mendel's laws. Usually, one locus controls a single trait. A pleiotropic gene is a single locus that controls multiple traits. If there is a loss of function mutation in a pleiotropic gene, the organism is affected in multiple ways. One example of such a trait can be found in the plant *Arabidopsis thaliana*. This plant has a mutant allele known as tu8. This gene was originally isolated as a mutant in the biochemical pathway that makes glucosinolate, a chemical used against pathogens. This tu8 mutation also causes the plant to be dwarfed, late-flowering, and heat-sensitive. Genetic experiments by researchers James Campanella and Jutta Ludwig-Mueller have shown that all these traits are controlled by a mutation in a single gene.

Cytoplasmic Inheritance

Finally, *cytoplasmic inheritance*, often known as *maternal inheritance* or *extranuclear inheritance*, is a phenomenon referring to any genetic traits not inherited from nuclear genes. For example, both chloroplasts and mitochondria contain their own genetic information that is inherited by every generation. This information is inherited in a different fashion from that of nuclear genes. Nuclear genes, in the form of chromosomes, are donated equally by each parent. The genetic information from chloroplasts and mitochondria is not donated equally. Offspring come from the joining of the male and female gametes, but the size of these gametes differs drastically. Male gametes, both animal sperm and plant pollen, are often one-one hundredth the volume of an egg cell. Because of their small size, male gametes often have little cytoplasm. Because the chloroplast and mitochondria reside in the cytoplasm, it is usually the case that none of the organellar DNA of the male gamete is included in the offspring. The female parent alone donates the chloroplast and mitochondrial alleles. Although maternal inheritance is the rule in most plants, a few groups, such as some members of the evening primrose family (*Onagraceae*) have displayed biparental inheritance of organellar DNA.

James J. Campanella

See also: Chromosomes; DNA in plants; DNA replication; Gene regulation; Genetic code; Genetic equilibrium: linkage; Genetics: Mendelian; Genetics: mutations; Mitosis and meiosis; Nucleic acids; Nucleus; Reproduction in plants; RNA.

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GERMINATION AND SEEDLING DEVELOPMENT

Categories: Anatomy; physiology; reproduction and life cycles

With germination, the growth of a seedling, spore, or bud begins. Seedling development begins with the close of germination.

To germinate, seeds must be nondormant and in a suitable environment. Seeds germinate within a restricted range of temperatures, moisture, oxygen, light, and freedom from chemical inhibitors. Wild seeds display many *adaptations* that predispose germination within specific habitats and seasons. By contrast, seeds of crops and other cultured plants usually lack controls that prevent germination. The control system was lost because some seeds in the population lacked controls and were chosen when they germinated in the care of a culturist. For that reason, most cultivated plants that start from seeds show little or no germination control. Most of the information on germination control, therefore, covers wild species of plants.

Seeds and Dormancy

Seeds are the exclusive means of regeneration for the annual flowering plants. In other plants, seeds are an alternative strategy to regeneration by *buds*, *bulbs*, *rhizomes*, *stolons*, or *tubers*. In those plants, the primary roles of the seed are to disperse the population and to reinvigorate the genetic diversity of the germ line.

Seed *dormancy* occurs in most plants, and when a seed is dormant it will not germinate, even if it is in the right environmental conditions. The dormant state may begin with maturation of the seed embryo, or it may develop in climate extremes after the seed falls from its parent. Dormancy prevents immediate germination when the mature seed is in an inappropriate environment, and it is a programmed phase in the life cycle. Dormancy's function ends, and a *germination window* opens, at a time when the emerging seedling will have the optimum chance for survival.

After-ripening removes the dormancy and allows the seed to respond to germination stimuli. Seeds of summer annuals after-ripen when exposed to winter and early spring temperatures, a treatment called *stratification*. Exposure to cold temperatures can also promote dormancy in some seeds.

Not all nongerminating seeds are innately dormant. There are also nondormant and conditionally dormant seeds. Neither type may germinate when the seeds mature, simply because the parent prevents contact with the soil and absorption of water or because the temperature range is below that necessary for germination. Wild seeds may experience a deepening of dormancy as a result of exposure to the temperatures of the dormant season. Nondormant seeds may simultaneously experience biochemical reactions that deepen dormancy and cause them to after-ripen.

Dormancy is caused by one or more conditions of the seed. Physiological dormancy of the embryo is the most common. It may be caused by the presence of an *inhibitor molecule*, an inadequate level of a growth hormone, or some other internal factor. Examples of the latter include blockages in membrane function or in synthesis of an enzyme or its nucleic acid messenger.

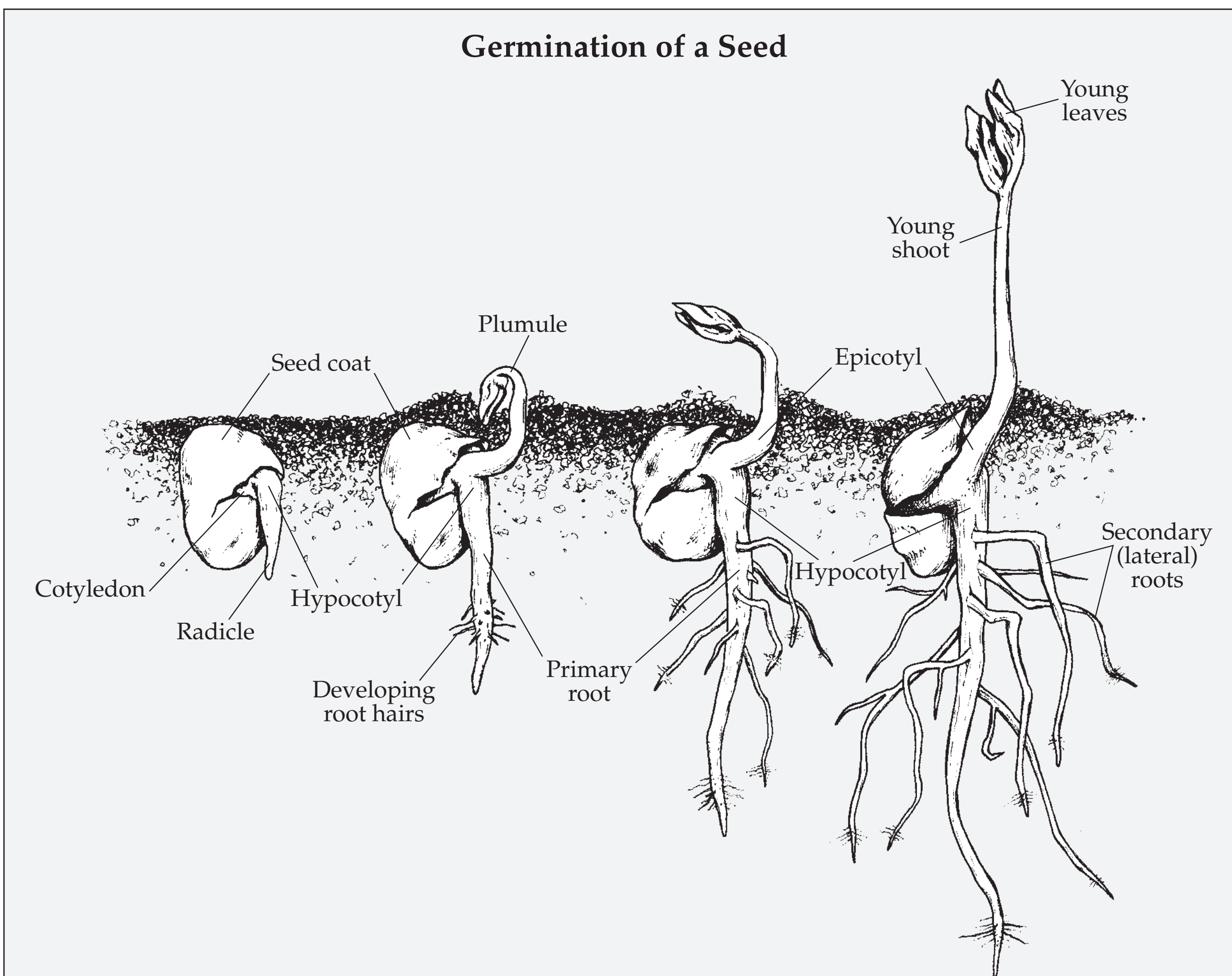
Other causes of dormancy are a hard or impervious seed coat, an underdeveloped embryo, or some combination of those factors. Some hard-coated seeds require physical scraping, such as tumbling down a swift-flowing stream and being scraped on the streambed. Others may require exposure to a forest fire or passage through the gut of an animal to weaken the seed coat.

Germination

The seeds from the previous year's crop of summer annuals wait to germinate in spring. Seeds of many species will germinate when soil temperatures reach a threshold constant. Others require daily fluctuations of temperature, waiting until the daily fluctuation becomes sufficiently large.

Seeds of most species require a light stimulus to germinate. The light is absorbed by the pigment *phytochrome*, which is positioned in the cotyledons of the embryo. Phytochrome acts as a shade detector. White light and, especially, red light, convert the phytochrome molecule to an active form. The rearrangement of the molecule causes it to attach a different part of itself to a new location on a cell membrane within the cotyledons of the seed. Transformed phytochrome allows seeds to germinate. By contrast, far-red light, which is absorbed by the transformed phytochrome molecule, transforms the molecule back to its original shape—that is, it deactivates it. When sunlight is transmitted through green leaves to the forest floor, much of the visible light with wavelengths shorter than 700 nanometers is absorbed or scattered. This *shade light* is rich in far red, and it tends to deactivate phytochrome.

Not all seeds germinate at the beginning of the following growing season. Light-demanding seeds that have become buried or have fallen into the shade will be stressed by the absence of an activat-



Kimberly L. Dawson Kurnizki

ing light signal, while the embryos experience an environment that is otherwise growth-promoting. Stressed seeds may enter a *secondary dormancy* and will need to undergo a second interval of after-ripening before again becoming nondormant. Seeds emerging from secondary dormancy may require a smaller light stimulus. Following primary dormancy, one or more complete light cycles may be necessary. By contrast, seeds may be fully activated by only a brief pulse of light when they emerge from secondary dormancy.

Many seeds become dry on the parent plant as a part of maturation. Drying is believed to end the seed-building phase and start the pregermination phase. Most domestic seeds require no after-ripening but will germinate if allowed to take up water. Water uptake is a first step in germination. Biochemical events that begin with water uptake in domestic seeds include metabolism along three separate pathways and an increased use of oxygen. Excessive moisture, even at temperatures too low for germination, may lower seed viability. Thus, seeds are best preserved under cold, dry conditions.

With proper storage, a reasonable percentage of seeds may live for many years. Record long-lived species include seeds of *Canna* (arrowroot, six hundred years), *Albizia* (mimosa and silk trees), and *Cassia* (about two hundred years). Seeds of *Verbascum* (mullein) have survived at 40 percent viability for one hundred years. Weed seeds in soil banks may need to wait for hundreds of years before the forest is cleared by catastrophe and the environment once again is favorable for such pioneer species. By contrast, recalcitrant seeds require their embryos to be kept moist, or viability is quickly lost; examples include trees with large seeds, such as walnut, oak, hazel, and chestnut. These seeds usually live less than one year.

Seedlings

Seedling development begins with the close of germination. Cells in the embryonic root (the *radicle*) begin to divide and grow. In some seeds, or in unusual environmental conditions, other parts of the embryo emerge before the radicle. Development of the seedling is marked by the growth and elongation of the embryo stem. Seeds are classified according to which part of the stem grows more rapidly. In the *epigeal* type, the *hypocotyl*, which is the basal part of the stem between the radicle and the embryonic leaves (the *cotyledons*), grows, thereby thrusting the cotyledons above the soil. In the *hypogeal* type, the *epicotyl* or upper part of the stem elongates, and the cotyledons remain underground.

Exposed to light, phytochrome in the cotyledons calls for an end to subterranean elongation, called *etiolation*, and the beginning of plantlike growth. Among its functions, phytochrome triggers the synthesis of chlorophyll; photosynthesis soon turns the cotyledons into sugar factories. At the same time, the epicotyl region of the embryo above the cotyledons is extending the *plumule* to form the first true, or foliage, leaves. In hypogeal seeds the first leaves emerge from the plumule.

Food reserves that are stored in the endosperm, cotyledons, and embryo will nourish the early growth of the plant until it can synthesize the necessary machinery for making its own food. Foods are stored in seeds as starch and other complex carbohydrates, fats, and proteins. Cereal grains contain large amounts (65-80 percent) of carbohydrates, which are stored in the endosperm. Seeds of legumes are famous for their high protein contents, which reach 37 percent in soybeans. The peanut, a legume, stands out by having both high protein (30 percent) and high fat content (50 percent). Legumes store food reserves in the embryonic leaves (cotyledons).

Food is transferred to the growing sites, primarily as sucrose and amino acids. Starches and other carbohydrates and fats are first converted to simple sugars and then to sucrose for transport. Synthesis of active phytochrome, second messengers, and the plant hormone gibberellin are involved in determining the rate of mobilization and transport. They promote synthesis of enzymes, such as those that break down food reserves into simple sugars.

The embryo selects one part of the root-stem axis for rapid growth, changing the relationship of the other parts to the external environment. The cotyledons are also versatile: They may act as first leaves or may remain attached to another part of the embryo, such as the endosperm. There, they act as absorptive organs to transport mobilized food reserves to the growing parts of the seedling. In onions, a single cotyledon performs both functions. The exposed part carries out photosynthesis, while the buried part absorbs foods from the endosperm.

Ray Stross

See also: Angiosperm life cycle; Angiosperm plant formation; Dormancy; Hormones; Plant life spans.

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GINKGOS

Categories: Evolution; gymnosperms; paleobotany; *Plantae*; taxonomic groups

The ginkgos, phylum Ginkgophyta, *constitute one of four phyla of the gymnosperms in the kingdom* Plantae. Ginkgo biloba, *the maidenhair tree, is the only living representative of the ginkgo family,* Ginkgoaceae, *a group of plants that have lived for millions of years and are identified by an abundant fossil record.*

The ginkgo is a hairless, deciduous tree with a straight trunk and pyramid-shaped foliage usually sparsely branched when young, becoming denser with age. Leaves are fan-shaped, 2 to 3 inches (5 to 7.5 centimeters) across, sometimes divided into two lobes. The ginkgo normally reaches heights of 80 to 100 feet (24 to 30 meters) and under favorable conditions grows to 125 feet (38 meters) or more. The bark is reddish-gray and corky, with irregular, wide fissures dividing rough plates. On old trees, the bark becomes gray, rough, and deeply furrowed.

Considerable diversity in branching habit occurs, sometimes with one side of the tree having erect branching and the other side spreading limbs. Young trees send out straight branches at a skyward angle and, until maturity, the sparse branching gives the tree an erratic appearance. Upon maturity, the branches round out and become widespread, yet retain an uneven crown.

As in many conifers, the long branches (shoots) and short, spurlike shoots of *Ginkgo biloba* are easily distinguished. The leaves are spirally arranged on both types but widely spaced on the long shoots, with leaves in crowded, rosettelike clusters on the short shoots. Branchlets (twigs) have a horizontal or drooping habit and are occupied with short, spurlike shoots. These shorter shoots increase in length only a fraction of an inch (2.5 centimeters) per year and may produce clusters of leaves annually for many years before abruptly lengthening out into long shoots bearing scattered leaves. The fan-shaped leaf has a marked resemblance to the fronds of the maidenhair fern, thus the common

Classification of Phylum *Ginkgophyta*

Class *Ginkgoopsida*
Order *Ginkgoales*
Family *Ginkgoaceae* (Ginkgo family)
Sole living species: *Ginkgo biloba* (maidenhair tree)

name: maidenhair tree. However, in its native China it is commonly called ducks-foot tree, also based on leaf shape.

The leaves, which grow on slender stalks up to 3 inches (7.5 centimeters) long, have numerous veins radiating out from the base to an irregularly notched leaf margin. There is no central midrib vein on the somewhat leathery, textured leaf. Stomata (breathing pores in the leaves) occur on both the upper and lower surfaces of the leaves. The leaves emerge yellow-green in spring but turn green toward midsummer and become golden in autumn. Leaves on vigorous young trees can grow up to 6 to 8 inches (15 to 20 centimeters) in width. There is a morphological distinction between leaves of long branches and short shoots, with the leaves of long branches generally bilobate to four-lobed and those of short shoots only fan-shaped to bilobate.

Elliptical, naked seeds resembling a small plum appear on female trees in early spring. Seeds range from 0.75 to 1 inch long (1.9 to 2.5 centimeters) and are covered by a thin, yellowish-orange, fleshy outer wall enveloping a woody shell which contains an edible kernel in the shell interior. When falling to the ground in autumn, the seed covering begins to diminish in thickness over several months, giving off the vile odor of butanoic and hexanoic acids (butter and Romano cheese fatty acids), and is eventually lost from most seeds. *Ginkgo biloba* wood is light, brittle, yellowish in color, and of little value. It is used as a base wood in highly lacquered furniture and small carved items.

Reproduction

The ginkgo is dioecious: Male and female reproductive structures are borne on separate trees. The male reproductive structures appear in May and are inch-long, catkinlike structures bearing numerous paired, pollen-bearing organs. The pollen grains are similar to the elliptical grain of cycads. The pollen organs and ovules are confined to the short shoots of each ginkgo tree and arise in the leaf axils or inner bud scales.

The female reproductive structure consists of a long stalk, bearing on each side an erect, naked ovule, which is surrounded at the base with a collarlike rim. The paired ovules are borne in groups of two to ten. The three-layered ovules include a fleshy exterior layer (sarcotesta), an inner flesh, and a stony shell (sclerotesta) between the two. This three-layered structure is called the integument. The nucellus (the central cellular mass of the body of the ovule containing the embryro) is mostly free from the surrounding integument, except at its base, where it develops a pollen chamber at its apex.

Similar to the cycads, the gingko reproduces by means of flagellated sperm cells, which are carried by the wind-borne pollen to the female reproductive structures within the ovule. In the ginkgo, the vascular system is weakly developed and consists of a pair of braided bundles in the interior fleshy layer of the integument. Upon maturation of the microgametophyte (male gametophyte), pollen tubes are produced, as are large, motile sperm cells similar to those of the cycads. Megagametophyte (female gametophyte) development is similar to that in cycads as well.

Natural Regeneration

Studies into the seedling development of *Ginkgo biloba* reveal a unique mechanism of clonal regeneration that may help explain the species' long survival in the natural setting. The organ of clonal regeneration in the gingko is called the *basal chichi*. These organs are part of aggregates of suppressed shoot buds and are located in embryonic tissue of *Ginkgo biloba* seedlings. When damage occurs to the seedling axis, one of these subsurface buds grows down from the tree trunk to form a woody, stemlike basal chichi. Regeneration of *Ginkgo biloba* by basal chichi promotes survival of the tree in the forests of China today and may have been a factor in the protracted survival of the order since the Mesozoic era.

Habitat and Range

Ginkgo biloba, a distinctive tree suited for use in singular or in group plantings on lawns or along streets, is widely cultivated in all temperate zones. It prospers in moderately moist, fertile soil in humid, temperate regions. It is extremely resistant to disease and pests, and it is highly tolerate of smoke, dust, wind, and ice.

Ginkgo biloba is apparently native in eastern China, with documented semiwild trees growing on the west peak of Tian Mu Mountain in the Tian Mu Reserve, Zhejiang Province. *Ginkgo biloba* is planted in the eastern United States, Europe, and along the Pacific coast.

Fossil Record

Among the plants, *Ginkgo biloba* is probably the best-known example of a "living fossil." Although the ancestors to the order *Ginkgoales* date to the Paleozoic era, it was at the close of the Triassic period when they became a dominant part of the Mesozoic flora. During the Jurassic period, especially the middle Jurassic, *Ginkgoales* reached zenith numbers of species and its widest distribution.

Jurassic and Cretaceous fossil localities reveal circumpolar *Ginkgophytes* sites, including Alaska, Greenland, Zemlya Frantsa Iosifa (Franz Joseph Land), and Mongolia, with the Siberian locations especially productive. Southern Hemisphere *Ginkgoales* localities include Patagonia at the southern tip of South America, South Africa, India, Australia, and New Zealand. European fossil sites are known in England, Scotland, Germany, Italy, Hungary, Turkestan, and Afghanistan. Western Canada and the United States have *Ginkgoites* leaf remains from the Upper Mesozoic and Lower Tertiary deposits. The presence of *Ginkgophytes* in high northern latitudes during the Early Cretaceous period and its presence in southern latitudes, such as Argentina, during the Jurassic, suggests that the dispersal of the plant was from the southern to northern latitudes during the Upper Mesozoic era.

During the Tertiary period, the decline of the *Ginkgophytes* was evident from the presence of only two of nineteen species remaining in the fossil record. One of the remaining two species is the *Ginkgo adiantoides*, which declined sharply during the Oligocene period. This decline continued into the Miocene period in North America, with *Ginkgo adiantoides* disappearing from the fossil record at the end of the Miocene. *Ginkgo adiantoides* did continue into the Pliocene in Europe, however. Since the Pliocene, the fossil record indicates that *Ginkgoales* have been represented by the extant living fossil, *Ginkgo biloba*.

Researchers propose that the decline of *Ginkgophyta* was a result of competition from the angiosperms (flowering plants) for similar plant habitats. Also, the *Ginkgophytes* became more restricted to northern temperate forests in the Tertiary period. When glaciation occurred in these areas during the Pleistocene, these forests were destroyed by climate change.

Mariana Louise Rhoades

See also: Conifers; Cycads and palms; Evolution of plants; Fossil plants; Leaf arrangements; Paleobotany; Pollination; Reproduction in plants; Seeds; Shoots; Water and solute movement in plants.

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GLYCOLYSIS AND FERMENTATION

Category: Cellular biology

Glycolysis is the beginning of the process of extracting usable energy from food. The disposal of the products of glycolysis when there is no oxygen available is the process of fermentation.

The simple sugar *glucose* is generally considered the starting point for looking at glycolysis and fermentation. Glucose is a simple *carbohydrate*, consisting of carbon, hydrogen, and oxygen. Most glucose is produced by plants; organisms that cannot photosynthesize must obtain glucose (or more complex carbohydrates) from their surroundings. Animals obtain food molecules by eating. Simpler forms of life, such as bacteria and yeast, simply absorb their food from their environment.

Breaking Chemical Bonds

The energy in glucose is locked up in the chemical bonds that hold the molecule together. The process of glycolysis breaks these chemical bonds in a series of carefully controlled chemical reactions. Each reaction can be greatly accelerated by the appropriate *enzyme*. Generally, cells have sufficient quantities of the necessary enzymes present at all times.

Each chemical step is regulated by either the amount of raw materials present or the amount of finished product. If the raw materials are in short supply, the rate of reaction will be slow. Also, if the finished products build up to a high concentration, the reaction will slow down. The energy of the chemical bonds in glucose must be released gradually. During most of the chemical steps, small amounts of energy are released. The amount of energy released is often not enough to perform significant biological work, in which case it is simply wasted as heat. The energy released during some steps, however, is captured in the special high-energy bond of *adenosine triphosphate* (ATP). ATP is one of the most important of the short-term energy storage molecules in cells and is a coenzyme for many important chemical reactions.

Adenosine Triphosphate

ATP belongs to a class of organic molecules known as *nucleotides*. It has an important role in the energy reactions in the cell. The term "triphosphate" indicates that there are three phosphate groups attached to the base molecule. The last two of these phosphates are held by a special kind of chemical bond known as a *high-energy bond*. It takes a greater amount of energy to form one of these bonds than to form the normal kinds of bonds that hold the atoms of other molecules together. When this bond is broken, a large amount of energy is released and is available to the cell to do work. Examples of such work are production of heat, synthesis of complex molecules, and movement of molecules across a membrane. When energy is required in a cell, the third phosphate of ATP is released. While the third phosphate group is routinely split off to release energy, the second one is rarely split off in cellular reactions. The cell must maintain a supply of ATP by means of the reverse reaction. The energy required for this reaction may come from fermentation when oxygen is unavailable. When oxygen is available, other components of cellular respiration are used, which include the *Krebs cycle* and *electron transport*.

Glycolysis

Energy from glycolysis is used to make ATP by two different processes. During glycolysis the glucose molecules are each split into two smaller molecules. The initial glucose molecules contain six carbon atoms each. Each molecule of glucose produces two molecules of pyruvic acid, and each pyruvic acid molecule contains three carbon atoms. During glycolysis, energy is released from the bonds of glucose molecules and is used to join free phosphate ions (also called *inorganic phosphate* or P_i) with molecules of adenosine diphosphate (ADP) to make ATP. This type of ATP synthesis is called substrate-level phosphorylation.

As a by-product, however, electrons are also stripped from glucose. These electrons are immediately trapped and held by another very important molecule, the electron carrier *nicotinamide adenine dinucleotide* (NAD). By convention, the empty electron carrier is denoted as NAD^+. When the molecule is carrying a pair of electrons, it is denoted as NADH, since the molecule also picks up a hydrogen nucleus, or proton. The electrons held by NADH represent potential energy. In the presence of oxygen, these electrons can be passed to the electron transport system to make ADP by *oxidative phosphorylation*, while at the same time regenerating NAD^+, which is required to maintain glycolysis. This second process for making ATP results in about eight times as much ATP per glucose molecule than from substrate-level phosphorylation in glycolysis. Because fermentation is carried out in the absence of oxygen, this process cannot be used. Instead, the NADH must be relieved of its electrons by an alternative process. The NAD^+ regeneration mechanism varies according to the type of organism.

Glucose molecules are relatively stable and do not split readily. For glucose molecules to split, they must be energized by the addition of two phosphate groups to each glucose molecule from two ATP molecules. The third phosphate from each ATP molecule is transferred, along with its high-energy bond. Therefore, the initial steps of glycolysis actually use ATP, depleting some of the cell's energy stores. Once glucose is energized, it readily splits under the influence of the appropriate enzyme. Each half of the glucose molecule then attaches another phosphate group from the cell's pool of P_i. In a series of reactions, each half of the glucose molecule generates two ATP molecules by substrate-level phosphorylation. Therefore, glycolysis results in a net gain of two molecules of ATP per molecule of glucose. At the end of glycolysis there are two three-carbon molecules of pyruvate left over for each original glucose molecule.

Fermentation

Under aerobic conditions, further energy from the chemical bonds of pyruvic acid is harvested by the Krebs cycle and electron transport system. When oxygen is not available (*anaerobic* conditions), however, the electrons must be removed from the NADH to regenerate NAD^+. While there are many ways of accomplishing this, the most common methods are alcoholic fermentation, as observed in yeast, where the end products are ethyl alcohol and carbon dioxide, and lactic acid fermentation, as observed in the muscles of a mammal during strenuous physical exercise. In any event, no further energy is gained for the cell.

In yeast cells cultured in the absence of oxygen, a carbon atom and two oxygen atoms are first split from pyruvic acid, releasing a molecule of carbon dioxide (CO_2). This CO_2 gas is responsible for the bubbles that make bread rise and the carbonation in champagne. The remainder of each pyruvic acid molecule then receives a pair of electrons from NADH, producing a molecule of ethyl alcohol (ethanol). The alcohol evaporates from bread when it is baked but is retained for its mildly euphoric effect in alcoholic beverages. As far as the yeast is concerned, the alcohol is only produced as a way of regenerating NAD^+. It is not a desirable product and will eventually kill the yeast cells. Most yeast cells cannot tolerate an alcohol concentration greater than about 12 percent.

Cellular respiration is the process by which organisms harvest usable energy in the form of ATP molecules from food molecules. Fermentation is the form of respiration used when oxygen is not available. Fermentation is much less efficient than aerobic cellular respiration. Fermentation harvests only two molecules of ATP for every glucose molecule used. Aerobic respiration reaps a yield of more than thirty molecules of ATP. Additionally, the typical products of fermentation, alcohol or lactic acid, are toxic to the organism producing them. Most forms of life will resort to fermentation only when oxygen is absent or in short supply. These are described as *facultative anaerobes*.

While higher forms of life, such as animals, can obtain energy by fermentation for short periods, they enter an oxygen debt, which must eventually be repaid. The yield of two molecules of ATP for each glucose molecule used is simply not enough to sustain their high demand for energy. A few simple forms of life, mostly bacteria, rely solely on fermentation for their source of ATP. To some of these, oxygen is actually poisonous. These are described as *obligate anaerobes*, and they are only found under the completely anaerobic conditions of the deeper layers of mud in saltwater and freshwater marshes.

James Waddell

See also: ATP and other energetic molecules; Carbohydrates; Krebs cycle; Oxidative phosphorylation; Photorespiration; Photosynthesis; Respiration.

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GNETOPHYTES

Categories: Evolution; gymnosperms; *Plantae*; taxonomic groups

The gnetophytes are a small group of vascular seed plants composing the phylum Gnetophyta*, which is one of four phyla of gymnosperms that have living representatives.*

The *Gnetophyta* include only three genera—*Ephedra*, *Gnetum*, and *Welwitschia*—each of which belongs to a separate family, in a single order, the *Gnetales*. The gnetophytes have a number of features in common with the flowering plants (phylum *Anthophyta*, the angiosperms), which has sparked scientific interest in the evolutionary relationships between the two groups; they are the only gymnosperms, for example, in which vessels occur. There are about ninety species of gnetophytes. They are diverse in form and size, and their distribution varies widely, from moist, tropical environments to extremely dry deserts. Most gnetophytes are shrubs or woody vines. The leaves occur oppositely or in whorls of three.

Like most other gymnosperms, the gnetophytes bear their reproductive structures in strobili, or cones. The gnetophytes differ from other gymnosperms in that both the seed-producing (ovulate or female) cones and the pollen-producing (male) cones are compound; that is, they are, in turn, composed of cones. Both male and female cones contain oppositely arranged bracts, or modified leaves, which bear short, fertile shoots at the axil (the angle between the bract and the stem that bears it). Most gnetophytes are *dioecious*, meaning that they bear their pollen and ovulate cones on separate plants.

Angiosperm-like Features

The gnetophytes share with the angiosperms a number of structural and developmental characteristics. One of these is the presence of water-conducting tubes, called *vessels*, in the secondary xylem, or wood. Vessels, although present in angiosperms, do not occur in gymnosperms other than gnetophytes. Another similarity is that *archegonia*—structures that protect the egg—which are typical of gymnosperms but absent from angiosperms, are not found in either *Gnetum* or *Welwitschia* (although they are present in *Ephedra*). In addition, the cones

Classification of Gnetophytes

Class *Gnetopsida*
- Order *Ephedrales*
  - Family *Ephedraceae* (Mormon tea family)
    - Genus *Ephredra*
- Order *Gnetales*
  - Family *Gnetaceae* (Gnetum family)
    - Genus *Gnetum*
  - Family *Welwitschiaceae*
    - Genus *Welwitschia* (tumboa)

of gnetophytes bear some resemblance to angiosperm flower clusters, and the leaves of *Gnetum* are similar in form, structure, and venation to those of the *Eudicotyledones* of the angiosperms.

Another feature common to angiosperms and gnetophytes—but not found in gymnosperms other than gnetophytes—is double fertilization. In double fertilization, there is union of each of two sperm nuclei with a nucleus in the female gametophyte (the gamete-producing generation in plants), rather than just a union of a single sperm and egg nucleus. Further, in at least some species of all three gnetophyte genera, the reproductive structures produce nectar that attracts insects, as in many angiosperms. Insects play a role in the pollination of gnetophytes, in contrast to the typical gymnosperm's reliance on the wind.

The similarities between gnetophytes and angiosperms have led scientists, who have long thought that the ancestor of the angiosperms is a gymnosperm, to look closely at the gnetophytes. The living gnetophytes are considered too specialized to include the angiosperm ancestor. In addition, evidence suggests that such shared features as similar-appearing vessels, similar-appearing reproductive structures, and the absence of archegonia were derived independently in the two groups. Scientists have still not determined, however, whether the gnetophytes and angiosperms share a close, common ancestor. Unfortunately, the fossil record for gnetophytes is too sparse to shed much light on this question. Although the gnetophytes were once more diverse than they are today, there is no indication that the group was ever rich in genera or abundant in individuals. The earliest known gnetophyte fossils date back 140 million years, to the Early Cretaceous period of the Mesozoic era, which is about as far back in time as the angiosperm fossil record goes.

Researchers have turned to cladistics (phylogenetic analyses) to study fossil, structural, and molecular evidence in an attempt to determine evolutionary relationships. The results of these studies have been inconsistent, and additional research will be needed. There is strong evidence, however, that, within the gnetophytes, *Ephedra* is the closest to the common ancestor of the group, and that *Gnetum* and *Welwitschia* are derived sister clades.

Ephedra

The genus *Ephedra* includes about sixty species, most of them adapted to semiarid and desert conditions. *Ephedra* is the only genus of gnetophyte that occurs in the United States, with twelve species growing in the desert Southwest, some of them ranging into Mexico. Another twelve species occur over a wide area in South America. The rest grow in the Eastern Hemisphere, from central Asia westward across southwest Asia and into Mediterranean Europe and North Africa.

Most species of *Ephedra* are scraggly, profusely branched shrubs. Some are vinelike, commonly climbing over other vegetation. The leaves of most species are small, dry, brown scales. Their reduced size may be related to the plants' need to minimize evaporative water loss in their dry environments. Photosynthesis is carried on mostly in the branches, which remain green while young. The branches are jointed, giving rise to the genus's common name, joint fir. Both the branches and the leaves are arranged two or three to a node. With its jointed stems and small leaves, *Ephedra* superficially resembles the horsetail, *Equisetum*. The stems of *Ephedra* form secondary xylem, or wood, as do the stems of conifers and many angiosperms. *Ephedra* wood is extremely hard.

The cones of *Ephedra* are borne in the leaf axils and are very tiny—the smallest in the gnetophyte group. The female cones have at their tips one or two ovules borne on very short stalks. The male cones are in spikelike clusters. Male and female cones are produced on the same plant or on different ones, depending on the species. The mature female cones are fleshy and berrylike and often brightly colored.

Stem extracts of *Ephedra* have a long history of use as folk medicines. Many Eurasian *Ephedra* species, especially *Ephedra sinica*, contain ephedrine, an alkaloid chemical that the Chinese have used for more than five thousand years as a decongestant drug, called Ma-huang, to treat asthma and hay fever. Ephedrine alkaloids have not been found in New World species of *Ephedra*, but Western countries manufacture synthetic ephedrine, which is used in cough medicines. European settlers in the American Southwest and Mexico brewed a beverage known as Mormon tea or Mexican tea from stem fragments of *Ephedra*.

Gnetum

The genus *Gnetum* includes approximately thirty species, which grow throughout the moist tropics. Most of these are woody vines that climb on trees in the rain forests of central Africa, Asia, and northern South America and on some Pacific islands. The best-known species, *Gnetum gnemon*, however, is a tree native to Indonesia that grows to 10 meters. It is cultivated for its edible seeds and tender young leaves.

Gnetum stems characteristically bear two broad, leathery leaves at each node and produce secondary xylem, or wood. In all *Gnetum* species, male and female reproductive structures are borne on separate plants. The cones, like those of *Ephedra*, look like berries, and the seeds may be brightly colored.

Welwitschia

The genus *Welwitschia* includes a single species, *Welwitschia mirabilis*. This low-growing, perennial plant is restricted to a 150-kilometer-wide strip of coastal desert in Angola, Namibia, and South Africa. In this extremely arid environment, where there may be no precipitation for several years at a time, *Welwitschia* may survive, at least in part, by using dew and condensate from fog that rolls in off the ocean at night. Young plants seem to become established mainly during rare wet years. Some living *Welwitschia* plants have been dated at fifteen hundred years old.

Described by some as the strangest living plant, *Welwitschia* bears little resemblance to other gymnosperms. Most of the plant is taproot, buried in sand to a depth of 1 to 1.5 meters. At its tip, the taproot divides into smaller roots that probably absorb water unavailable to less deeply rooted plants. The exposed part of *Welwitschia* includes a massive, squat stem that emerges only a short distance above the ground. The stem widens with age, becoming up to a meter across, and may develop a crusty, barklike covering on its surface. This broad, woody, concave disk, having ceased elongating from the tip, produces only two leaves during the plant's lifetime. The wide, strap-shaped leaves continue to grow from their bases at a rate of 8 to 15 centimeters per year, for the life of the plant. Battered by wind and hot sand, the leaves break off at their tips and split lengthwise, giving older plants the appearance of having numerous leaves. With their worn tips, the leaves seldom exceed 2 meters in length, although they may reach 6 meters.

The only real branches that *Welwitschia* produces are the branch systems of the pollen and ovulate cones, which are borne on separate plants. These branch systems develop in the axils of the leaves, although they appear to grow from around the rim of the stem cup. The pollen cones, which are red, are produced in groups of two or three at the end of each branch. Ovulate cones are also red. Droplets of nectar lure flies to pollinate the plant. The seeds, generally only one to a cone, have winglike extensions that may aid dispersal by the wind.

Jane F. Hill

See also: Angiosperms; Angiosperm life cycle; Angiosperm plant formation; Cladistics; Eudicots; Evolution of plants; Gymnosperms; Medicinal plants.

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GRAINS

Categories: Agriculture; economic botany and plant uses; food

Grains are the fruits or seedlike fruits of plants, particularly members of the grass family, Poaceae. *Important cereal grain crops are all produced by annual grasses and are dry (desiccant) fruits with the ovary wall fused to the seed coat. Inside the fruit wall-seed coat covering (the bran) is a small embryo (germ) and a large amount of stored food (endosperm).*

Grains were the first domesticated crops and allowed the development of all of the great early civilizations. Several factors contribute to the importance of grains in agriculture: ease of growth, storage, and preparation; high yields; and high-energy, easily digestible content (starch). The wild relatives of cereal grains all disperse their seeds by the shattering, or breaking apart, of mature fruiting stalks. Harvesting these wild species is a problem because the seeds are flung everywhere when the fruiting stalk is disturbed. A first step in the domestication of all grains was the elimination of shattering so that inflorescences could be harvested. For grasses, such as wheat, that produce many stems, or tillers, arising from the base of the plant, selection led to synchrony in the production of the tillers so that all the inflorescences of a plant would set fruit at the same time. For grasses, such as corn, that had a thick main stem, selection led to the elimination of secondary branches and a concentration of seeds in one or a few large inflorescences. The second half of the twentieth century saw selection for shorter stature that allows grains to grow better in tropical regions. While thirty-five species of grasses have been domesticated, only five are major crops today: *wheat*, *rice*, *corn*, *sorghum*, and *barley*.

Wheat

Wheat is the most widely cultivated grain in the world and was among the earliest grains to be domesticated. Archaeological deposits from the Middle East, the native home of wheat, containing domesticated wheat seeds have been dated to ten thousand years ago. The first species of wheat domesticated was the diploid einkorn wheat (*Triticum monococcum*), soon followed by the tetraploid, free-threshing emmer wheat (*T. turgidum*), which made it easier for people to separate the fruits from the papery tissues, or chaff, in which they are enclosed. Today, emmer wheats are grown throughout the world and are especially well suited to making pasta and pastries. Bread wheat (*T. aestivum*) was the last to be domesticated. This species is a hexaploid, and its increased cell size has as an important secondary effect: the high production of proteins, known as glutens, that allow bread wheat to form an elastic dough that produces light, spongy bread.

While some wheat is eaten as a grain in such dishes as tabbouli, most wheat is used for flour: whole wheat if the bran and germ are ground along with the starchy endosperm and white if the bran and embryo are removed. Because white flour (even organic flour) lacks the vitamins present in whole wheat flour, federal law in the United States requires that it be enriched with five nutrients: riboflavin, niacin, folic acid, thiamin mononitrate, and iron.

Rice

The acreage devoted to rice (*Oryza sativa*) is less than that of wheat, but more rice is produced annually than wheat, and more people in the world depend on rice as their primary food. Rice was domesticated in the Yangtze River region of China, probably more than nine thousand years ago. In most of the world, rice is grown by germinating seeds and growing seedlings in a nursery. Seedlings are then planted by hand in fields covered with water. Rice does not need to grow in standing water, but it needs high rainfall if the fields are not irrigated. Because rice contains no gluten, it is not used for leavened bread, but it is well suited for cooking because the seeds retain their shape and have a soft, chewy consistency. The two major types of rice are long-grained *Indica*, preferred in India, and short-grained *Japonica*, preferred in China and Japan because of the sticky grains that adhere to one another upon cooking. Removing the bran produces white rice, which lacks the vitamins and fiber of brown rice. Consequently, rice is often enriched with vitamin B_1.

Corn

Corn (*Zea mays*) is the only major grain native to the New World. It was domesticated in southern Mexico about eight thousand years ago from an annual grass known as *teosinte*. Corn plants are monoecious (having both pistillate and staminate flowers on one plant), with male flowers forming the tassel on the top of a corn plant and the female flowers packed inside the ear. The silks of an ear are the styles, one leading to each kernel of corn. Much of the U.S. crop is used for animal feed, but a large portion is converted to cornstarch or corn syrup to be used in the brewing, paper making, and processed food industries. A by-product of the cornstarch industry is corn oil, extracted from the germs.

Sorghum

Sorghum (*Sorghum bicolor*) is native to sub-Saharan Africa, where it was domesticated by five thousand years ago. Grain sorghums are a major source of food for millions of people in Africa and India, but in the New World sweet sorghum (sorgo) is grown primarily for animal feed. The plants are robust, with modern cultivars having a single, thick stem bearing a mass of seeds at the apex. Sorghum is the most drought-tolerant of the major grains and is therefore widely grown in arid regions. In addition to the grain sorghums and sorgos, other varieties yield rough fiber for brushes and booms.

Barley

Barley (*Hordeum vulgare*) was probably the first grain to be domesticated; ancient cultivated fruits found in the Near East have been dated to 10,500 years ago. Initially, barley was preferred over wheat and was used to make flat breads, pastes, gruel, and beer. Barley became less popular after the domestication of emmer and then bread wheat. However, it has remained the grain of choice for brewing beer because of its superior flavor after malting. Malting consists of germinating the grain just enough for it to produce enzymes that break down the starch into simple sugars that yeast can then ferment.

Beryl B. Simpson

See also: Agricultural revolution; Agriculture: experimental; Agriculture: world food supplies; Corn; Plant domestication and breeding; Plants with potential; Rice; Vegetable crops; Wheat.

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GRASSES AND BAMBOOS

Categories: Agriculture; angiosperms; economic botany and plant uses; food; gardening; *Plantae*

Grasses are monocotyledonous flowering plants (phylum Anthophyta, the angiosperms*) belonging to the family* Poaceae, *formerly* Gramineae. *The family is widespread and economically very valuable. All the grasses are herbaceous except for the bamboos, some of which are treelike.*

Grasses arose seventy million to eighty million years ago, in the Late Cretaceous period of the Mesozoic era. They succeeded partly because they concentrate their growth lower down on the leaf and stem than other plants do and thus can regenerate quickly when fire or herbivores remove the top part of the plant. This makes them ideal for human uses such as lawns and pasture for domestic livestock. Grasses are a very important food source for humans. Grasses provide all cereal grains—barley, corn, millet, oats, rice, rye, and wheat. Other grasses used for food include sorghum, sugarcane, and bamboo.

The grass family is important botanically and ecologically, too. With about 650 genera and 7,500 to 10,000 species, it is the fourth largest angiosperm family. In number of individual plants, it far outranks any other flowering plant family, composing the natural vegetation of about one-quarter of the earth's land surface. The family is especially abun-

PhotoDisc

Grasses are a very important food source for humans and provide all cereal grains, including wheat.

dant in semiarid climates and has the widest range of all the angiosperm families. Grasses provide a vital food source for many grazing, wild animals. By binding the soil with their roots, grasses protect it from erosion. In addition, grasses build up the soil when they die and decompose.

Stems, Roots, and Leaves

The aboveground stems of grasses are called *culms*. The roundness of culms distinguishes grasses from similar-looking plants, the sedges and rushes, which have differently shaped stems. Grass culms are divided into *nodes*, or joints, which are solid, and internodes (the regions between the nodes), which are usually hollow. Elongation of the culm occurs mainly at the bases of the internodes, rather than at the stem tip as in most plants. Grasses range in height from only a few centimeters, in annual bluegrass, to 30 or 40 meters, in treelike bamboos. Grasses may have underground stems, or *rhizomes*. The roots are slender and fibrous and form an extensive system that may compose a large proportion of the plant's total biomass. This large root system helps grasses obtain water in dry regions.

The leaves of grasses are generally arranged alternately on the stem and have no petiole, or stalk. The lower part of the leaf, the *sheath*, is wrapped around the culm like a split tube and is attached at its base to a node. The upper part of the leaf, the *blade*, diverges from the culm and is slender and elongated, tapering to a point at the tip.

Flowers and Fruits

Pollinated by the wind, grass flowers are simple and inconspicuous individually. They have stamens and pistils—the essential male and female reproductive structures—but lack petals and sepals, which most other angiosperms use to lure insect pollinators. Many grass flowers have three stamens and a single pistil that has two stigmas. Long, dangling anthers in the stamens and long, feathery stigmas help the wind transfer pollen efficiently from stamen to pistil.

Identification of grass species is based to a considerable extent on flower arrangement and characteristics of modified leaves, called bracts, that surround the flowers. Individual flowers, called florets, are usually arranged in clusters, called spikelets. Each floret and spikelet typically has at its base a pair of bracts. The spikelets may be crowded on an unbranched stalk, forming a spike, or borne at the ends of stalks having many branches, in a panicle.

Common Grasses of the United States

Common Name	*Scientific Name*
American beachgrass	*Ammophila breviligulata*
Baltic rush	*Juncus balticus*
Basin wildrye	*Leymus cinereus*
Basket rush	*Juncus textilis*
Beaked panicgrass	*Panicum anceps*
Bermudagrass	*Cynodon dactylon*
Big bluestem	*Andropogon gerardii*
Billion-dollar grass	*Echinochloa frumentacea*
Bitter panicgrass	*Panicum amarum*
Blue grama	*Bouteloua gracilis*
Bluebunch wheatgrass	*Pseudoroegneria spicata*
Broomsedge bluestem	*Andropogon virginicus*
Buffalograss	*Buchloe dactyloides*
Bushy bluestem	*Andropogon glomeratus*
California bulrush	*Schoenoplectus californicus*
Canada wildrye	*Elymus canadensis*
Caucasian bluestem	*Bothriochloa bladhii*
Cereal rye	*Secale cereale*
Cheatgrass	*Bromus tectorum*
Common rush	*Juncus effusus*
Common threesquare	*Schoenoplectus pungens*
Cosmopolitan bulrush	*Schoenoplectus maritimus*
Crested wheatgrass	*Agropyron cristatum*
Deergrass	*Muhlenbergia rigens*
Deertongue doc	*Dichanthelium clandestinum*
Desert wheatgrass	*Agropyron desertorum*
Eastern gamagrass doc	*Tripsacum dactyloides*
Fall panicgrass	*Panicum dichotomiflorum*
Field brome	*Bromus arvensis*
Florida paspalum	*Paspalum floridanum*
Hard fescue	*Festuca trachyphylla*
Indian ricegrass	*Achnatherum hymenoides*
Indian woodoats	*Chasmanthium latifolium*
Indiangrass	*Sorghastrum nutans*
Inland saltgrass	*Distichlis spicata*
Intermediate wheatgrass	*Thinopyrum intermedium*
Italian ryegrass	*Lolium perenne* ssp. *multiflorum*

(continued)

Common Grasses of the United States *(continued)*

Common Name	*Scientific Name*
Kentucky bluegrass	*Poa pratensis*
Knotgrass	*Paspalum distichum*
Little bluestem	*Schizachyrium scoparium*
Maidencane	*Panicum hemitomon*
Nutgrass	*Cyperus rotundus*
Orchardgrass doc	*Dactylis glomerata*
Perennial ryegrass	*Lolium perenne*
Prairie cordgrass	*Spartina pectinata*
Purpletop tridens	*Tridens flavus*
Red fescue	*Festuca rubra*
Redtop	*Agrostis gigantea*
Reed canarygrass	*Phalaris arundinacea*
Salt rush	*Juncus lesueurii*
Saltmeadow cordgrass	*Spartina patens*
Sandberg bluegrass	*Poa secunda*
Santa Barbara sedge	*Carex barbarae*
Seashore paspalum	*Paspalum vaginatum*
Siberian wheatgrass	*Agropyron fragile*
Sideoats grama	*Bouteloua curtipendula*
Slender wheatgrass	*Elymus trachycaulus*
Slough sedge	*Carex obnupta*
Smooth brome	*Bromus inermis*
Smooth cordgrass	*Spartina alterniflora*
Snake River wheatgrass	*Elymus wawawaiensis*
Splitbeard bluestem	*Andropogon ternarius*
Streambank wheatgrass	*Elymus lanceolatus*
Switchgrass	*Panicum virgatum*
Tall fescue	*Lolium arundinaceum*
Tall flatsedge	*Cyperus eragrostis*
Tall oatgrass	*Arrhenatherum elatius*
Texas cupgrass	*Eriochloa sericea*
Timothy	*Phleum pratense*
Torpedo grass	*Panicum repens*
Tule	*Schoenoplectus acutus* var. *occidentalis*
Vanilla grass doc	*Hierochloe odorata*
Weeping lovegrass	*Eragrostis curvula*
Western wheatgrass	*Pascopyrum smithii*

Note: ssp. = subspecies; var. = variety

Source: U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA. Accessed April 11, 2002.

The grass fruit, called a caryopsis, or grain, consists of a single seed with its seed coat firmly adherent to the thin fruit wall. Wind plays a major role in dissemination of the fruits. Grasses may germinate, grow, set seed, and die in the same year (*annuals*) or live and produce seed for many years (*perennials*).

Bamboos

The bamboos are perennial, often treelike, grasses belonging to the *Bambusoideae*, a subfamily that is thought to be an early offshoot in the grass family lineage. Bamboo taxonomy is poorly understood. One estimate holds that there are roughly 45 genera and 480 species.

Like other grasses, bamboos have jointed culms, which are hollow except at the nodes, where there are partitions. The culms, which originate from rhizomes, are often called *canes*. The canes are light and elastic. Their hardness is due not to secondary xylem, or wood, as in most trees and shrubs, but rather to scattered fibers in the outer walls of the cane internodes.

Canes of some bamboo species grow at rates as high as a meter a day. The upper nodes of fully elongated culms give rise to small, horizontal branches. Leaves are borne on these branches or on branches of these branches. The blades are narrow and often short. Although some bamboos flower every year, many bloom only at the end of their lifetimes, which may range from 10 to 120 years.

Bamboos are distributed mainly in tropical and subtropical regions, with large concentrations in Asia and South America. A few species reach mild temperate areas. In the United States, there is a single native species, *Arundinaria gigantea*, called cane. It forms canebrakes in southern bottomlands. Bamboos are grown as ornamentals in many parts of the world. Dense bamboo thickets are sometimes planted as living fences or barricades. In Asia, bamboos are very significant economically, providing materials for building, matting, and many other purposes. The young shoots are popular as food in eastern Asia.

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See also: Asian flora; Corn; Erosion and erosion control; European flora; Fruit: structure and types; Grains; Grasslands; North American flora; Pollination; Rice; Savannas and deciduous tropical forests; Wheat.

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GRASSLANDS

Category: Ecosystems

Grasslands are areas of intermittent rainfall which favor grass growth. The grass helps the soil become rich by facilitating the accumulation of nutrients and decaying plant material.

Grasslands once covered about a quarter of the world's land surface. Grasses' growth patterns help enrich the soil immensely. Because their soils become among the world's richest, grasslands are so intensely farmed and grazed that only small patches of natural grassland remain.

Climate and Geographic Location

Annual precipitation between 10 and 32 inches (25-80 centimeters), often with a dry period late in the growing season, supports grassland. Grassland temperature patterns vary. Fire and grazing favor grasses and often combine with climate to maintain grasslands.

Extensive grasslands generally are found in continental interiors. In North America, grasslands occur from the eastern foothills of the Rocky Mountains to the Mississippi River, from south central Canada to northeastern Mexico, in eastern Washington and Oregon, and in California's Central Valley. Grasslands on other continents include the steppes of Europe and Asia, areas fringing the major deserts of Africa and Australia, and the Pampas of South America.

Types of Grasslands

Extensive grasslands are often divided into *tall-grass*, *mixed-grass*, and *short-grass* regions. In prehuman settlement North American grasslands, the tall-grass prairie occurred in the moist eastern zone. Big bluestem, Indian grass, and switch grass grew 6-10 feet (2-3 meters) tall in this region. The short-grass prairie or plains occupied the drier western extreme. There, blue grama and buffalo grass seldom grew taller than 8 inches (20 centimeters). Mixed-grass prairie grew in between, with a mixture of tall, short, and middle-height grasses. Boundaries between regions were broad zones of gradual change.

Grasses and Grasslands

Grasses are well adapted to occupy regions with intermediate annual precipitation, fires, and grazing animals. Grasses have their main center of growth at or below the ground. Their slender, widespread roots compete intensely for nutrients and moisture, especially near the surface. The aboveground parts of the plants grow densely, and the entire aboveground plant dies every year, covering the ground with a dense mulch. These characteristics present difficulties for plants invading grasslands, as the grass roots usurp moisture and nutrients and the leaves and mulch intercept sunlight.

Under very dry conditions, when grasses cannot grow densely, shrubs and succulents (such as cacti) dominate, and deserts occur. With heavy rainfall and infrequent dry periods, trees compete well with grasses, and forests dominate the landscape. Grasslands are often bordered by forests at their moist edges and deserts at their dry boundaries. Under intermediate rainfall conditions, however, grasses are favored over all competitors.

Fire and grazing by animals tip the balance further in favor of the grasses. The late-season dry period typical of grasslands and the mulch built up after a year or more of growth are ideal conditions for the spread of fires. Whether started by lightning or by humans, fires spread quickly through the dried mulch. The tops of plants burn to the ground, but often little damage occurs underground. Because the primary growth center of most nongrass plants is above ground and that of grasses is below ground, fire is more harmful to woody plants and nonwoody, nongrass plants (*forbs*).

Because grazing removes the tops of plants, it does more damage to forbs and woody plants than to grasses. Many grasses actually increase growth after light grazing. Most extensive grasslands are occupied by large grazing animals, such as the bison and pronghorn of North American grasslands. These and other grazers played important roles in the maintenance of the native grasslands and in the lives of the people who lived there.

Grassland Soils

The presence of grasslands is determined by climate, fire, and grazing, but grasses impact their environment as well. In addition to their competitive role in excluding trees, shrubs, and forbs, grasses contribute to soil formation. All the aboveground parts of grass plants die each year, become mulch, and slowly decompose into the soil. Rainfall is generally insufficient to wash nutrients out of the reach of the grass roots, so the soil accumulates both nutrients and decaying plant material. The world's richest soils develop under these conditions.

Human Impact on Grasslands

Because of their soils, grasslands became agricultural centers. Domestic grasses became the predominant crops—corn in the tall-grass country and wheat in the mixed-grass region. The short-grass plains were too dry to support grain crops but became an important region for grazing domestic animals.

In the process of learning what activities the grasslands could and could not support, Americans changed the grasslands of the continent forever. Farming reduced native tall-grass prairie to one of the world's rarest habitats. Although grazing had less impact on the short-grass plains, vast areas have been *overgrazed* severely. Grasslands in other parts of the world have been similarly abused. Given the importance of grasslands to humanity, serious conservation measures must be taken to restore their productivity.

Carl W. Hoagstrom

See also: Biomes: types; Grasses and bamboos; Grazing and overgrazing; Rangeland.

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GRAZING AND OVERGRAZING

Categories: Animal-plant interactions; economic botany and plant uses; environmental issues; soil

Animals that eat grass, or graze, can actually help the earth produce richer land cover and soil. When the land suffers ill effects because of too much grazing, overgrazing has occurred.

The effects of overgrazing occur where there are more grazing animals than the land and vegetation can support. Overgrazing has negatively affected regions of the United States, primarily in the Southwest. Areas that have been severely damaged by overgrazing typically show declining or endangered plant and animal species.

Herbivores are animals that feed on plant material, and grazers are herbivores that feed specifically on grass. Examples are horses, cows, antelope, rabbits, and grasshoppers. Overgrazing occurs when grazer populations exceed the *carrying capacity* of a specified area (the number of individual organisms the resources of a given area can support). In overgrazing conditions, there is insufficient food to support the animal population in question. Depending on the grazer's strategy, emigration or starvation will follow. Grasslands can handle, and even benefit from, normal grazing; only overgrazing adversely affects them.

Grasses' Defenses Against Grazing

Grasslands and grazers coevolved, so grasses can withstand grazing within the ecosystem's carrying capacity. All plants have a site of new cell growth called the meristem, where growth in height and girth occurs. Most plants have the meristem at the very top of the plant (the apical meristem). If a plant's apical meristem is removed, the plant dies.

If grasses had an apical meristem, grazers—and lawn mowers—would kill grasses. Grasses survive mowing and grazing because the meristem is located at the junction of the shoot and root, close to the ground. With the exception of sheep, grazers in North America do not disturb the meristem, and sheep do so only during overgrazing conditions. At proper levels of grazing, grazing actually stimulates grass to grow in height in an attempt to produce a flowering head for reproduction. Grazing also stimulates grass growth by removing older plant tissue at the top that is functioning at a lower photosynthetic rate.

Grazers

Mammalian grazers have high, crowned teeth with a great area for grinding to facilitate opening of plants' cell walls as a means to release nutrients. The cell wall is composed of cellulose, which is very difficult for grazers to digest. Two major digestive systems of grazing strategies have evolved to accommodate grazing. *Ruminants*, such as cows and sheep, evolved stomachs with four chambers to allow regurgitation in order to chew food twice to maximize cellulose breakdown. Intestinal bacteria digest the cellulose, releasing fatty acids that nourish the ruminants. Other grazers, such as rabbits and horses, house bacteria in the cecum, a pouch at the junction of the small and large intestines. These bacteria ferment the plant material ingested. The fermented products of the bacteria nourish these grazers.

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Impacts in the Southwest

As previously mentioned, in the United States the negative effects of overgrazing are most intense in the Southwest. Some ecologists believe that one significant factor was the pattern of early European colonization of the area. Missions were abundant in the Southwest, and the missions owned cattle that were rarely slaughtered, except on big feast days. Because Catholic missionaries received some financial support from their religious orders in Europe, mission cattle were not restrained as strictly as were

Image Not Available

gions where certain species have been removed. Desertification is the intensification and expansion of deserts at the expense of neighboring grasslands. When overgrazing occurs along desert perimeters, plant removal leads to decreased shading. Decreased shading increases the local air temperature. When the temperature increases, the air may no longer cool enough to release moisture in the form of dew. Dew is the primary source of precipitation in deserts, so without it, desert conditions intensify. Even a slight decrease in desert precipitation is serious. The result is hotter and drier conditions, which lead to further plant loss and potentially to monocultures.

Overgrazing of grasslands, combined with the existence of nonnative species in an ecosystem, can result in the endangerment of species of native grasses. At one time, cattle in the Southwest fed exclusively on native grasses. Then nonnative plant species arrived in the New World in the guts of cows shipped from Europe. They began to compete with the native grasses. European grass species have seeds with prickles and burs; southwestern native grasses do not, making them softer and more desirable to the cattle. Hence European grasses experienced little, if any, grazing, while the much more palatable southwestern native grasses were grazed to the point of overgrazing. The result was drastic decline or loss of native grassland species. In such cases animals dependent on native grassland species must emigrate or risk extinction. For example, many ecologists conjecture that the Coachella Valley kit fox in California is threatened because of the loss of grassland habitat upon which it is dependent.

Solutions

Desertification is usually considered irreversible, but the elimination of grazing along desert perimeters can help to prevent further desertification. One kind of attempt to reestablish native grass species involves controlled-burn programs. Nonnative grassland species do not appear to be as fire-resistant as native grass species. Controlled burn programs are therefore being used in some overgrazed grassland areas to try to eliminate nonnatives and reestablish native grass species. If successful, such programs will improve the health of the ecosystem.

Jessica O. Ellison

See also: Biological invasions; Grasses and bamboos; Grasslands; Sustainable agriculture.

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GREEN ALGAE

Categories: Algae; *Protista*; taxonomic groups; water-related life

The green algae are a diverse group of eukaryotic organisms classified in the phylum Chlorophyta. *They are considered eukaryotic because individual cells possess a prominent structural feature known as a nucleus, which houses the chemicals responsible for heredity and metabolic regulation. The phylum is one of several algal phyla in the kingdom* Protista, *where algae are grouped based upon pigmentation, carbohydrate storage reserves, and cell wall composition.*

Green algae are found in moist soils and freshwater and saltwater habitats; most are believed to be freshwater-dwelling. The phylum consists of at least eight thousand species. Some estimates place this number at seventeen thousand species. Several shared characteristics support the hypothesis that these organisms and terrestrial plants derived from a common ancestor.

General Characteristics

The green algae, or chlorophytes, may be unicellular, multicellular, colonial, or filamentous. Multicellular forms may demonstrate some tissue differentiation but not to the complexity displayed by terrestrial plants. Colonial algae tend to cluster in a pattern resembling a hollow sphere or disc. Some filamentous forms are coenocytic, meaning they have lost a portion or all of their cross walls.

The cell walls consist of cellulose. There are usually two layers of cellulose fortified by pectin. Some unicellular forms have a lorica (thin wall or cuticle), which is separated from the protoplast by a gelatinous matrix or water.

The phylum *Chlorophyta* is named for the prominent green chloroplast, a cell structure containing pigments that carry out photosynthesis, similar to that found in higher plants. The chloroplasts are green because the accessory pigments, which include xanthophylls and various carotenoids, do not mask the chlorophylls, the principal photosynthetic pigments, present. All classes contain chlorophylls *a* and *b*. Chlorophyll *c* has been found in a few species of the class *Prasinophyceae*. The chloroplasts are double-membraned structures with thylakoids (membranous folds) stacked in groups of from two to six.

The storage carbohydrate is starch. Starch grains can be found clustered around pyrenoids (protein bodies), if they are present. However, they are found generally scattered throughout the fluid portion of the chloroplast. Chlorophytes possess either two or four flagella (whiplike appendages for motility) at least once during their life cycle, although some forms have a single flagellum. In addition to providing motility, flagella may play a key role in the sexual process for some unicellular forms.

There is considerable debate over the classification of green algae. Most taxonomists currently classify *Chlorophyta* in the kingdom *Protista*. Because of the many similarities to terrestrial plants, many taxonomists feel that *Chlorophyta* should have its own kingdom. Living species of charophytes are grouped into three classes: *Chlorophyceae*, *Charophyceae*, and *Ulvophyceae*.

Chlorophyceae

The class *Chlorophyceae* is the largest in terms of the number of species listed. Members have two or more flagella; a diverse array of sexual and asexual reproductive strategies; production of a zygospore following sexual reproduction; and mitosis that involves phycoplasts (microtubules that separate daughter nuclei during division). Representative genera include *Chlamydomonas*, *Pandorina*, *Volvox*, and *Gonium*.

Chlamydomonas species are unicellular, with two apical flagella and a cup-shaped chloroplast. *Gonium* is a colonial species with four or more cells with no functional or morphological differentiation. *Pandorina* species form spherical colonies with limited differentiation and structural organization. Colonies of *Volvox* can consist of up to sixty thousand cells and demonstrate some structural specialization. Portions of the colony have cells with large flagella and stigmata. These cells appear to be specialized for colony motility. The posterior region consists of cells with small flagella and no stigmata. These seem to be responsible for reproduction.

Charophyceae

Charophyceae contains asymmetrical cells that may or may not be motile. Motile cells have two apical flagella. Sexual reproduction is characterized by the formation of a zygospore and zygotic meiosis. This class is similar to land plants in that nuclear envelopes dissolve during mitosis, which is not the case for the other two classes. The genus *Chara* includes members that resemble vascular plants. Chara species have a central axis and branchlike extensions. These organisms demonstrate apical growth that begins with an apical cell, which is analogous to the apical meristems of terrestrial plants. *Spirogyra* is a well-known filamentous genus that is distinguished by spiral chloroplasts. Sexual reproduction is characterized by the formation of a conjugation filament between two cells that allows for gamete transfer.

Ulvophyceae

Ulvophyceae is a diverse class of primarily marine organisms that can consist of small colonial forms, filamentous forms, thin sheets of cells, or coenocytic complexes. Reproduction is by alternation of generations, with meiosis occurring in spores. There may be two or more flagella, if flagella are present. The genus *Ulva*, also known as sea lettuce, displays a green sheet of cells that are found in intertidal waters. Reproduction involves an isomorphic alternation of generations. *Ulothrix* contains freshwater filamentous algae that can attach to surfaces via a holdfast. Ulothrix asexually generates zoospores and aplanospores. Species are able to reproduce sexually by formation of a heterothallic zygote/zygospore from isogamous gametes.

Reproductive Strategies

Chlorophytes reproduce sexually, which involves alternating haploid (organisms with half the complete chromosome set) and diploid stages. *Haplobiontic* haploid organisms consist of mature haploid forms that produce gametes by mitosis (division resulting in offspring cells identical to the parent form). Compatible gametes fuse and form a diploid zygote, which divides by meiosis (division resulting in four haploid offspring cells) to form four spores. A haplobiontic diploid organism consists of mature diploid forms that produce gametes by meiosis. *Diplobiontic* green algae are more complex, with a zygote undergoing mitosis. This results in the formation of a haploid and diploid thalli. The haploid thallus is referred to as the gametophyte, and the diploid thallus is referred to as the sporophyte. Gametophytes generate gametes, while sporophytes produce spores. This pattern is referred to as an alternation of generations.

The thalli may be identical (isomorphic) or different (heteromorphic). If a thallus produces both sperm and eggs, it is considered homothallic. If the egg and sperm are produced on separate thalli, the organism is heterothallic. Gametes may be isogamous (indistinguishable and motile) or heterogamous (two distinct types). Male gametes develop in gametangia known as antheridia. Female gametes develop in either oogonia (single-celled gametangia) or archegonia (multicelled gametangia). Zygotes often form thick-walled resting structures called zygospores.

The most common type of spore is the zoospore, which is a flagellated cell. Cells can form single zoospores or divide mitotically to produce many zoospores. Zoospores mature into vegetative cells within minutes or days, depending upon the species. Vegetative cells may or may not keep their flagella. Zoospores are typically formed in compartments called sporangia but may be formed following meiosis in a zygote. Most zoospores resemble members of the chlorophyte genus *Chlamydomonas*. Thick-walled, nonmotile spores called akinetes may be formed and can produce zoospores via mitosis or form filamentous structures. Some chlorophytes form aplanospores, which are nonmotile.

Ecology

Chlorophytes are found in diverse habitats all over the world. While most inhabit temperate, freshwater environments, marine and terrestrial forms also exist. Terrestrial forms include some living on moist soils, some on moist rocks, and some in snow-covered areas. Some terrestrial forms are specialized as *lichens*, a close association between an alga and a fungus, or living on animals such as turtles or sloths.

Because they are photoautotrophic, capable of making their own carbohydrates using sunlight energy, chlorophytes are critical to life on earth. Green algae are the planet's largest food source. They fix approximately 1,010 tons of carbon per year. As a result, they also contribute significantly to oxygen production.

Stephen S. Daggett

See also: Algae; Brown algae; *Charophyceae*; *Chlorophyceae*; Chrysophytes; Cryptomonads; Diatoms; Eutrophication; Evolution of plants; Lichens; Marine plants; Photosynthesis; Phytoplankton; *Protista*; Red algae; *Ulvophyceae*.

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GREEN REVOLUTION

Categories: Agriculture; economic botany and plant uses; food; history of plant science

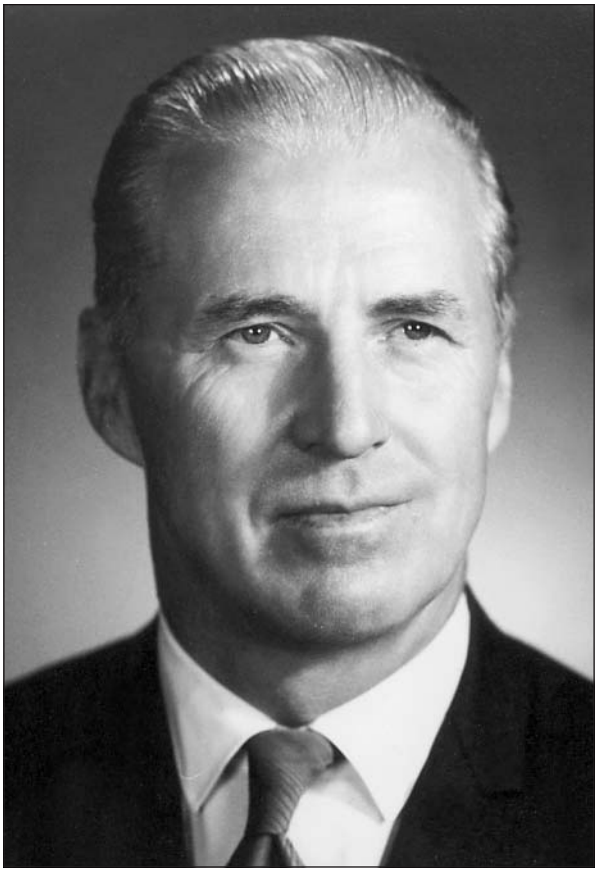
The Green Revolution implemented advances in agricultural science to raise food production levels, particularly in developing countries. These advances are associated with the spreading use of high-yield varieties (HYV) of wheat, rice, and corn developed through advanced methods of genetics and plant breeding.

Yield Increases

The Green Revolution can be traced back to a 1940 request from Mexico for technical assistance from the United States to increase wheat production. By 1944, with the financial support of the Rockefeller Foundation, a group of U.S. scientists were researching methods of adapting the new high-yield variety (HYV) wheat that had been successfully used on American farms in the 1930's to Mexico's varied environments. A major breakthrough is attributed to Norman Borlaug, who by the late 1940's was director of the research in Mexico. For his research and work in the global dissemination of the Mexican HYV wheat, Borlaug won the 1970 Nobel Peace Prize.

From wheat, research efforts shifted to rice production. Through the work of the newly created International Rice Research Institute in the Philippines, an HYV rice was developed. This so-called miracle rice was widely adopted in developing countries during the 1960's. Later research has sought to spread the success of the Green Revolution to other crops and to more countries.

Approximately one-half of the yield increases in food crops worldwide since the 1960's are attributable to the Green Revolution. Had there not been a Green Revolution, the amount of land used for agriculture would undoubtedly be higher today, as would the prices of wheat, rice, and corn, three crops that account for more than 50 percent of total human energy requirements. There is a concern, however, that the output benefits of the Green Revolution have had some negative equity and environmental effects.



Norman Borlaug was awarded the Nobel Peace Prize in 1970 for his research and work in the global dissemination of the Mexican high-yield varieties of wheat.

Equity and Environmental Issues

The Green Revolution has promoted input-intensive agriculture, which has, in turn, created several problems. In theory, a small-scale farmer will get benefits from planting the HYV seeds that are similar to those reaped by a large farm. In practice, however, small-scale farmers have had more difficulty in gaining access to Green Revolution technology. To use the new seeds, fields need adequate irrigation and the timely application of chemical fertilizers and pesticides. In many developing countries, small-scale farmers' limited access to credit makes the variety of complementary inputs difficult to obtain. Greater use of fertilizers is associated with rising nitrate levels in water supplies. Pesticides have been linked to community health problems. Long-term, intensive production has resulted in compaction and salinization of soil and other problems.

Because agriculture is increasingly dependent on fossil fuels, food prices have become more strongly linked to energy supplies of this type. This issue raises concerns about the sustainability of the new agriculture. Biotechnological approaches to generating higher yields, the expected future path of the Green Revolution, will raise an additional set of equity and environmental concerns.

Bruce Brunton

See also: Agriculture: modern problems; Agriculture: world food supplies; Corn; Genetically modified foods; Grains; High-yield crops; Hybridization; Rice; Sustainable agriculture; Wheat.

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GREENHOUSE EFFECT

Categories: Environmental issues; pollution

The greenhouse effect is a natural process of atmospheric warming in which solar energy that has been absorbed by the earth's surface is reradiated and then absorbed by particular atmospheric gases, primarily carbon dioxide and water vapor. Without this warming process, the atmosphere would be too cold to support life. Since 1880, however, the surface atmospheric temperature appears to be rising, paralleling a rise in the concentration of carbon dioxide and other gases produced by industrial activities.

Since 1880, carbon dioxide, along with several other gases—chlorofluorocarbons (CFCs), methane, hydrofluorocarbons (HFCs), perfluorocarbons (PFCs), sulfur hexafluoride, and nitrous oxide—have been increasing in concentration and have been identified as likely contributors to a rise in global surface temperature. These gases are called *greenhouse gases*. The temperature increase may lead to drastic changes in climate and food production as well as widespread coastal flooding. As a result, many scientists, organizations, and governments have called for curbs on the production of greenhouse gases. Since the predictions are not definite, however, debate continues about the costs of reducing the production of these gases without being sure of the benefits.

Global Warming and Human Interference

The greenhouse effect occurs because the gases in the atmosphere are able to absorb only particular wavelengths of energy. The atmosphere is largely transparent to short-wave solar radiation, so sunlight basically passes through the atmosphere to the earth's surface. Some is reflected or absorbed by clouds, some is reflected from the earth's surface, and some is absorbed by dust or the earth's surface. Only small amounts are actually absorbed by the atmosphere. Therefore, sunlight contributes very little to the direct heating of the atmosphere. On the other hand, the greenhouse gases are able to absorb long-wave, or infrared, radiation from the earth, thereby heating the earth's atmosphere.

Discussion of the greenhouse effect has been confused by terms that are imprecise and even inaccurate. For example, the atmosphere was believed to operate in a manner similar to a greenhouse, whose glass would let visible solar energy in but would also be a barrier preventing the heat energy from leaving. In actuality, the reason that the air remains warmer inside a greenhouse is probably because the glass prevents the warm air from mixing with the cooler outside air. Therefore the greenhouse effect could be more accurately called the "atmospheric effect," but the term greenhouse effect continues to be used.

Even though the greenhouse effect is necessary for life on earth, the term gained harmful connotations with the discovery of apparently increasing atmospheric temperatures and growing concentrations of greenhouse gases. The concern, however, is not with the greenhouse effect itself but rather with the intensification or enhancement of the greenhouse effect, presumably caused by increases in the level of gases in the atmosphere resulting from human activity, especially industrialization. Thus the term *global warming* is a more precise description of this presumed phenomenon.

A variety of other human activities appears to have contributed to global warming. Large areas of natural vegetation and forests have been cleared for agriculture. The crops may not be as efficient in absorbing carbon dioxide as the natural vegetation they replaced. Increased numbers of livestock have led to growing levels of methane. Several gases that appear to be intensifying global warming, including CFCs and nitrous oxides, also appear to be involved with *ozone depletion*. Stratospheric ozone shields the earth from solar ultraviolet (short-wave) radiation; therefore, if the concentration of these ozone-depleting gases continues to increase and the ozone shield is depleted, the amount of solar radiation reaching the earth's surface should increase. Thus, more solar energy would be intercepted by the earth's surface to be reradiated as long-wave radiation, which would presumably increase the temperature of the atmosphere.

However, whether there is a direct cause-and-effect relationship between increases in carbon dioxide and the other gases and surface temperature may be impossible to determine because the atmosphere's temperature has fluctuated widely over millions of years. Over the past 800,000 years, the earth has had several long periods of cold temperatures—during which thick ice sheets covered large portions of the earth—interspersed with shorter warm periods. Since the most recent retreat of the glaciers around ten thousand years ago, the earth has been relatively warm.

Problems of Prediction

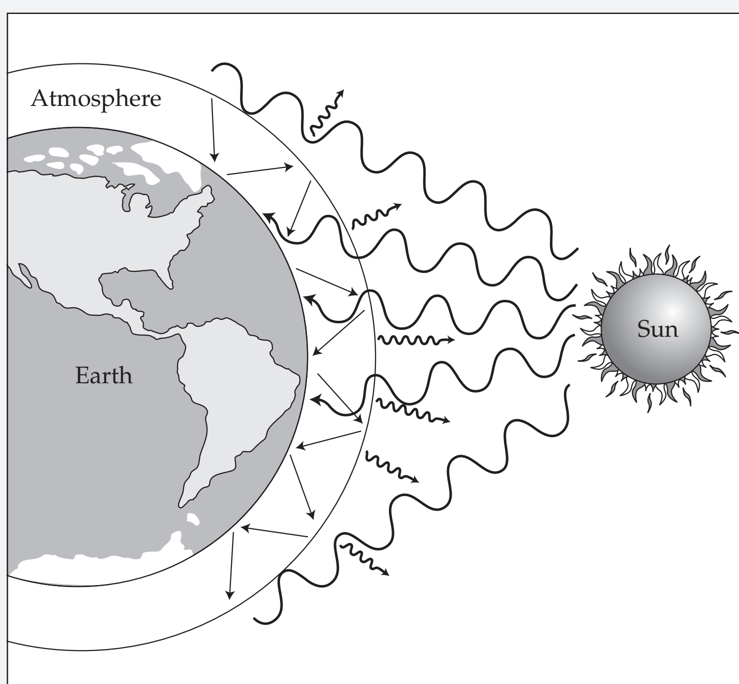
How much the temperature of the earth might rise is not clear. So far, the temperature increase of around 1 degree Fahrenheit is within the range of normal (historic) trends. The possibility of global warming became a serious issue during the late twentieth century because the decades of the 1980's and the 1990's included some of the hottest years recorded for more than one century. On the other hand, warming has not been consistent since 1880, and for many years cooling occurred. The cooling might have resulted from the increase of another product of fossil fuel combustion, sulfur dioxide aerosols, which reflect sunlight, thus lessening the amount of solar energy entering the atmosphere. Similarly, in the early 1990's temperatures declined, perhaps because of ash and sulfur dioxide produced by large volcanic explosions. In the late 1990's temperatures appeared to be rising again, thus indicating that products of volcanic explosions may have masked the process of global warming. The United States Environmental Protection Agency (EPA) states that the earth's average temperature will probably continue to increase because the greenhouse gases stay in the atmosphere longer than the aerosols.

Proper analysis of global warming is dependent on the collection of accurate temperature records from many locations around the world and over many years. Because human error is always possible, "official" temperature data may not be accurate. This possibility of inaccuracy compromises examination of past trends and predictions for the future. However, the use of satellites to monitor

The Greenhouse Effect

Clouds and atmospheric gases such as water vapor, carbon dioxide, methane, and nitrous oxide absorb part of the infrared radiation emitted by the earth's surface and reradiate part of it back to the earth. This process effectively reduces the amount of energy escaping to space and is popularly called the "greenhouse effect" because of its role in warming the lower atmosphere. The greenhouse effect has drawn worldwide attention because increasing concentrations of carbon dioxide from the burning of fossil fuels may result in a global warming of the atmosphere.

Scientists know that the greenhouse analogy is incorrect. A greenhouse traps warm air within a glass building where it cannot mix with cooler air outside. In a real greenhouse, the trapping of air is more important in maintaining the temperature than is the trapping of infrared energy. In the atmosphere, air is free to mix and move about.



U.S. Greenhouse Gas Emissions, 1990-1999

Type	*1990*	*1994*	*1995*	*1996*	*1997*	*1998*	*1999*
Carbon dioxide (carbon)[1]	1,350.5	1,422.5	1,434.7	1,484.1	1,505.2	1,507.4	1,526.8
Methane gas[1]	31.74	31.17	31.18	30.16	30.11	29.29	28.77
Nitrous oxide[2]	1,168	1,310	1,257	1,246	1,226	1,223	1,224
Chloroflurocarbons[2]	202	109	102	67	51	49	41
Halons[2]	2.8	2.7	2.9	3.0	3.0	3.0	3.0
Hydrofluorocarbons[2]							
HFC-23	3.0	3.0	2.0	3.0	3.0	3.4	2.6
HFC-125	(Z)	0.3	0.5	0.7	0.9	1.1	1.3
HFC-134a	1.0	6.3	14.3	19.0	23.5	26.9	30.3
HFC-143a	(Z)	0.1	0.1	0.2	0.3	0.5	0.7
Perfluorocarbons[2]							
CF-4	3	2	2	2	2	2	2
C-2F-6	1	—	1	1	1	1	1
C-4F-10	(Z)	(Z)	(Z)	(Z)	(Z)	(Z)	(Z)
Sulfur hexafluoride[2]	1	1	2	2	2	2	1

Note: Emission estimates were mandated by Congress through Section 1605(a) of the Energy Policy Act of 1992 (Title XVI). Gases that contain carbon can be measured either in terms of the full molecular weight of the gas or just in terms of their carbon content.

1. In millions of metric tons.

2. In thousands of metric tons.

Z. Less than 500 metric tons.

— Represents or rounds to zero.

Source: Abridged from U.S. Energy Information Administration, *Emissions of Greenhouse Gases in the United States*, annual. From *Statistical Abstract of the United States: 2001* (Washington, D.C.: U.S. Census Bureau, 2001).

temperatures has probably increased the reliability of the data.

Predictions for the future are hampered in various ways, including lack of knowledge about all the components affecting atmospheric temperature. Therefore, computer programs cannot be sufficiently precise to make accurate predictions. A prime example is the relationship between ocean temperature and the atmosphere. As the temperature of the atmosphere increases, the oceans would absorb much of that heat. Therefore, the atmosphere might not warm as quickly as predicted. However, the carbon dioxide absorption capacity of oceans declines with temperature. Therefore, the oceans would be unable to absorb as much carbon dioxide as before, but exactly how much is unknown. Increased ocean temperatures might also lead to more plant growth, including phytoplankton. These plants would probably absorb carbon dioxide through photosynthesis. A warmer atmosphere could hold more water vapor, resulting in the potential for more clouds and more precipitation. Whether that precipitation would fall as snow or rain and where it would fall could also affect air temperatures. Air temperature could lower as more clouds might reflect more sunlight, or more clouds might absorb more infrared radiation.

To complicate matters, any change in temperature would probably not be uniform over the globe. Because land heats up more quickly than water, the Northern Hemisphere, with its much larger landmasses, would probably have greater temperature increases than the Southern Hemisphere. Similarly, ocean currents might change in both direction and temperature. These changes would affect air temperatures as well. In reflection of these complications, computer models of temperature change range widely in their estimates. Predicted increases range from 1.5 to 11 degrees Celsius (3 to 20 degrees Fahrenheit) over the early decades of the twenty-first century.

Mitigation Attempts

International conferences have been held, and international organizations have been established to research and minimize potential detriments of global warming. In 1988 the United Nations Environment Programme and the World Meteorological

Organization established the International Panel on Climate Change (IPCC). The IPCC has conducted much research on climate change and is now considered an official advisory body on the climate change issue. In June, 1992, the United Nations Conference on Environment and Development, or Earth Summit, was held in Brazil. Participants devised the Framework Convention on Climate Change, considered the landmark international treaty. It required signatories to reduce and monitor their greenhouse gas emissions.

A more advanced agreement, the Kyoto Accords, was developed in December, 1997, by the United Nations Framework Convention on Climate Change. It set binding emission levels for all six greenhouse gases over a five-year period for the developed world. Developing countries do not have any emission targets. It also allows afforestation to be used to offset emissions targets. The Kyoto agreement includes the economic incentive of trading emissions targets. Some countries, because they have met their targets, would have excess permits, which they might be willing to sell to other countries that have not met their targets.

Margaret F. Boorstein

See also: Acid precipitation; Air pollution; Carbon cycle; Climate and resources; Ozone layer and ozone hole debate; Photorespiration; Rain forests and the atmosphere; Respiration.

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GROWTH AND GROWTH CONTROL

Category: Physiology

The processes of primary and secondary growth take a plant from early cell division to its adult form. Growth control factors regulate these processes.

Plant growth is of two distinct types: *primary growth* and *secondary growth*. Primary growth results in increased length of stems or roots. Secondary growth increases the width of the plant and allows differentiation of cells into various distinct tissue types. Both types of growth occur in plant tissues called *meristems*. A meristem consists of tissue where extensive cell division takes place, and thus plant growth. There are two general types of meristems. Primary growth occurs at the *apical meristems*, and secondary growth occurs at the *lateral meristems*, which are known as the *vascular cambium* and the *cork cambium*.

Meristems

Apical meristems are located at the growing tips of the plant; there are apical meristems in the roots and in the buds on shoots of the aboveground part of the plant. New cells produced at the meristems are initially undifferentiated. They enlarge in the adjacent *zone of elongation*, mostly by increasing their water content. These cells eventually differentiate into the plant's primary tissue types: *dermal*, *vascular tissue*, and *ground tissues*.

Other meristematic tissue occurs along the stem, and lateral buds are capable of producing branches with their own meristems, but most elongation occurs from the apical meristem. Apical dominance prevents excessive branching and in some plants prevents all branching. If the apical meristem is removed by removing the end of the stem, the lateral buds will be released from apical dominance, and greater branching results. Eventually, one of the lateral meristems will grow more than the others and will impose apical dominance, becoming the new apical meristem.

Secondary growth increases the girth (diameter) of the stems and roots of woody plants. Lateral growth of the vascular cambium produces new vascular tissue, called secondary *xylem* and *phloem*. In trees and shrubs, this continual lateral growth produces wood. Cork cambium produces cells at the outer edges of roots and stems. At maturity these cells are dead and form the bark, their primary function being structural support and protection. The walls of cork cells contain a protective waxy substance called *suberin*.

Gametophytes and Sporophytes

All vascular plants, as well as mosses and liverworts and many algae, display a type of life cycle referred to as *alternation of generations*, which involves two distinct life-forms, the *gametophyte* and *sporophyte*. The sporophyte generation is genetically diploid and, as the name implies, produces spores by meiosis. Spores germinate and develop into gametophytes, which are genetically haploid and produce gametes (eggs and sperm) by mitosis. Sporophytes are larger than gametophytes and represent the dominant, or more noticeable, generation and typically live much longer than gametophytes. Trees, shrubs, herbs, and ferns all represent sporophytes. Gametophytes are extremely small by comparison and are therefore unknown to most nonscientists. They are free-living in ferns as tiny, heart-shaped masses of cells that grow on or just under the surface of the soil and are often smaller than the letters on this page. In flowering plants and gymnosperms, gametophytes are enclosed in the reproductive tissues of flowers and cones on the sporophytes that later develop into seeds. In mosses and liverworts, gametophytes are larger and represent the dominant generation, and the sporophyte grows from the structure on the end. Algae are more diverse. In some groups both gametophytes and sporophytes are indistinguishable, whereas in other groups one or the other is larger.

Both the gametophyte and the sporophyte develop from single cells—the *spores* and the *zygotes*, respectively. In seed plants, the first cell division of the zygote often defines the root cell line (or its equivalent) and the stem cell line (or its equivalent). The body produced by this early development is initially linear in many cases, laying out the primary axis of the plant body. The embryo grows from the zygote and as it matures is included in integuments that develop into the seed coat. A primary root and primary stem grow from a root apical meristem and a shoot apical meristem, respectively.

Primary and Secondary Tissue

In many species, the new cells in the sporophyte are produced primarily by the division of apical meristems, thus consisting almost exclusively of primary tissues. There are, however, some plants in which the sporophytes grow in girth. Some of these—such as the *calamites* (giant horsetails), the *Lepidodendron* (tree lycopods), and the seed ferns—are known only from the fossil record. Others are the trees and shrubs, so-called woody plants, that characterize the modern forests.

The wood of woody plants is composed almost entirely of secondary xylem—xylem that is not derived from the apical meristems but instead grows from the vascular cambium, a cylindrical meristem located under the bark. The bark of woody plants, also a secondary tissue, is composed of phloem and corky layers. The corky layers develop from a second cylindrical meristem, the cork cambium.

In addition to the secondary tissues, many plants as they grow produce secondary organs: branch stems and branch roots. These secondary organs are not derived from the original axis of the plant. In the early stages of their growth they are composed of primary tissues that are essentially identical to the primary tissues of primary organs. Cambial growth will produce secondary tissues in these branch stems and roots. The patterns of secondary tissue formation determine the form of the wood and bark of woody species. The patterns of secondary organ formation determine the architecture of the plant: the shape of the crown and the root system. This architecture plays an important role in the ability of the plant to compete for sunlight, water, and soil nutrients.

Growth Control

The patterns of secondary organ formation are controlled both by genetic factors and by environmental conditions. Horticulturists use plants as a source of dwarfing stocks that have a genetic predisposition to form branches early. In many cases, the dwarfing results from a failure of the stem to elongate in the *internodes* (the regions between the nodes, where leaves and lateral branches originate). Dwarfing appears to be particularly influenced by plant hormones called gibberellins, which stimulate internodal elongation in *dicots*. The effect of gibberellins is also influenced by the concentration of the other hormones within the plant.

Likewise, the architecture of columnar plants is under genetic and hormonal control. The Lombardy poplar, for example, has greatly reduced branching compared to the European poplar. This elongation

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Many plants as they grow produce secondary organs: branch stems and branch roots. These secondary organs are not derived from the original axis of the plant. The patterns of secondary organ formation determine the architecture of the plant: the shape of the crown and the root system. This architecture plays an important role in the ability of the plant to compete for sunlight, water, and soil nutrients.

of the principal axis is similar to that found in forest trees growing in the shade of the surrounding forest. The shaded environment stimulates the growth of the main axis of many tree species while inhibiting growth of the secondary stems. As a result, the stem reaches above the surrounding trees and is better able to compete for light.

The inhibition of secondary stem formation seems to be influenced primarily by hormones called auxins. High auxin concentrations inhibit the development of secondary stems, while low auxin levels stimulate the formation of branches. In some species, high cytokinin levels also stimulate secondary stem growth. Because cytokinins are produced in large quantities in the root tips, and auxins are produced in large quantities in the stem tip, the relationship between these two chemicals reflects the balance between the root system and the stem system.

Less is known about the mechanisms of control of branching in the root system. Some species, especially *monocots*, have many secondary roots of approximately equal size. Others have dominant primary roots, called *taproots*, with little development of secondary roots. Carrots carry this pattern to an extreme.

The pattern of secondary tissue formation is determined by an interplay between genetic factors and environmental conditions. Many plants complete their life cycles in a single year. This quick passage from seed to seed is under genetic control. Annuals rarely develop woody tissue; perennials survive many seasons and show increases in stem girth throughout their lives.

The annual rings seen in the cross-section of a tree are a result of seasonal variations in the production of secondary xylem. Variations in the thickness of annual rings are the result of genetic controls and environmental factors such as mean temperature, damage from insect pests or other pathogens, and water and nutrient availability. Even wind can have significant effects. Strong prevailing winds cause an effect called wind pruning, which results in reduced branching and shorter distances between the annual rings on the windward side.

Secondary tissues are extraordinarily complex. The patterns of cell division, apparently under genetic control, are influenced by a whole concert of hormones. Hormonal gradients and seasonal gradients of sugars and amino acids may play a role in these patterns of secondary tissue formation. The activity of mature phloem tissues and the concentrations of auxins, gibberellins, cytokinins, and perhaps of the gaseous hormone ethylene may all be important in regulating the activity of the cambia.

Craig R. Landgren, updated by Bryan Ness

See also: Angiosperm life cycle; Germination and seedling development; Hormones; Plant life spans; Plant tissues; Roots; Seeds; Shoots; Stems.

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text places plant growth in context of the biology of plants and places plants in context with the living and nonliving world. Chapter 31, "Vascular Plant Structure," provides a simple review of plant cell types, tissues, and organs. Chapter 32, "Plant Development," deals clearly with many questions concerning growth and growth controls.

GROWTH HABITS

Categories: Angiosperms; gardening; physiology

Plant habit, also known as plant life form, is the characteristic shape, appearance, or growth form of a plant species. It develops from specific genetic patterns of growth in combination with environmental factors and is part of the organization of every plant.

Growth of Plants

Development of a plant body is accomplished through growth, defined as increase in number of cells and size of a species. Rates of growth in plants are achieved in two ways: first, by *geometric increase*, in which all cells of the organism divide simultaneously, especially in a young embryonic plant; second, by *arithmetic increase*, in which only one cell undergoes division, especially in mature plants with localized growth in a region at the root and shoot apices. Generally, plants grow by a combination of both kinds of cell division to produce variations of form that finally develop a specific *habit* that is unique to a particular plant species.

Evolution of Growth Habits

The primary purpose for the evolution of different growth habits in plants is adaptation for permanent survival and reproduction of new individuals, typically under changing climatic conditions. Water availability, especially during the growing season, is the single most important environmental factor that limits plant distribution and productivity on a global basis. Competition in the past among plants for available water, nutrients, space, and light enhanced the evolution of adaptive growth forms in plants.

Some plants developed wood as a mechanism to counteract the destructive effects of wind, ice, mechanical damage, and fire. *Erect* and *dense* growth habits evolved to resist wind effects and other mechanical damages. Plants without wood adapted *prostrate*, *mat-forming*, *spreading*, *creeping*, or *climbing* habits.

As animals interacted with plants and in the past, both evolved simultaneously. Various plants developed prostrate and mat-forming habits in

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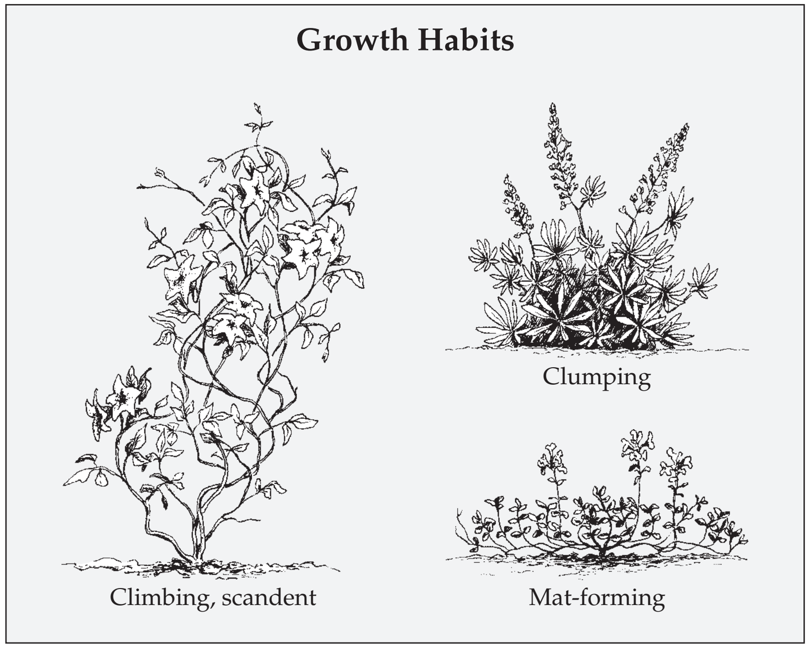
order to endure intense grazing and trampling, or erect and tall growth forms to escape browsing and grazing.

In the past, individual plants that were able to adapt, survive, and produce more offspring were selected naturally for success. Different plants with varied growth habits colonized different habitats, becoming the dominant plants (largest or most abundant), and thereby the principal contributors in characterizing and sustaining different biomes. The various kinds of growth habits which evolved result in a variety of forms. It is not uncommon for one species of plant to exhibit growth habits among its different varieties.



Three common growth habits, genetically determined forms of growth influenced by availability of light and water, wind exposure, soil conditions, and other environmental factors. There are many more such forms, including those shown above as well as erect, dense, prostrate, spreading, stemless, mounding, trailing, and other forms.

Climbing Plants

Climbing plants are also called *vines*. The stems trail along or coil around other plants or structures as they grow upward. Examples include cucumber (*Cucumis sativus*), morning glory (*Ipomea* species), and grape vine (*Vitis* species). Climbers characterize moist forests and woodlands.

Clump-Forming Plants

Clump-forming or *tussocky plants* exhibit an aggregate of several shoots growing in a bunch from a common base, especially in grasses. Examples include the bunch grasses *Andropogon* and *Aristida* mosses (such as *Polytrichum* species) and sedges (*Carex stricta*). They characterize grasslands and are common in the prairies of the United States. They also grow in sandy locations, wetlands, and disturbed habitats.

Dense Plants

Dense plants grow many small, woody canes or stems very close together in an upright fashion. The majority are shrubs. Examples include *Ephedra*, southern arrowwood (*Viburnum dentatum*), mountain laurel (*Kalmia latifolia*), and creosote bush (*Larrea tridentata*). They characterize woodlands, grasslands, coastal vegetation, and deserts.

Erect Plants

In *erect plants*, one main stem grows in an upright position clearly above ground level. This is common in trees. Examples include banana (*Musa*), oak (*Quercus*), pine (*Pinus*), maple (*Acer*), and palm. They mainly characterize forests and woodlands and some grasslands.

Mat-Forming Plants

Mat-forming plants have many *stolons* (creeping stems) that grow in a trail along soil or water surfaces and spread out to produce a matlike cover. Examples include the grasses *Cynodon* and *Digitaria*, Kentucky bluegrass (*Poa pratensis*), crab grass (*Digitaria sanguinalis*), the aquatic ferns *Salvinia* and *Azolla*, and mosses, such as *Sphagnum*. They characterize grasslands, bogs, wetlands, secondary forest floors, and cultivated habitats.

Mound-Forming Plants

Mound-forming plants grow to form a rounded shape resembling a mound or swollen bump. Examples include the barrel cactus (*Ferocactus* and *Echinocactus*), several other species of cacti (such as *Gymnocalycium*), and *Euphorbia gymnocalycioides*. They characterize deserts, grasslands, and the tundra.

Open Plants

Upright, woody stems or canes growing in an erect fashion characterize *open plants*. Their growth resembles a dense habit but has fewer stems and an open, airier structure. Examples include some bamboos (*Bambusa*), black willow (*Salix nigra*), smooth alder (*Alnus serrulata*), and meadowsweet (*Spirea*). This is characteristic of some shrubs and small trees of forests, woodlands, wetlands, and grasslands.

Prostrate Plants

The stems of prostrate plants grow flat on the soil surface or almost touching (hugging) the ground but not trailing. Examples include the herbaceous milk-purslane weed (*Euphorbia supina*), common mullein (*Verbascum thapsus*), and some species of juniper. They are common in the tundra, grasslands, wetlands, and disturbed habitats.

Scandent Plants

Scandent plants have prominent stems in a leaning position. Examples include sugarcane (*Saccharum officinarum*), coconut palm (*Cocos nucifera*), bearberry (*Arctostaphylos uva-ursi*), blackberry (*Rubus fruticosus*), and some bamboos (*Bambusa*). They characterize the dwarfed, woody trees in the timberline of the tundra, savanna, forest undergrowth, and coastal habitats.

Spreading Plants

Spreading plants exhibit a sprawling type of growth, resulting from profuse lateral branching in mostly woody or succulent stems. Examples include common juniper (*Juniperus communis*), blueberries (*Vaccinium*), prickly-pear cactus (*Opuntia*), Sumacs (*Rhus*), and ferns (such as *Adiantum*). They characterize forest undergrowth, grasslands, sandy coastal areas, deserts, cultivated lands, and some areas of the tundra.

Stemless Plants

Stemless plants have no visible stem aboveground and are composed mainly of leaves or leaflike structures. Examples include common dandelion (*Taraxacum officinale*), *Aloe vera*, sisal (*Agave*), onion (*Allium cepa*), and liverworts (such as *Marchantia polymorpha*). They characterize aquatic and wetland vegetation, deserts, some grasslands, cultivated land, and wasteland.

Samuel V. A. Kisseadoo

See also: Angiosperm cells and tissues; Angiosperm evolution; Angiosperm plant formation; Angiosperms; Arctic tundra; Biomes: types; Bryophytes; Community-ecosystem interactions; Conifers; Deserts; Savannas and deciduous tropical forests; Shoots; Species and speciation; Taiga; Wood.

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GYMNOSPERMS

Categories: Gymnosperms; *Plantae*; taxonomic groups

Pine trees are a familiar example of gymnosperms, a series of evolutionary lines of woody vascular seed plants that produce seeds not encased in an ovary.

Two kinds of higher plants—the gymnosperms and *angiosperms*—have developed to become the dominant type of land plant. With the exception of a few aquatic angiosperms, they do not require water for pollen transfer and are thus free to live in a wide variety of habitats. Gymnosperms and angiosperms differ primarily in the amount of protection they provide their *ovules* (the part that, after fertilization, becomes a weed), with gymnosperms usually providing less than angiosperms.

Progymnosperms

The first group of gymnosperms to appear was the *progymnosperms*. These plants evolved from the trimerophytes about 365 million years ago. *Archaeopteris*, the best-known progymnosperm, was described in 1871 by Sir William Dawson. Dawson believed that *Archaeopteris* was an ancient *fern*. He reached this conclusion because the large, leafy branch systems of *Archaeopteris* resembled a fern frond. In 1960 Charles Beck showed that these branch systems were borne on a stem having typical gymnospermous wood. This discovery led to the recognition of the progymnosperms as a distinct plant group which completely altered biologists' view of gymnosperm evolution.

Archaeopteris reached an estimated height of about 18 meters (59 feet). The main axis of the plant gave rise to a series of lateral branch systems, bearing primary branches in a single plane. The flattened branch system resembled a fern frond. The primary branches were covered with spirally arranged leaves. Some leaves bore *eusporangia* (spore-bearing structures that originate from a few cells). The earliest progymnosperms were *homosporous*, meaning that all their spores looked alike. Later progymnosperms were *heterosporous*, producing two types of spores, large megaspores and smaller microspores. Seeds have not been found attached to any progymnosperm.

Classification of Gymnosperms

Division *Cycadophyta*
- Class *Cycadopsida*
  - Order *Cycadales*
    - Families:
      - *Cycadaceae* (cycads)
      - *Zamiaceae* (sago palms)

Division *Ginkgophyta*
- Class *Ginkgoopsida*
  - Order *Ginkgoales*
    - Family:
      - *Ginkgoaceae* (ginkgoes)

Division *Coniferophyta* (conifers)
- Class *Pinopsida*
  - Order *Pinales*
    - Families:
      - *Araucariaceae* (araucarias)
      - *Cephalotaxaceae* (plum yews)
      - *Cupressaceae* (cypress)
      - *Pinaceae* (pines)
      - *Podocarpaceae* (podocarps)
      - *Taxodiaceae* (redwoods)
  - Order *Taxales*
    - Family:
      - *Taxaceae* (yews)

Division *Gnetophyta*
- Class *Gnetopsida*
  - Order *Ephedrales*
    - Family:
      - *Ephedraceae* (Mormon teas)
  - Order *Gnetales*
    - Families:
      - *Gnetaceae* (gnetums)
      - *Welwitschiaceae*

Source: U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Two major lines of gymnospermous evolution arose from the progymnosperms—the cycadophyte and the coniferophyte lines. Two plant groups make up the cycadophyte line: the pteridosperms, or seed ferns, and the cycads. These plants have large, compound, frondlike leaves. The cordaites (known only from the fossil record) and the conifers make up the coniferophyte line, all of which have simple leaves.

Pteridosperms and Cordaites

The *pteridosperms* and the *cordaites* appeared first. These plants were common in the wet tropical and subtropical coal swamps that covered much of the central United States between 345 million and 225 million years ago. One of the best-known pteridosperms is *Medullosa*. *Medullosa* had an upright stem between 3 and 8 meters (10 and 26 feet) high. The lower portion of the stem was covered with adventitious roots (roots that develop from stems or leaves, rather than from other roots). A number of large compound leaves arose from the stem tip. Ovules and pollen organs occurred singly on the leaves and not in cones. Pteridosperm pollen organs consisted of a number of elongate eusporangia that were commonly fused to form a ring. The seeds of *Medullosa* were quite large. Some reached lengths of up to 11 centimeters. Unlike other pteridosperms, *Medullosa* had multiple vascular bundles in the stem. Other gymnosperms have only a single conductive strand in their stems.

The cordaites were derived from Archaeopteris-like progymnosperms. Some species of *Cordaites* were trees, others were shrubs, and some were similar to modern mangroves. *Cordaites* was common in swamp, floodplain, and upland environments. Long strap-shaped leaves up to 1 meter in length occurred at its branch tips. It resembled modern mangroves in having stilt roots.

Cones developed between the upper surface of some leaves and the stem of cordaites. Four rows of *bracts* were borne on the cone axis. Above each bract was a dwarf shoot that terminated in either male or female reproductive structures. Swedish botanist Rudolf Florin believed that the woody seed-bearing scale of modern pine could be derived from the dwarf shoot of cordaites through a series of extinct coniferalean intermediates. His interpretation has been adopted in many textbooks. It has also been shown that the conifers did not evolve directly from the cordaites, although both groups undoubtedly shared a common ancestor.

Cycadeoids, Cycads, and Conifers

When the coal swamps dried up, the pteridosperms and the cordaites were replaced by the *cycads*, *cycadeoids*, and *conifers*. The cycads and cycadeoids evolved from the medullosan seed ferns. The cycads and cycadeoids were among the dominant plants during the age of the dinosaurs. The conifers are related to the cordaites.

Some cycadeoids had slender, branching trunks, while others were short and stumpy. Both types had compound leaves. Cycadeoid cones contained both male and female reproductive structures. Earlier researchers thought that the cones of the beehivelike cycadeoids resembled primitive angiosperm flowers, but detailed reinvestigation of the cones showed that this was not true. The cycadeoids became extinct about sixty-five million years ago.

The cycads were more abundant in the past than they are now. Eleven genera and 160 species exist worldwide. They are dispersed in the modern tropics—in Africa, Cuba, Mexico, Australia, India, China, and Japan. *Zamia floridana* (coontie) is the only cycad native to the United States. Some cycads

Welwitschia: The Strangest Gymnosperm

There are many unusual plants in Africa, but one of the most unusual is *Welwitschia mirabilis*, a resident of the Namib Desert. It has a short, swollen stem only about 4 inches (10 centimeters) high, which terminates in a disc-like structure. Coming off the top of the stem are two straplike leaves. These two leaves last for the lifetime of the plant and continue to grow very slowly. As they grow, they twist and become shredded, so that an individual plant appears to have many leaves. The reproductive structures rise from the center of the stem, and, instead of flowers, *Welwitschia* has small cones.

Welwitschia is such a successful survivor of the Namib that it easily lives for hundreds of years. Some specimens have been dated to about two thousand years old. Older plants can reach tremendous sizes, with the top of the stem sometimes reaching 5 feet (1.5 meters) in diameter. Specimens of *Welwitschia* are extremely difficult to grow in cultivation, requiring special desert conditions and room for the deep taproot.

Pinaceae *(the pine family) is the largest family of living gymnosperms, containing about two hundred species in ten genera. Unlike a few conifers, such as the bald cypress and dawn redwood, which shed their leaves in the fall, pines are evergreens.*

are small, unbranched trees that grow to 18 meters (59 feet) tall and resemble palm trees. Others have subterranean stems, and only their leaves and cones show above the ground. All the cycads possess stiff, leathery, compound leaves, often with very sharp tips on each leaflet. The male and female reproductive structures are borne at the end of the stem in separate cones on different plants. Cycad cones are the largest cones that have ever been produced. Cycad ovules are also very large. Some reach lengths of 6 centimeters. Their ripe seeds are often brightly colored.

The dominant group of living gymnosperms is the conifers. About 550 species are divided among 51 genera. Conifers are most abundant in temperate areas, such as the northern parts of North America, Europe, and Asia, and New Zealand and southern Australia. The conifers are divided into seven families—the *Araucariaceae* (examples are the kauri pine and Norfolk Island pine), *Podocarpaceae* (typified by the yellow woods), *Pinaceae* (pine, spruce, hemlock, and fir), *Cupressaceae* (juniper and arborvitae), *Taxaceae* (yew), *Cephalotaxaceae* (cultivated in the United States as plum-yew or cow's-tail pine, it also has at least one Asian genus), and *Taxodiaceae* (bald cypress, redwoods). Some researchers separate the *Taxaceae* from the conifers on the basis of their arillate ovule (an ovule that forms an additional seed coat to the normal one). Several extinct conifer families are also known.

Ovule and Seed Complexes

The most distinctive features of the gymnosperms are their ovule and seed complexes. In the center of the ovule is the female *gametophyte*. Surrounding the female gametophyte are layers of tissue called the *nucellus* and the *integument*. The nucellus is a nutritive tissue from which the developing female gametophyte draws its nourishment. The integument surrounds the nucellus and is the outermost layer of the ovule. After fertilization, the integument develops into the seed coat.

The gymnosperms have exploited land habitats more successfully than the lower plants and pterophytes because gymnosperms do not require water for pollen transfer. The male gametophyte (pollen grain) is carried to the female gametophyte (ovule) through the air. The ovule exudes a sticky fluid (the pollination drop), which traps the pollen grains. As the sticky fluid dries, the pollen grains are drawn through the *micropyle* into the ovule. The *archegonia* (the organs that contain the eggs) are located directly below the micropyle. When the sperm are released, they fertilize the egg; a fertilized ovule is called a seed.

Modern Gymnosperm Types

Pines are the standard example of gymnosperms. *Pinaceae* (the pine family) is the largest family of living gymnosperms. It contains about two hundred species in ten genera. Pine trees are typically conical and represent the sporophyte generation. The leaves are needle-shaped and confined to short, lateral shoots. Unlike a few conifers, such as the bald cypress and dawn redwood, which shed their leaves in the fall, pines and most conifers are evergreens.

Sexual reproduction typically takes three years to complete. In the first year, the pollen (male) and seed (female) cones are formed. The cones are borne on different parts of the same plant. The small, upright male cones are borne in clusters on the lower branches of the tree. The mature seed cones are very large and hang down from the upper branches. In the spring, the male cones shed millions of pollen grains into the air. Only a few grains reach an ovule. Once there, the male gametophyte must wait from twelve to fourteen months before the female gametophyte matures and fertilization occurs. The seeds mature in the fall of the third year and are shed.

Included within the gymnosperms are four plants whose affinities are uncertain—ginkgo, or the maidenhair tree (*Ginkgo biloba*), and the gnetophytes (families *Gnetum*, *Ephedra*, and *Welwitschia*). Ginkgo is a large tree covered with fan-shaped leaves that turn golden yellow before being shed in the fall. Although a common ornamental in the United States, ginkgo is native to southeastern China. *Gnetum* is a broad-leaved vine found in the tropical rain forests of South America, western Africa, and southeastern Asia. *Ephedra* is found worldwide in cool, arid regions. Sixteen species of *Ephedra* grow in the western United States. Most species are highly branched shrubs with scalelike leaves. *Welwitschia mirabilis* is the most unusual plant species within the four families. The exposed portion of the stem gives rise to two strap-shaped leaves that are never shed and never stop growing during the life of the plant. *Welwitschia* is found only in coastal desert and inland savanna regions in southwestern Africa.

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See also: Conifers; Cycads and palms; Ginkgos; Gnetophytes; Seedless vascular plants.

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HALOPHYTES

Categories: Angiosperms; economic botany and plant uses; *Plantae*; soil; water-related life

Halophytes are salt-resistant or salt-tolerant plants that thrive and complete their life cycles in soils or waters containing high salt concentrations. Despite high salt content in the tissues of halophytes, they can be grown and harvested as food or animal fodder.

The Salinity-Plant Relationship

Salts are ionic molecules that typically dissolve in water and split into cations (positively charged ions) and anions (negatively charged ions). Rain dissolves salts from minerals in rocks and soil. These dissolved salts then either enter surface waters or percolate down to an aquifer. In arid regions where there is low rainfall, water evaporates quickly, leaving its salt load behind, leading to the development of saline soils, salt lakes, and brackish groundwater. Even in areas that are only moderately arid, excessive irrigation can cause soil salinity to rise with time, which can lead to loss of agricultural lands, because most crop plants tolerate very little salt in the soil. White, powdery, or crystalline residues coating the ground are indications of especially heavy salt accumulation.

Most plants can tolerate salts at very low levels,

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Halophytic (salt-tolerant) trees, such as mangroves, can be harvested for wood and fuel. Mangrove roots serve as critical habitat and nutrient filters for many other species.

but many cannot live in soils or water with high concentrations of salts. The salts in saline areas are often dominated by sodium chloride, forming sodium and chloride ions in water. High concentrations of these ions prevent the growth of *glycophytes*, salinity-intolerant plants. Glycophytes grow only in areas with fresh water containing less than 125 parts per million of soluble salts. Halophytes can be *true halophytes* or *semi-halophytes*; both can thrive in areas with slightly to highly saline water containing soluble salts of 125 to 5,000 parts per million. Only the true halophytes can survive in areas with excessively saline water, containing greater than 5,000 parts per million soluble salts. The concentration of soluble salts is about 850 parts per million in Colorado River water and about 35,000 parts per million in seawater.

Water Potential

Movement of water between soil and plants occurs by osmosis. Water moves from an area of low solute concentration (low salt concentration) to an area of higher solute concentration. A common measure of the tendency of aqueous solutions to "attract" water is called *osmotic potential*. The osmotic potential of pure water is zero, which means that when coming into contact with water containing solutes, pure water will move into it. The osmotic potential of water with solutes is always expressed as a negative number, and the higher the concentration of solutes, the more negative the osmotic potential. Therefore, the osmotic potential in plants and growth media (water and soil) is always more negative than that of pure water. The osmotic potential in plants must always be more negative than the osmotic potential in soils, so that water can move from soil into the cells of plant roots. If large concentrations of soluble salts are present, as in saline or excessively fertilized soils, osmotic potential in the soil becomes more negative than in plants, causing water to move from roots to soils. As a result, glycophytes wilt and die, while halophytes possess adaptations that enable them to survive.

Growth and Survival Mechanisms

Many halophytes are considered *facultative halophytes*, indicating that they can grow in saline and nonsaline habitats. Others are *obligate halophytes* which can survive only in a saline environment. Some *Salicornia* species (pickleweed, for example) cannot survive under freshwater conditions. Although some halophytes can grow normally in nonsaline soils, they are less abundant than glycophytes, suggesting that they may compete poorly with glycophytes in nonsaline environments.

Some halophytes require fresh water for germination, whereas others readily germinate in saline environments. Some germinate only during the rainy season, to take advantage of the relatively low salt concentration. Seed germination in the goosefoot family (*Chenopodiaceae*) is unique in that the hypocotyl (the stem between the cotyledons and the radicle), rather than the radicle (or embryonic root), emerges first. After the lower tip of the hypocotyl touches the soil, the radicle begins to emerge. The roots are ready to tolerate the salts, storing the absorbed salts in the hypocotyl tissues. In saltbush (*Atriplex*), germination is regulated by storing salts in the seed coat, and the developing embryo is desalinized in the seed.

In mangroves (*Avicennia* and *Rhizophora* species), seeds mature without undergoing dormancy and germinate while the fruit is still attached to the mother plant, which provides water and nutrients during germination. A seedling on the mother tree produces a long hypocotyl. This heavy hypocotyl causes the mature seedlings to fall on the mud, where they continue to mature.

Resistance of halophytes to salt stress involves two different adaptations: salt tolerance, which involves accumulating salts in the plant's cells, and salt avoidance, which involves adaptations to minimize the concentrations of salt in the cells or adaptations to bar salts from entering through plant roots. These two adaptations have led to the designations "salt accumulators" and "salt excluders," respectively.

Salt Accumulators

Salt accumulators absorb salts throughout the growing season, resulting in an increase in salt concentration in the cells and thus maintaining a water potential that is more negative than that of the soil. The difference in osmotic potential between plant cells and soil water forces the water to enter the cells by passing through the cell membrane via osmosis. Water in leaf cells escapes as vapor through pores, or stomata, a process called evapotranspiration. Evapotranspiration also helps move water from the roots up the stem to the leaves.

Salt accumulators, such as saltbush (*Atriplex*), smooth cordgrass (*Spartina alterniflora*), saltgrass

(*Distichlis spicata*), and tamarisk (*Tamarix petandra*), have specialized cells called salt glands located on the surfaces of their leaves, used for storing excess sodium chloride. As the glands fill with salt they eventually burst, releasing salts that form a crystalline coating on the leaves. The crystals fall or are dissolved by rain, which returns the salt to the soil. Other halophytes can accumulate and concentrate the salts in their cells up to a certain toxic concentration, at which point the salts cause the plant to die.

Some salt accumulators avoid salt stress by minimizing salt concentration in the cytosol of their leaf cells. Leaf cells regulate cytosolic salt levels by transporting sodium and chloride ions into the central vacuole. A high salt concentration in the vacuole causes it to take up more water and swell. As the water-filled vacuole pushes the cytosol toward the cell membrane and cell wall, the cell maintains its turgidity, typical of *succulent* halophytes, such as pickleweed (*Salicornia virginica*).

Salt Excluders

Some *salt excluders* avoid salt stress by defoliation or abscission (leaf release). When cytosolic salt concentrations approach toxic levels, excess sodium chloride accumulates in petioles, stems that connect leaves to the main stem). The petiole, including the leaf, dies and then detaches from the stem, dropping to the ground. The removal of salt-concentrated parts desalinates the plant, thus preventing buildup of sodium and chloride ions to toxic levels.

Other salt excluders avoid salt toxicity at the roots. The root epidermis (outer layer of cells) of some halophytes may not allow the passage of sodium and chloride ions through the cell membrane. Roots also have an endodermis (inner layer of cells) that contains waxy strips surrounding each cell, to obstruct the entry of sodium and chloride ions. Although this mechanism is less common, selective permeability of the cell membrane (the transport of other ions rather than sodium and chloride ions) into the roots of halophytes is possible. In some plants, root cells are capable of actively pumping excess sodium and chloride ions out into the surrounding soil.

Halophytes as Crops

In arid regions, farmers often use groundwater to irrigate their crops. Even when salt concentrations in the groundwater are relatively low, salt can gradually accumulate in the soil as a result of high evaporation rates in these areas. Eventually, such soils become so salinized that most traditional crop plants cannot survive. Growing halophytes as crops could be a way to use salinized soils. Also, as the human population increases and fresh water becomes an expensive commodity, irrigating halophytes with salt water could be a way of conserving fresh water.

Some halophytes growing in deserts, estuaries, and seashores are potential sources of food, fuel, and forage. The seeds of eelgrass (*Zostera marina*) and saltgrass could be ground to make flour. Seeds of *Salicornia* species are a potential source of vegetable oil. Halophytic trees, such as mangrove, could be harvested for wood and fuel. Eelgrass and saltbush could be used as forage for livestock. Common reed (*Phragmites australis*) is a marsh plant used since ancient times for roofing and making baskets. Coconut palms (*Cocos nucifera*), found in occasionally inundated shorelines, yield oil from the nuts. Traditional uses of the coconut palm include weaving leaflets into baskets and mats, converting husks into charcoal, and using fibers to make brushes and mats. Other halophytes could be sources of waxes, gums, and pharmaceuticals.

Domingo M. Jariel

See also: Active transport; Adaptations; Aquatic plants; Irrigation; Osmosis, free diffusion and facilitated diffusion; Plants with potential; Root uptake systems; Soil salinization; Water and solute movement in plants; Wetlands.

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HAPTOPHYTES

Categories: Algae; *Protista*; taxonomic groups; water-related life

The algal phylum Prymnesiophyta, *or* Haptophyta, *is a monophyletic taxon that contains two hundred to three hundred extant species that are 4-40 microns in size.*

The phylum *Haptophyta* is divided into two subclasses, the *Prymnesiophycidae* and *Pavlovophycidae*, that differ significantly from one another (see below). The phylum is usually classified within the kingdom *Chromista* with other algae containing chlorophyll *a* and *c* (excluding dinoflagellates), but their exact relationship to the heterokont algae remains unclear.

Although a few freshwater species are known, most are marine, and species diversity within the phylum is greatest in nutrient-poor waters of the tropical and subtropical open oceans. Most are motile biflagellate single cells or nonmotile coccoid (walled unicells) cells. Colonial, filamentous, and palmelloid forms are also known.

Cell Structure

Prymnesiophyte cells are typically eukaryotic. The nucleus is positioned centrally or nearer the posterior end of the cell and lies between the chloroplasts. Most cells probably possess a single highly branched mitochondrion, although it is possible that multiple mitochondria may be present in some species. An exceptionally large Golgi body (dictyosome) with many cisternae is located anteriorly, just beneath the flagellar basal region.

The motile cells of most prymnesiophytes bear two equal or slightly subequal heterodynamic flagella that lack mastigonemes (hairlike appendages) and arise from a shallow apical depression. However, the longer flagellum in members of the *Pavlovophycidae* is adorned with fibrous hairs and knobscales. Further differences between the *Prymnesiophycidae* and *Pavlovophycidae* are evident in the flagellar and mitotic apparatuses. In the *Prymnesiophycidae* the flagellar root system originating near the two basal bodies consists of three to four microtubular roots, the nuclear envelope breaks down prior to division, the mitotic spindle axis is straight, and a fibrous microtubular organizing center (MTOC) is absent. In contrast, the *Pavlovophycidae* flagellar root system includes only two roots, the nuclear envelope remains intact during division, the mitotic spindle is V-shaped, and a fibrous MTOC is present.

A *haptonema*—a thicadlike structure that, along with two flagella, extends from the cell wall—is found in many, but not all, species and gives this phylum its name. However, the haptonema is unique to the *Prymnesiophyta*. In many coccolithophorids the haptonema is reduced (vestigial) or absent. The haptonema, which may have evolved by duplication of a portion of the flagellar apparatus, arises between the flagellar basal bodies and at its base is composed of three to eight singlet microtubules. The microtubules are arranged in an arclike or crescentlike fashion and are surrounded by a layer of the endoplasmic reticulum. The movement of the haptonema (which does not beat) and flagella are highly coordinated. When present, the haptonema may be long or short and may or may not be capable of coiling. Coiling is induced by a rapid uptake of calcium from the environment. The haptonema can be used for attachment (in fact, the Greek word *haptein* means "to fasten") and, at least in some species, is used to capture prey (such as bacteria and smaller eukaryotes). In phagotrophic species a single membranebound food vacuole is posteriorly located, and the haptonema delivers captured prey to this organelle. The haptonema is also involved in tactile responses; for example, upon contact with an obstacle it may stimulate a change in the direction of swimming.

Chloroplasts and Nutrition

Most prymnesiophytes possess two chloroplasts that are surrounded by four membranes; in most species investigated, the outer membrane is studded with ribosomes and is confluent with the nuclear envelope. A girdle lamella, a thylakoid encircling the periphery of the plastid that is found in some other algae containing chlorophyll *a* and *c*, is absent. In members of the *Prymnesiophycidae*, eyespots are absent. Eyespots are present beneath an invagination of the plasmalemma in members of the *Pavlovophycidae* but usually are not associated with a flagellar swelling as in many other algal taxa.

The photosynthetic pigments of prymnesiophytes are diverse. All contain chlorophylls a, c_1, c_2, beta carotene, diadinoxanthin, and diatoxanthin, but chlorophyll c_3, fucoxanthin, 19′-hexanoyloxyfucoxanthin and 19′-butanoyloxyfucoxanthin are present or absent in different combinations in other species.

Pyrenoids are present and may be immersed (embedded within the chloroplast) or bulging, in which case they protrude from the periphery of the chloroplast and into the surrounding cytosol. Pyrenoids may be traversed by one or a few thylakoid membranes.

Most prymnesiophytes are photoautotrophs and, in addition to using photosynthesis for nutrition, probably are also capable of directly obtaining inorganic or organic nutrients dissolved in the surrounding water. A number of species, particularly those possessing a relatively long and flexible haptonema, are phagotrophic and ingest bacteria and smaller eukaryotes. Thus, mixotrophic species (those that combine photoautotrophic and heterotrophic means of obtaining food) are common among prymnesiophytes.

Cell Covering

Members of the *Pavolophycidae* lack body scales. However, cells of species placed in the *Prymnesiophycidae* are covered by organic base plate scales, mineralized calcium carbonate scales, or a combination of both that are external to the plasmalemma. Nearly 70 percent of all known species of prymnesiophytes are known as coccolithophorids. The external covering of these cells is composed of mineralized calcium carbonate (calcite) scales termed *coccoliths*. Individual coccoliths are intricately arranged around the cell to form a coccosphere. Both organic scales and coccoliths are produced within the Golgi complex and are released onto the cell surface near the point of flagellar insertion. An organic base plate scale serves as a matrix for coccolith calcification that may occur inside or outside the cell; thus, organic scales and mineralized scales are homologous structures.

Organic base plate scales are microfibrillar and composed of proteins, celluloselike and pectinlike substances. The microfibrils on the proximal side of the scale are arranged radially, whereas those on the distal surface are arranged spirally. In species bearing only organic scales (such as *Chrysochromulina*, *Phaeocystis*, and *Prymnesium*), one or more layers of organic scales may be present.

In coccolithophores the coccoliths are external to the organic scales (when present). *Pleurochrysis* is an example of a coccolithophorid that possesses organic scales as well as coccoliths, whereas the widely distributed coccolithophorids *Emiliana* and *Gephyrocapsa* bear mineralized scales only. There is tremendous diversity in coccolith morphology, ranging from those that are platelike to highly ornamented forms with rims and spines. The taxonomy of species within the group is based primarily upon structural differences among coccoliths. However, some species may bear coccospheres composed of morphologically different coccoliths, and transitions between coccolith types are now known to be associated with different life history phases. An accurate account of the biodiversity of prymnesiophytes species remains uncertain because different life history phases bearing different scales are often considered separate species.

The function of coccoliths is not known with certainty. It is likely that they serve multiple functional roles in some species, whereas in other species more specific functions may be attributed to morphologically different coccoliths. Coccoliths are effective at deterring only smaller grazers (such as protozoans), and coccolithophorids are readily eaten by other organisms. It has been suggested that coccoliths protect the delicate plasmalemma from osmotic, chemical, and physical disruption or invasive bacteria and viruses. Coccoliths, which may be shed or produced when needed, may also play a role in buoyancy control. The long spines on the coccoliths of *Rhabdosphaera* and other coccolithophores also reduce sinking rates. Calcification and photosynthesis in most coccolithophorids appears to be physiologically linked. It is possible that the carbon dioxide released during calcification may be used in the dark reactions of photosynthesis and that coccoliths increase the amount of surface area available for light capture.

There are more than one thousand different types of fossilized coccoliths, and these are among the most commonly used microfossils for stratigraphic analyses in the petroleum industry. In addition, because some coccolithophorids are restricted to water masses defined by a particular temperature range, fossil coccoliths are frequently used as paleoclimatic indicators. Because their calcium carbonate scales are birefringent, satellite imagery can be used to deduce the relative abundance and position of prymnesiophyte blooms.

Life History

Most prymnesiophytes are biflagellate motile single cells that reproduce asexually via binary fission. Life history stages may include transitions between nonmotile and motile forms and also the production of different scales (organic versus mineralized) and the production of mineralized scales of different morphologies. Thus, during their life histories flagellate cells may be morphologically transformed into amoeboid, coccoid, colonial, palmelloid (walled cells embedded in a mucilaginous envelope), or filamentous life forms. For example, *Pleurochrysis* possesses a nonmotile benthic colonial or filamentous haploid stage that alternates with a diploid motile coccolith bearing stage. Some life histories include alternations between two motile cell stages that bear completely different types of coccoliths. In *Hymenomonas* and *Ochrosphaera*, diploid coccolith-bearing cells alternate with cells possessing only organic scales.

Phylogeny and Fossil Record

Although they may have originated earlier, the coccoliths of prymnesiophytes first appear in the fossil of the Late Triassic, approximately 220 million years ago (mya). The abundance of coccolith fossils reached its peak during the Late Cretaceous (95-63 mya). Fossil records indicate that perhaps 80 percent of all coccolithophorids went extinct during the Cretaceous-Tertiary (K-T) event at the end of the Cretaceous period. Today's prymnesiophytes represent a radiation of the minority of species that survived the K-T extinction event, which also brought about the demise of dinosaurs.

According to most scholars, the most primitive prymnesiophytes are those lacking body scales and possessing a haptonema. Flagellates bearing organic scales are believed to have diverged next. The absence of a haptonema and the presence of coccoliths are considered derived features for the group, and these characteristics are found in most coccolithophorids.

Environmental Importance

Prymnesiophytes, particularly coccolithophorids, play important roles in coastal and open ocean environments. For example, they are integral contributors in global carbon and sulfur cycles.

Coccoliths that are shed, derived from dead cells, are ingested and expelled are transported to the sea floor. In some areas the accumulation of coccoliths has led to the formation of enormous deposits of chalk or limestone, a notable example being the White Cliffs of Dover in England. By this sedimentary process, calcium and carbon are cycled from the oceans back into the lithosphere. The ocean is the largest long-term sink of inorganic carbon on the planet, and carbonate deposits cover one-half of the sea floor, an area equal to one-third the surface of the earth. Coccoliths account for approximately 25 percent of the total yearly vertical transport of carbon to the deep sea. Blooms of coccolithophorids (such as *Emiliania*, *Pheocystis*) release dimethylsulfide that becomes aerosolized and subsequently acts as a nucleating agent for water droplets in the atmosphere, ultimately producing acid rain. Because coccoliths reflect light, large blooms may also have a cooling effect on the local climate.

Other species of prymnesiophytes, including some species of *Chrysochromulina*, *Prymnesium*, and *Phaeocystis*, are known to form blooms that are toxic to other marine organisms or that interfere with marine fisheries. On the other hand, *Pavolova* and *Isochrysis* are widely used as food in the aquaculture industry.

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See also: Algae; Heterokonts; *Protista*.

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HARDY-WEINBERG THEOREM

Categories: Evolution; genetics

The Hardy-Weinberg theorem is the principal that, in the absence of external pressures for change, the genetic makeup of an ideal population of randomly mating, sexually reproducing diploid organisms will remain the same, at what is called Hardy-Weinberg equilibrium.

Population genetics is the branch of genetics that studies the behavior of genes in populations. The two main subfields of population genetics are theoretical (or mathematical) population genetics, which uses formal analysis of the properties of ideal populations, and experimental population genetics, which examines the behavior of real genes in natural or laboratory populations.

Population genetics began as an attempt to extend Gregor Mendel's laws of inheritance to populations. In 1908 Godfrey H. Hardy, an English mathematician, and Wilhelm Weinberg, a German physician, each independently derived a description of the behavior of allele and genotype frequencies in an ideal population of randomly mating, sexually reproducing diploid organisms. Their results, now termed the Hardy-Weinberg theorem, showed that the pattern of allele and genotype frequencies in such a population followed simple rules. They also showed that, in the absence of external pressures for change, the genetic makeup of a population will remain at an equilibrium.

Because evolution is change in a population over time, such a population is not evolving. Modern evolutionary theory is an outgrowth of the "New Synthesis" of R. A. Fisher, J. B. S. Haldane, and Sewell Wright, which was developed in the 1930's. They examined the significance of various factors that cause evolution by examining the degree to which they cause deviations from the predictions of the Hardy-Weinberg theorem.

Predictions

The predictions of the Hardy-Weinberg theorem hold if the following assumptions are true:

(1) The population is infinitely large.

(2) There is no gene flow (movement of genes into or out of the population by migration of gametes or individuals).

(3) There is no mutation (no new alleles are added to the population by mutation).

(4) There is random mating (all genotypes have an equal chance of mating with all other genotypes).

(5) All genotypes are equally fit (have an equal chance of surviving to reproduce).

Under this very restricted set of assumptions, the following two predictions are true:

(1) Allele frequencies will not change from one generation to the next.

(2) Genotype frequencies can be determined by a simple equation and will not change from one generation to the next.

The predictions of the Hardy-Weinberg theorem represent the working through of a simple set of algebraic equations and can be easily extended to more than two alleles of a gene. In fact, the results were so self-evident to the mathematician Hardy that he, at first, did not think the work was worth publishing.

If there are two alleles (A, a) for a gene present in the gene pool (all of the genes in all of the individuals of a population), let p = the frequency of the A allele and q = the frequency of the a allele. As an example, if $p = 0.4$ (40 percent) and $q = 0.6$ (60 percent), then $p + q = 1$, since the two alleles are the only ones present, and the sum of the frequencies (or proportions) of all the alleles in a gene pool must equal one (or 100 percent). The Hardy-Weinberg theorem states that at equilibrium the frequency of AA individuals will be p^2 (equal to 0.16 in this example), the frequency of Aa individuals will be $2pq$, or 0.48, and the frequency of aa individuals will be q^2, or 0.36.

The basis of this equilibrium is that the individuals of one generation give rise to the next generation. Each *diploid* individual produces *haploid* gametes. An individual of genotype AA can make only a single type of gamete, carrying the A allele. Similarly, an individual of genotype aa can make only a gametes. An Aa individual, however, can make two types of gametes, A and a, with equal probability. Each individual makes an equal contribution of gametes, as all individuals are equally fit, and there is random mating. Each AA individual will contribute twice as many A gametes as each Aa individual. The frequency of A gametes is equal to the frequency of A alleles in the gene pool of the parents.

The next generation is formed by gametes pairing at random (independent of the allele they carry). The likelihood of an egg joining with a sperm is the frequency of one multiplied by the frequency of the other. AA individuals are formed when an A sperm joins an A egg; the likelihood of this occurrence is $p \times p = p^2$ (that is, $0.4 \times 0.4 = 0.16$ in the first example). In the same fashion, the likelihood of forming an aa individual is $q^2 = 0.36$. The likelihood of an A egg joining an a sperm is pq, as is the likelihood of an a egg joining an A sperm; therefore, the total likelihood of forming an Aa individual is $2pq = 0.48$. If one now calculates the allele frequencies (and hence the frequencies of the gamete types) for this generation, they are the same as before: The frequency of the A allele is $p = (2p^2 + 2pq)/2$ (in the example $(0.32 + 0.48) \div 2 = 0.4$), and the frequency of the a allele is $q = (1 - p) = 0.6$. The population remains at equilibrium, and neither allele nor genotype frequencies change from one generation to the next.

The Real World

The Hardy-Weinberg theorem is a mathematical model of the behavior of ideal organisms in an ideal world. The real world, however, does not approximate these conditions very well. It is important to examine each of the five assumptions made in the model to understand their consequences and how closely they approximate the real world.

The first assumption is infinitely large population size, which can never be true in the real world, as all real populations are finite. In a small population, chance effects on mating success over many generations can alter allele frequencies. This effect is called *genetic drift*. If the number of breeding adults is small enough, some genotypes will not get a chance to mate with one another, even if mate choice does not depend on genotype. As a result, the genotype ratios of the offspring would be different from those of the parents. In this case, however, the gene pool of the next generation is determined by those genotypes, and the change in allele frequencies is perpetuated. If it goes on long enough, it is likely that some alleles will be lost from the population, because a rare allele has a greater chance of not being included. Once an allele is lost, it cannot be regained.

How long this process takes is a function of population size. In general, the number of generations it would take to lose an allele by drift is about equal to the number of individuals in the population. Many natural populations are quite large (thousands of individuals), so that the effects of drift are not significant. Some populations, however, especially of endangered species, are very small: A number of plant species are so rare that they consist of a single population with less than one hundred individuals.

The second assumption is that there is no gene flow, or movement of genotypes into or out of the population. Individuals that leave a population do not contribute to the next generation. If one genotype leaves more frequently than another, the allele frequencies will not equal those of the previous generation. If incoming individuals come from a population with different allele frequencies, they also alter the allele frequencies of the gene pool.

The third assumption concerns mutations. A mutation is a change in the deoxyribonucleic acid (DNA) sequence of a gene—that is, the creation of a new allele. This process occurs in all natural populations, but new mutations for a particular gene occur in about 1 of 10,000 to 100,000 individuals per generation. Therefore, mutations do not, in themselves, play much part in determining allele or genotype frequencies. Mutation, however, is the ultimate source of all new alleles and provides the variability on which evolution depends.

The fourth assumption is that there is *random mating* among all individuals. A common limitation on random mating in plants is *inbreeding*, the tendency to mate with a relative. Because plants have a limited ability to move, and pollinators may not carry pollen very far, the plants in a population tend to mate with nearby individuals, which are often relatives. Such individuals tend to share alleles more often than the population at large.

The final assumption is that all genotypes are equally *fit*. Considerable debate has focused on the question of whether two alleles or genotypes are ever equally fit. Many alleles do confer differences in fitness; it is through these variations in fitness that natural selection operates. Newer techniques of molecular biology have revealed many differences in DNA sequences that appear to have no discernible effects on fitness.

As the cornerstone of population genetics, the Hardy-Weinberg theorem pervades evolutionary thinking. The advent of techniques to examine genetic variation in natural populations has been responsible for a great resurgence of interest in evolutionary questions. One can now test directly many of the central aspects of evolutionary theory. In some cases, notably the discovery of the large amount of genetic variation in most natural populations, evolutionary biologists have been forced to reassess the significance of natural selection compared with other forces for evolutionary change.

Richard Beckwitt

See also: Population genetics; Species and speciation.

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HELIOTROPISM

Categories: Movement; physiology

Heliotropism is a growth movement in plants that is induced by sunlight. It is sometimes called solar tracking, a directional response to the sun. Because plants react in a similar way toward artificial sources of light, heliotropism is sometimes termed phototropism, a growth movement induced by any light stimulus.

Plants that orient their leaves to receive maximum sunlight are called diaheliotropic. *Diaheliotropism* is the tendency of leaves or other organs of a plant to track the sun by turning their surfaces toward it. Tracking the sun maximizes the amount of direct solar radiation received. Diaheliotropic movements can increase radiation interception, enhance photosynthesis, and increase growth rates of plants.

Plants that move their leaves to avoid sunlight are called paraheliotropic. *Paraheliotropism* is a plant response to minimize surface exposure to the sun. By orienting leaves and other plant organs parallel to the sun's rays, light absorption is minimized. It is a process that some plants use to reduce dehydration by reducing leaf temperatures and water loss during times of drought.

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Solar Tracking

Alfalfa, cotton, soybean, bean, and some wild species of the mallow family *Malvaceae* are plant species that exhibit *solar tracking*. Heliotropic plants change the orientation of their leaves toward the sun. This solar tracking mechanism can occur as a continuous adjustment throughout the day so that the leaf blades are always oriented perpendicular to the sun's rays. The leaves are in a nearly vertical position, facing the eastern horizon as the sun rises.

During the morning and later afternoon, when solar radiation is not at its most intense, the leaves move to a horizontal orientation. When there is increased solar radiation near midday, the leaves move to become more vertical so that they are not damaged by overheating. At sunset, the leaves are nearly vertical, facing the west when the sun sets. During the night, the leaves assume a horizontal position and reorient just before dawn, to start the solar tracking cycle over again. Leaves only track the sun on clear days. They stop when clouds block the sun.

Mechanisms

In many cases, the leaves of solar tracking plants are controlled by a specialized organ called the *pulvinus*. This organ is a swollen part of the petiole that may occur where it joins the stem, the leaf blade, or both. It contains motor cells that generate mechanical forces that control the orientation of the petiole and thus the leaf blade. The forces are produced by changes in the turgor in the pulvinus. The cells of this organ have highly elastic cell walls that allow them readily to change size and shape. The cells of the upper pulvinus have the capability of increasing their turgidity with water uptake, while the lower pulvinus can lose water very easily. The net effect is a force that moves the petiole.

Another mechanism producing heliotropism is produced by small mechanical changes along the length of the petiole and by movements of the younger parts of the stem. Heliotropic plants are continuously moving their leaves, leaflets, and pinnules to readjust to prevailing light conditions. Movements occur rather rapidly, every fifteen to sixty seconds, which is just slow enough to be imperceptible to most humans.

Alvin K. Benson

See also: Growth habits; Leaf arrangements; Leaf shapes; Nastic movements; Photoperiodism; Photosynthesis; Thigmomorphogenesis.

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HERBICIDES

Categories: Agriculture; pests and pest control

Herbicides are a class of pesticide used to kill or otherwise control weeds and other unwanted vegetation.

Herbicides are used to control grasses, weeds, and other plant pests. These chemical compounds kill plants or inhibit their normal growth. In general, herbicides work by interfering with photosynthesis, so that a plant dies from lack of energy or by a combination of *defoliation* (leaf removal) and *systemic* herbicidal action.

Herbicides are used to clear rights-of-way beneath power lines and along railways and roads. In agriculture and forest management, they are used

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to control weeds or to remove the leaves from some crop plants to facilitate harvesting. While herbicides may be employed in lieu of tillage, their use is more often in conjunction with tillage and other agronomic practices. During wartime, defoliants and other herbicides have been used to destroy plants that an enemy uses for cover during battle or for food.

Types of Herbicides

Herbicides may be *selective* or *nonselective*. Selective herbicides, such as amitrole, atrazine, monuron, pyridine, 2,4-dichlorophenoxyacetic acid (2,4-D), and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), target a particular plant and will kill or stunt weeds among crop plants without injuring the crop. For example, 2,4-D targets soft-stemmed plants, while 2,4,5-T is effective against woody plants. Cereals (grains) are crops particularly suited for treatment with 2,4-D, because the compound does not harm narrow-leafed plants but kills broad-leaved weeds. Selective toxicity minimizes the environmental impact of an herbicide.

Nonselective herbicides (also called broad-spectrum or general-usage herbicides) are toxic to all plants. Examples include dinoseb, diquat, paraquat, and arsenic trioxide. Nonselective compounds are best suited for areas where all plant growth is to be suppressed, such as along railroad rights-of-way.

Some compounds, known as *contact herbicides*, kill only those plant parts to which they are directly applied. Others, called systemic herbicides, are absorbed through the plant's foliage or roots and carried to other parts of the plant. When mixed with the soil, some herbicides kill germinating seeds and small seedlings.

Popular *inorganic* herbicides include ammonium sulfate, sodium chlorate, sulfuric acid solutions, and borate formulations. Among the *organic* herbicides are the organic arsenicals, substituted amides and ureas, nitrogen heterocyclic acids, and phenol derivatives. Phenoxyaliphatic acids and their derivatives, a major group of organic herbicides, are selective poisons that readily travel from one part of a plant to another.

History

Agricultural societies have used simple chemical herbicides, such as ashes and common salts, for centuries. In 1896 a fungicidal compound known as Bordeaux mixture (a combination of copper sulfate, lime, and water) was found to be effective against some weeds. Subsequently, copper sulfate was employed as a selective weed killer in cereal crops. By the early 1900's sodium arsenate solutions and other selective inorganic herbicidal mixtures had been developed.

In the early 1940's a new generation of herbicidal compounds emerged. In an attempt to mimic natural plant hormones, the defoliant 2,4-D was created. At low concentrations, 2,4-D promotes retention of fruit and leaves; at higher concentrations, it overstimulates plant metabolism, causing leaves to drop off. A related chemical, 2,4,5-T, came into general use in 1948. The years after World War II saw the first large-scale application of herbicides in agriculture and other areas. The new defoliants rapidly gained acceptance because of their effectiveness against broad-leaved weeds in corn, sorghum, small grains, and grass pastures.

A few years after their development, these defoliants were employed as chemical weapons. During its conflict with communist guerrillas in Malaya during the late 1940's and early 1950's, Britain sprayed 2,4,5-T on crops and jungle foliage to deprive the guerrillas of food and cover. The United States conducted a similar antifood and antifoliage campaign in South Vietnam during the 1960's. In this campaign, dubbed Operation Ranch Hand, massive quantities of herbicidal mixtures were sprayed from aircraft onto Vietcong food plantations, infiltration routes, staging areas, and bases. The quantity and frequency of the spraying greatly exceeded recommended levels; in addition, mechanical problems or military need often forced aircraft to dump their herbicide loads all at once, drenching the jungle below. Soldiers, civilians, and the environment were subjected to unusually high concentrations of defoliants.

One of the herbicides used in this campaign was Agent Orange, a mixture that included 2,4-D and 2,4,5-T. Commercial preparations of 2,4,5-T contain varying amounts of *dioxin*, a highly toxic contaminant. Agent Orange has been implicated in the increased incidence of stillbirths and birth defects among the Vietnamese living in the areas sprayed, in illnesses suffered by American and Australian soldiers who were involved in the operation, and in birth defects among the children of these veterans. In 1970 the United States placed severe restrictions on domestic and agricultural use of 2,4,5-T, at about the same time the defoliation campaign was halted.

U.S. Regulation of Herbicides

In 1947 the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) authorized the U.S. Department of Agriculture (USDA) to oversee registration of herbicides and other pesticides and to determine their safety and effectiveness. In December, 1970, the newly formed Environmental Protection Agency (EPA) assumed statutory authority from the USDA over pesticide regulations. Under the Federal Environmental Pesticide Control Act of 1972, an amendment to FIFRA, manufacturers must register all marketed pesticides with the EPA before the product is released. Before registration, the chemicals must undergo exhaustive trials to assess their potential impact on the environment and human health. An EPA decision to grant registration is based on the determination that unreasonable adverse effects on human health or the environment are not anticipated within the constraints of approved usage. Since October, 1977, the EPA has classified all pesticides to which it has granted registration as either restricted-usage (to be applied only by certified pest control operators) or unclassified (general-usage) pesticides.

Karen N. Kähler

See also: Agriculture: modern problems; Biopesticides; Genetically modified foods; Pesticides.

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HERBS

Categories: Angiosperms; economic botany and plant uses; food; medicine and health

The term "herb" has a variety of meanings but is most frequently used in one of three ways. To a botanist, an herb is a plant with a soft, flexible stem and a life cycle that is completed in one growing season. A person interested in medicinal plants would use the word "herb" to describe any plant with medicinal properties. In a culinary situation, an herb is a plant used to impart flavor to food.

Herb or Spice?

Herbs and spices are both used in cooking to modify the taste and smell of food. A clear distinction between herbs and spices is difficult to draw, but there are some broad differences that are useful to know. Plants referred to as herbs, such as basil (*Ocimum basilicum*) or rosemary (*Rosmarinus officinalis*), typically have been used in temperate regions throughout much of recorded history. Herbs can be distinguished from spices in that herbs are the leaves of nonwoody plants, used for their flavor or therapeutic properties. Spices, in contrast, are derived from other parts of plants, such as buds, stems, or bark, and are more strongly flavored, often because of the essential oils produced in these plant parts. More often than not, the leaf is the important plant part used for seasoning. The word "spice" also evokes a more exotic connotation, referring to plants obtained from distant places such as India or Ceylon. Spices are typically native to tropical areas.

History of Herbs

Herbs and spices have been used for thousands of years to add zest to meals, to help preserve food, and even to cover up the taste and smell of spoiled food. The Sumerians were known to have used laurel (*Laurus nobilis*), caraway (*Carum carvi*), and thyme (*Thymus vulgaris*) more than five thousand years ago. Other early records suggest that onion (*Allium cepa*) and garlic (*Allium sativum*) were also used. At least as early as 1000 B.C.E., the Egyptians used garlic and mint (*Mentha*) along with many other plants, for medicine, in religious ceremonies, or in embalming. The Greeks and Romans greatly expanded the uses of herbs to include their use as symbols, magical charms, cosmetics, dyes, perfumes, and air purifiers.

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Most of the historical information on herbs deals more directly with the medicinal properties of the plants. The first book available to the Europeans was *De materia medica* written by Pedanius Dioscorides, a Greek physician, in 100 C.E. This work on herbal medicine was so important that it was one of the first books printed after the printing press was developed. *De materia medica* continued to be the authoritative reference on the use of herbs in medicine for sixteen centuries. Another early work on medicinal herbs is *Pen-ts'ao* (*The Great Herbal*), a sixteenth century Chinese pharmacopoeia, attributed to Li Shih-chen, which lists more than eighteen hundred plants and medical preparations. The use of herbs as medicines began to decline in the seventeenth century as new ways of treating illnesses developed, but herbal remedies continue even today in natural and homeopathic medicines.

Common Herbs

Among the herbs most commonly used in cooking are members of the *Lamiaceae*, or mint, family. Mint, rosemary, basil, oregano (*Origanum vulgare*), sage (*Salvia officinalis*), thyme (*Thymus vulgaris*), and marjoram (*Origanum majorana*) are the most frequently used members of this family. These herbs are important staples in most cuisines of the Mediterranean region. The key features that most mint family members share are square stems and simple leaves (having undivided blades) attached in groups of two leaves in an opposite position on the stem. The flowers are also distinct in that the tips of the petals are grouped into two clusters that bear a resemblance to lips.

The most commonly used herb in the United States today is parsley, *Petroselinum crispum*, a member of the *Apiaceae*, or carrot, family. Other important members of this family include dill (*Anethum graveolens*), cilantro (*Coriandrum sativum*, also known as coriander), fennel (*Foeniculum vulgare*), cumin (*Cuminum cyminum*), anise (*Pimpinella anisum*), celery (*Apium sativum*), and caraway. Members of this family are easy to recognize, particularly when in flower. The leaves are compound (having blades subdivided into leaflets), and the petiole (base of the leaf) is expanded such that the base wraps around the stem. The flowers are small and occur in clusters known as umbels. Umbels are clusters of flowers in which the flowers have stems of varying lengths so that all are located in one plane, forming a broad, flat inflorescence. Depending on the plant, the leaves or "seeds" or both might be used to impart characteristic musky flavors to a dish. Botanically, these are not simply seeds but seeds plus dried portions of the fruit. The fruit splits apart during maturation, forming two structures that appear to be "seeds." This type of fruit is called a schizocarp (*schizo* meaning "split," *carp* meaning "body") and is characteristic of members of the carrot family.

Chemistry of Herbs

Plants used as herbs contain compounds called aromatic oils, or *essential oils*. These are relatively small compounds of low molecular weight that are easily separated from the plant. The essential oil of a particular plant is usually mixture of compounds, rather than one single ingredient. Essential oils impart the characteristic taste and odor of the herbs. In nature, oils often serve as attractants to animals pollinating flowers or dispersing fruits. Many of the compounds may also act in defense against the invasion of fungi, bacteria, or predation by herbivores.

Additional Uses

A discussion of herbs would not be complete without mentioning some of the uses of these plants not related to food or medicine. Crushing the plant releases the aromatic volatiles, making them useful as perfumes to cover up odors on bodies or in spaces. Undoubtedly this practice began by simply crushing the plant to release the odor into the air or rubbing the crushed plant onto an object. Burning the plant is another way to release its odors. The Egyptians were quite skilled at the art of perfumery and passed these skills on to the Greeks and Romans. Additionally, herbs were commonly used in the nineteenth century as components of floral bouquets designed to deliver messages to recipients. The flowers had particular meanings; for example, roses meant love. The herbs were added for greenery to deliver additional messages. Rosemary was used to denote friendship, and basil meant hatred.

Joyce M. Hardin

See also: Biochemical coevolution in angiosperms; Medicinal plants; Spices.

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HETEROKONTS

Categories: Algae; economic botany and plant uses; microorganisms; pests and pest control; *Protista*; water-related life

Heterokonts are a group of closely related phyla with flagella in pairs, one long and one short. They include oomycetes, chrysophytes, diatoms, and brown algae.

The term "heterokont" refers either to the flagellar arrangement of biflagellate cells in which the two *flagella* differ in length (as in *anisokonts*), type of motion, or ornamentation, or to those organisms (and organisms evolutionarily derived from such lineages) in which biflagellate cells with heterokont flagella are produced at some point during their life cycle. The most common heterokont flagellar arrangement consists of a posteriorly directed whiplash flagellum and an anteriorly directed tinsel flagellum. The tubular tinsel flagellum characteristically bears two rows of stiff, glycoproteinaceous, tripartite hairs previously referred to as mastigonemes but now increasingly referred to as *stramenopili*. Such organisms are often referred to as stramenopiles.

Although alternative heterokont arrangements in which two nontinsel flagella differ are found in other unrelated groups (such as the dinoflagellates or endoparasitic slime molds (plasmodiophorids), these organisms are unrelated to the stramenopila-bearing (stramenopilous) heterokonts and are not generally referred to as heterokont genera.

Evolutionary Relationships

Stramenopilous heterokonts are a diverse group of protists containing tubulocristate mitochondria that are phylogenetically related by the presence of stramenopili (usually associated with the tinsel flagellum, otherwise on the cell surface). Their precise relationship to other eukaryotes is poorly defined, but they clearly represent one of the early independent lineages associated with the crown eukaryotic radiation (which included plant, animal, and fungal lineages). The inclusion of major autotrophic (many of the algal forms contain chlorophyll *a* and *c*) and heterotrophic groups has led to a conflicting nomenclature.

The initially proposed kingdom *Chromista* presumes heterotrophs were derived from ancestral autotrophs, while the more recently proposed kingdom *Stramenopila* implies a heterotrophic ancestor, with autotrophs as the derived forms. Relationships between the autotrophic and heterotrophic taxa, however, are still not clearly resolved. Heterotrophic heterokonts (heterokont fungi) include the fungal-like oomycetes, hyphochytriomycetes, thraustochytrids, and labyrinthulids. Autotrophic heterokonts (heterokont algae) include the chromophytic algal groups, represented by diatoms, brown algae, golden algae, and yellow-green algae.

Oomycetes

Often referred to as the oomycetous water molds, the oomycetes (*Peronosporomycetes*) form the largest and most ubiquitous group of heterotrophic stramenopiles. Free-living forms occupy diverse ecological niches ranging from freshwater and marine to terrestrial environments. Both terrestrial and marine forms include saprophytic and obligately, or facultatively, parasitic genera.

Hosts include a range of nematodes, arthropods, molluscans, algae, and plants. Several of the plant pathogens have impacted the cultural and economic history of humans. These include the causative agents for a variety of root rots, downy mildews, white rusts, and late blights. Downy mildews of grapes (*Plasmopara*) and tobacco (*Peronospora*) were responsible for the near-decimation of the French wine industry and the Cuban tobacco industry in the late 1870's and the 1980's, respectively. Similarly, *Phytophthora infestans*, the causative agent of potato late blight, was responsible for the Irish Potato Famine of the mid-1840's and, during World War I, for the starvation of German civilians in 1915-1916.

Diatoms

Diatoms are the most diverse and abundant of the photosynthetic heterokonts. They are among the most important aquatic photosynthesizers and are probably the most numerous aquatic eukaryotes. Found as single cells or chains of cells in marine, freshwater, and terrestrial environments, they often dominate the phytoplankton of nutrient-rich waters. The cells are enclosed in a highly ornamented silica box (*frustule*). These frustules are of either the centric type, with apparent radial symmetry, or of the pennate type, with apparent bilateral symmetry. The chloroplasts of diatoms commonly contain the carotenoid fucoxanthin as an accessory photosynthetic pigment. A single tinsel flagellum, but no whiplash flagellum, is evident in sperm cells of those species in which sexual reproduction is known. A few species have been associated with fish kills, while some species of *Pseudo-nitzschia* produce the toxin domoic acid, responsible for amnesiac shellfish poisoning in humans. In the newer taxonomic systems they are included in the phylum *Ochrophyta* rather than the phylum *Bacillariophyta*.

Chrysophytes

Chrysophytes are often referred to as the golden algae because of the dominance of the pigment fucoxanthin. The phylum *Chrysophyta* had previously included a loosely related assemblage of algal forms, such as haptophytes, synurophytes, and diatoms. The term "chrysophycean," referring to the class *Chrysophyceae* of the *Ochrophyta*, now more appropriately includes those chrysophytes phylogenetically related by ultrastructural, pigment, and molecular analyses. These chrysophyceans are unified by the use of chlorophylls a, c_1, and c_2, the accessory pigments fucoxanthin and violaxanthin, and a silica-walled resting stage (stomatocyst, stomatopore). They are present as unicellular or colonial forms. Representative genera include *Ochromonas*, *Dinobryon*, and *Chrysocapsa*.

Brown Algae

The brown algae (phaeophyceans) are primarily marine algae and range in linear length from microscopic filaments to several meters (up to 60 meters and 300 kilograms in the giant kelp *Macrocsystis pyrifera*). Many species exhibit specialized organs and tissues such as leaflike *blades*, rootlike *holdfasts*, and cells resembling sieve elements of higher land plants. Like other ochrophytes, they have two forms of chlorophyll c as well as fucoxanthin and violaxanthin. Species of *Laminaria*, *Fucus*, and *Macrocystis* are primary sources of alginates used in a variety of industrial applications, from the textile industry (prints) to food processing (as a thickening agent).

M. E. S. Hudspeth

See also: Algae; Brown algae; Chrysophytes; Diatoms; Oomycetes; Phytoplankton; *Protista*.

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HIGH-YIELD CROPS

Categories: Agriculture; economic botany and plant uses; food

High-yield agricultural crops are those that have been bred, genetically modified, or fertilized to increase their production yields.

The health and well-being of the world's growing population are largely dependent on the ability of the agricultural industry to raise high-yielding food and fiber crops. No one knows for certain when the first crops were cultivated. At some time in the past, people discovered that seeds from certain wild grasses could be collected and later planted where they could be controlled during the growing process and eventually harvested for food. Agriculture was firmly established in Asia, India, Mesopotamia, Egypt, Mexico, Central America, and South America at least six thousand years ago.

Development of Modern Agriculture

Farming practices have undergone many changes, but until the nineteenth century most farms and ranches were family-owned, and people primarily practiced subsistence agriculture. Just as in almost all other industries, the arrival of the Industrial Revolution dramatically changed the agriculture industry. Inventions such the cotton gin in 1793, the mechanical reaper in 1833, and the steel plow in 1837 led the way to mechanization of most farms and ranches. The Industrial Revolution produced significant societal changes, as people involved in agricultural production left the farms to work in city factories. Fewer and fewer people were required to produce more and more agricultural crops for an increasing number of consumers.

As the population continued to grow, it became necessary to select and produce higher-yielding crops. The *Green Revolution* of the twentieth century helped make this possible. Agricultural scientists developed new, higher-yielding varieties of numerous crops, particularly the seed grains. Tremendous increases in the global food supply resulted from the use of these higher-yielding crops, along with improved farming methods.

Improved Yields

There are two major ways to improve yield in seed grains such as wheat: produce more seed per seed head or produce larger seeds. Numerous agricultural practices are required to produce higher yields, but one of the most important is the selection and breeding of genetically superior cultivars. When a plant with a potentially desirable gene mutation appears to improve a yield characteristic, seeds are collected and studied to see whether they consistently produce plants with higher yields.

This selection process remains one of the major means of improving yield in agricultural crops. Advances in the understanding of genetics have made it possible to breed some of the desirable characteristics that have resulted from mutation into plants that lacked the characteristic. In addition, the advent of *recombinant DNA technology* makes it possible to transfer genetic characteristics from one plant to any other plant.

The high-yielding varieties led to an increased reliance on *monoculture*. This practice of growing only one crop over large areas has made efficient, mechanized farming possible, with relatively few workers. It has also decreased the genetic variability of many agricultural plants, increased the need for commercial fertilizers and pesticides, and produced an increased susceptibility among crops to damage from a host of biotic and abiotic factors. For example, most pests prey upon specific plant species. If many fields are planted in one crop, the entire farm—and possibly the whole community—is susceptible should a pest strike. The corn blight that destroyed more than 15 percent of the North American crop in 1970 would have been less severe if a single cultivar of corn had not been so heavily planted in the United States.

The major high-yielding crops, in terms of land devoted to their culture and the total amount of produce, are wheat, corn, soybeans, rice, potatoes, and cotton. Each of these crops originated from a low-yielding native plant that was gradually converted into one of the highest-yielding plants in the world.

High-Yield Grains

Throughout the world, large portions of agricultural land are devoted to the production of wheat (*Triticum sativum*). Wheat is the staple of forty-three countries and 35 percent of the people of the world. It also provides 20 percent of the total food calories for the world's population.

The cultivation of wheat is older than the written history of humankind. Its place of origin is unknown, but many authorities believe wheat may have grown wild in the Tigris and Euphrates Valleys and spread from there to the rest of the Old World. Wheat is mentioned in the first book of the Bible, was grown by Stone Age Europeans, and was reportedly produced in China as far back as 2700 B.C.E. Wheat is widely adapted throughout the world and can grow in many climates; about the only places where wheat does not grow are those with climates that are continually hot and moist.

The total production of rice (*Oryza sativa*) is similar to that of wheat, and it is the principal food crop for nearly half of the world's population. Rice has been under cultivation for so long that its country of origin is unknown; however, botanists believe that the plant originated in Southeast Asia. Rice was being cultivated in India as early as 3000 B.C.E. and spread from there throughout Asia.

Image Not Available

Although rice is currently produced on all continents, more than 90 percent of the total world crop is grown in Asia. Rice was introduced into the United States in 1694, and the total U.S. crop is produced in just six states. The per capita consumption of rice is less than 10 pounds per person in the United States; however, in some Southeast Asian countries, the per-capita consumption can be as high as 325 pounds per person.

Corn (*Zea mays*) ranks third behind wheat and rice in world production of cereal grain. Corn may be the Americas' greatest contribution to agriculture. The earliest traces of the human use of corn date back to about 5200 B.C.E. It was probably first cultivated in the high plateau region of central or southern Mexico and was the basic food plant of all pre-Columbian advanced cultures and civilizations, including the Inca of South America and the Maya of Central America.

Corn is still produced primarily in the Western Hemisphere, although some is produced in Europe. It makes up more than 50 percent of the acreage devoted to all seed grains in the United States. Of the total grain crop produced, approximately 85 percent is fed to animals.

High-Yield Potatoes, Soybeans, and Cotton

The potato (*Solanum tuberosum*) is the New World's second gift to world agriculture. The white potato is capable of nourishing large populations, especially in cooler regions where many other crops will not grow. It contains large stores of energy, high-quality protein, and valuable minerals and vitamins.

Potatoes are indigenous to South America and probably originated in the central Andean region. The potato has become one of the world's great food crops because it combines, in one crop, the desirable characteristics of high yield, low cost, and nutrition as well as palatability. Potatoes are grown in practically all countries of the world. As the potato is better adapted to cool, humid climates, total production and average yields are much higher in northern Europe than in the United States.

Soybeans (*Glycine max*) have been an important food crop in Asian countries, particularly China and Japan, since long before the time of recorded history. Soybeans will grow in nearly all soil types except extremely deep sand and are adapted mainly to temperate regions with fairly humid, warm growing seasons. Hence, soybeans are now grown in much of the New World.

Cotton (*Gossypium*), with a total annual production of more than 13 million tons, is by far the most important fiber crop in the world. Humans heavily rely on it for clothing and other textiles. Cotton enters the daily life of more people than any other product except salt.

Cotton fiber has been known and highly valued by people throughout the world for more than three thousand years. Like most crop plants that have been in cultivation a long time, cotton has an obscure origin. A vigorous cotton industry was present in India as early as 1500 B.C.E. From India, the cultivation of cotton spread to Egypt and then to Spain and Italy. In the New World, a different species of cotton was being grown in the West Indies and South America long before the Europeans arrived. Although cotton is native to tropical regions, it has been adapted to humid, subtropical climates where there are warm days, relatively warm nights, and a frost-free season of at least two hundred days.

Genetic Engineering

The importance of plant nutrition was discovered during the nineteenth century, and the use of fertilizers has dramatically increased crop yields. Advances in the understanding of genetics in the early part of the twentieth century made it possible for people to breed desirable characteristics into plants, and people began to breed plants to increase yields. At about the same time, the development of large-scale chemical synthesis and processing made it possible to produce a variety of chemical agents to control plant pests, but many of these chemicals were found to be hazardous to the environment.

Developing plants with high natural resistance would decrease the reliance on chemical pesticides, so plant breeders started to breed not only for increased yields but also for increased resistance. Plant breeders began to examine older, abandoned cultivars, discarded breeders' stock, wild plant relatives, and native or foreign cultivars and occasionally induced mutations for increased yields or resistance to pests. When a particularly attractive trait was found, genetic crosses were made until progeny that showed improved yields and increased resistance were obtained. These developments in plant resistance have been partially responsible for the tremendous advances in the production of high-yield crops during the last half of the twentieth century.

To cope with the need for crop varieties that will both provide higher yields and exhibit greater resistance to pests and disease (thus avoiding the use of too many chemicals), new biotechnologies, including genetic engineering, are being refined. Total crop production can also be raised by using biotechnology to engineer plants that will flourish under what may have previously been considered marginal growing conditions, such as salty soil. As the population grows, the agricultural industry will feel the pressure to produce more food, with the added element of pressure to make crop production more friendly to the environment. Biotechnology has the potential to play a major role in the development of a long-term, sustainable, environmentally friendly agricultural system.

The future development of higher-yielding crops that can be harvested mechanically and the production of new types of equipment to facilitate the harvesting process will also be important improvements in the production of high-yielding crops.

D. R. Gossett

See also: Agricultural crops: experimental; Agriculture: modern problems; Agriculture: world food supplies; Biopesticides; Biotechnology; Corn; Fertilizers; Genetically modified foods; Green Revolution; Horticulture; Hybridization; Monoculture; Plants with potential; Resistance to plant diseases; Rice; Wheat.

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HISTORY OF PLANT SCIENCE

Categories: Disciplines; history of plant science

The study of plants has, since the fifth century B.C.E., expanded from the broad-based discipline of natural philosophy to include the specialized studies of genetics, ecology, and microbiology.

Plant Science in Antiquity

Natural philosophy, the "science" of its day, arose in Greece during the 500's B.C.E. and included speculations about plants, such as whether domesticated plants descended from wild plants. Full-fledged science began at the Lyceum in Athens, founded by Aristotle in 335 B.C.E. Upon Artistotle's departure from Athens in 323, his colleague Theophrastus became head of the Lyceum. He was author of two botanical treatises which cover general natural history. *Historia plantarum* ("Enquiry into Plants" in *Enquiry into Plants and Minor Works on Odours and Weather Signs*, 1916) emphasizes description of plants, their parts, and their locations, and *De causis plantarum* (*De Causis Plantarum*, 1976-1990) emphasizes *physiology*. The works include accounts of crops, fruit trees, and medicinal plants, but the stronger emphasis is on abstract knowledge. Greek physicians and pharmacists were more practical-minded, as is seen in Pedanius Dioscorides' *De materia medica*, compiled during the first century C.E. Although it concerns medicinal plants, practically all plants had medicinal uses, and Dioscorides was the first to give a species-by-species description of the different plants known in much of the Mediterranean region.

The Romans were heavily influenced by Greek civilization, yet Romans were more practical and less abstract thinkers than the Greeks; there were no important Roman scientists. Instead of botanical treatises, Romans wrote agricultural manuals, of which the longest and most thorough was Lucius Junius Moderatus Columella's in the early first century C.E. He used Greek sources, especially the work of Theophrastus of Eresos, and also Roman sources and his own experiences. Columella's near contemporary, Gaius Plinius Secundus (also known as Pliny the Elder), was one of the Roman compilers of encyclopedias; he also used Greek and Roman sources, but his goal was to educate and entertain. However, that did not preclude dispensing practical knowledge. His lengthy accounts of plants emphasized useful species and included curious folklore.

Middle Ages and Renaissance

Before the western Roman Empire declined in the later 400's C.E., original contributions to natural history were already rare. The eastern Empire persisted for another millennium, but it was politically and economically static, if not stagnant, and its main cultural contribution was to transmit Greek learning to the Arabs during the 700's and to the Italians during the 1400's. Arabic-language science was superior to Roman science and sometimes equal to ancient Greek science. It was studied and enlarged over a much broader geographical area than ancient science had been. Generally, Arabic-language authors did not use Roman sources, the exception being on the Iberian Peninsula, where Ibn al-ʿAwwam compiled his agricultural treatise during the second half of the 1100's. Dioscorides' manual was translated into Arabic and became the foundation of Arabic pharmacopoeias. Arabic-language science surpassed Greek science in the extent of its knowledge but rarely in theoretical understanding.

In the year 1000 C.E. both the Byzantine and Islamic civilizations were more prosperous and sophisticated than Latinized Western Europe, and yet by 1400 Western Europe had surpassed both adjacent civilizations in cultural achievements. There is no simple answer as to why Western Europe made a greater investment in higher education than any other civilization in the world, but it did so, and that investment paid off in science. While Western Europe's culture was rather rudimentary, scholars took the opportunity to translate important works of ancient or medieval authors from Arabic or Greek into Latin and then built upon them. The most impressive botanical example was Albertus Magnus's *De vegetabilibus et plantis*, written during the 1200's without access to Theophrastus's works but in the Lyceum tradition. Albertus used Greek and Arabic sources available in Latin translations and also Latin authors and his own experiences. However, medicine was much more important than natural history in the universities, and *De materia medica* was where most botanical studies focused.

During the 1450's Johann Gutenberg developed a printing press that used movable type. It was an important step for botany and medicine because science books were prominent among early printed works. Scholars of the Italian Renaissance were enthusiastic about ancient Greek and Roman civilizations and studied living plants to decide which ancient names and descriptions fit the species they found. This concern then spread northward during the 1530's, as seen in Euricius Cordus's *Botanologican*, Otto Brunfels's illustrated herbal, and Jean Ruel's development of terminology to describe parts of plants. Leonhard Fuchs combined Ruel's concern for terminology with Brunfels's concern for illustrations in his elaborate herbal (1542). In Italy, Pier Andrea Mattioli tied the old text of Dioscorides to the new trend in illustration (1544), while in France and the Low Countries three scholars—Rembert Dodoens, Charles de L'Écluse, and Matthias L'Obel—sought new species to name and describe for their herbals. Konrad Gesner and Valerius Cordus did equally outstanding research, yet the influence of each was impaired by death before their works were fully published.

Scientific Revolution

The precise investigations contrived by Nicolaus Copernicus, Galileo Galilei, and Isaac Newton made ancient astronomy and physics obsolete, and Andreas Vesalius and William Harvey did the same for ancient anatomy and physiology. Innovations in botany were more evolutionary than revolutionary. Luca Ghini developed the botanic garden and herbarium as teaching and research aids, and his student Andrea Cesalpino wrote the first true textbook of botany (1583). Joachim Jung developed morphological terminology beyond that of Ruel and Cesalpino but without benefit of a microscope.

When the microscope became available to Robert Hooke, he described plant cells and mold fungi

(1665). Following his lead during the 1670's were Nehemiah Grew and Marcello Malpighi, who described the anatomy of plant tissues. The Dutch microscopist Antoni van Leeuwenhoek examined small plants and discovered bacteria but not bacteria's role in disease. Cesalpino chose fruit as a key to plant classification, but Fabio Colonna decided that flowers provided a better guide to relationships. Colonna's judgment was strengthened by the discovery of the sexuality of plants, which Grew suspected and Rudolph Jakob Camerer demonstrated. Johann Hedwig later demonstrated sexuality in bryophytes and algae but failed to understand sexuality in ferns and fungi.

The age of exploration and the scientific revolution coalesced when explorers returned to Europe with previously unknown plants. Brothers Gaspard and Jean Bauhin facilitated knowledge of the increase in known species by using binomial nomenclature in their descriptions of about six thousand species. Engelbert Kämpfer botanized in Iran and Japan, published a travel book, and brought home a herbarium that eventually reached the British Museum. John Ray traveled only in Western Europe, including Britain, but his *Historia generalis plantarum* (1686-1704; *A Catalogue of Mr. Ray's English Herbal*, 1713) provided a synthesis of knowledge from many explorers' observations and specimens. Joseph Pitton de Tournefort's contributions to botany were enhanced by his explorations in the Levant, yet his main influence came from careful studies on plant genera.

In the eighteenth century the Swedish naturalist Carl Linnaeus formalized the system of binomial nomenclature and his sex-based classification system in response to all the newly discovered plants. The ease with which species could then be identified stimulated the search for still more species, which he named and classified. Some of his students, including Pehr Kalm and Carl Peter Thunberg, traveled far abroad and returned with observations and specimens. Michel Adanson explored Senegal within a French context and also devised a natural classification. John Bartram and his son William responded to European interest by discovering American plants to describe and send abroad. Joseph Banks, sailing with Captain James Cook, initiated an important partnership between British botanists and the navy, which blossomed during the 1800's. Seeds and live plants brought back to Europe commonly were planted in botanic gardens located at universities and in capital cities, where they were accessible to botanists. Directorships of these gardens provided employment for some botanists.

Experimentation came late to botany. Edme Mariotte set a good example (1679) with his experiments in plant physiology, but his results were rather inconclusive. More successful was Stephen Hales, whose inspiration came from animal physiology; he devised methods to measure the movements of sap in vines and saplings and correlate movements with sunlight. Although his experiments were well published (1727), he had no followers, and his experiments during the later 1700's addressed different issues. John Turberville Needham and Georges-Louis Leclerc de Buffon thought they had demonstrated spontaneous generation of life, but Lazzaro Spallanzani was skeptical and conducted superior experiments that showed they were mistaken. Spallanzani's work inspired Jean Senebier, who translated Spallanzani's works into French and became himself an outstanding experimentalist. Another experimental tradition arose within a chemical context, which utilized Hales's apparatus. Chemists explored ways to generate gases and to identify them. This led Joseph Priestley, Horace Bénédict de Saussure, and Jan Ingenhousz to conduct experiments on live plants in glass enclosures during the 1770's. Camerer (1694) and Josef Gottlieb Kölreuter in the later 1700's were among the early experimenters on sexual reproduction in flowers.

Taxonomic Botany

Taxonomic botany, as formally organized by Linnaeus, became the main scientific specialty during the 1800's because many new species were still being discovered in all parts of the world. Outstanding collectors included Alexander von Humboldt, Robert Brown, Joseph Dalton Hooker, George Englemann, and Edward Lee Greene. The accumulation of herbaria specimens and plantings in botanic gardens enabled botanists to produce encyclopedic accounts of species, such as those by Augustin Pyramus de Candolle and his son Alphonse Louis de Candolle and by George Bentham and Hooker.

Phytogeography

Phytogeography developed using those same plant collections and taxonomic encyclopedias. Linnaeus had begun writing on this subject, and

Karl Ludwig Willdenow, who trained Humboldt, carried it further. However, Humboldt's extensive explorations, collections, environmental measurements, and scientific publications became the real foundation of phytogeography (1808). In 1820, Augustin de Candolle introduced the concept of competition among species as a factor in the distribution of species, and his son Alphonse de Candolle wrote an important synthesis of phytogeography, *Géographie botanique raisonée* (1855, 2 volumes). August Heinrich Rudolph Grisebach achieved another world synthesis in 1872. Hewett Cottrell Watson founded British phytogeography (1835) and devoted his career to a study of the distribution of all British species and their variability. Asa Gray, an American who specialized in taxonomic botany, became, through his association with Joseph Hooker and Charles Darwin, the United States' leading phytogeographer.

Evolution and Heredity

Ideas on the evolution of species made little headway until the French Revolution (1789); then two naturalists wrote books discussing it in plants and animals. Although the British became enemies of the Revolution, Erasmus Darwin favored it. Both he and Jean-Baptiste Lamarck published speculative hypotheses that viewed struggle as a source of new traits, to be followed by the inheritance of the new traits. Johann Wolfgang von Goethe speculated in a more idealistic way about species varying from a basic type.

Paleobotany was less popular than vertebrate paleontology, but Alexandre and Adolphe-Théodore Brongniart, father and son, made important discoveries. Franz Unger followed in their footsteps. It became obvious to them that fossil species differed from living species, causing Unger to speculate on changes in species. Charles Darwin, who read his grandfather's books, outdid Erasmus Darwin with a carefully developed theory of evolution by natural selection. Alfred Russel Wallace had read many of the same scientific works as Charles Darwin, and he had also read *Darwin's Journal of Researches* (1839) before publishing his own ideas on evolution that resembled Darwin's theory of natural selection. That theory remained controversial for decades after its publication in Darwin's *On the Origin of Species by Means of Natural Selection* (1859), but it also stimulated much study of both fossil and living species to discover the details of evolution. Charles Edwin Bessey took up the challenge of explaining the history of plant evolution.

Heredity was a weak link in Darwin's theory of evolution, awaiting the advent of *genetics*. Karl Gärtner conducted numerous empirical studies but without achieving a theoretical breakthrough. When Gregor Mendel, an inconspicuous monk, developed experiments on peas which clarified patterns of inheritance, his thinking was beyond his audience's comprehension, including Karl Wilhelm von Nägeli, to whom he turned for encouragement. Mendel's 1866 article was only appreciated in 1900, when three botanists—Karl Franz Joseph Erich Correns, Erich Tschermak, and Hugo de Vries—independently rediscovered it and Mendel's laws. Meanwhile, others followed cell division more and more closely, demonstrating that chromosomes carry hereditary material (genes) and that those chromosomes divide in a regular way during both mitosis and meiosis.

Cytology, Fertilization, and Alternation of Generations

Studies on *cytology*, *fertilization*, and *alternation of generations* advanced considerably during the 1800's because advances in the quality of microscopes and slide-preparation techniques allowed botanists to achieve a more precise understanding than had been possible earlier. Charles-François Brisseau de Mirbel initiated French cytology with studies on plant anatomy, seeds, and embryos (1800-1832). Brown used a microscope to discover the cell nucleus. Matthias Jakob Schleiden, who used the improved microscopes, is credited with establishing the cell theory in plants—after his colleague. Theodor Schwann had done so for animals, though Schleiden misunderstood cell division. Nevertheless, his botany textbook (1942-1943) inspired others to investigate cellular processes. Hugo von Mohl advanced microscopy and developed the protoplasm concept. Wilhelm Friedrich Benedict Hofmeister and Nathanael Pringsheim studied fertilization and alternation of generations in diverse groups of plants. Later, Walther Flemming and Eduard Adolf Strasburger used improved techniques to study chromosomes during mitosis and meiosis.

Microbiology and Mycology

Microbiology and *mycology* also benefited from advances in microscopy and cytology. Ferdinand

Julius Cohn, Anton de Bary, and Louis Pasteur all made their main contributions during the 1850's, 1860's, and 1870's. Cohn studied unicellular algae and bacteria. De Bary founded mycology with studies on sexual reproduction in fungi and on the two-stage life cycle of wheat rust. Pasteur vindicated Schwann's claim that alcohol fermentation is caused by yeast and discovered anaerobic metabolism. Pasteur also investigated the causes of various diseases, several of which were bacterial. Robert Koch developed bacteriological techniques that enabled him to demonstrate clearly the bacterial cause of several diseases.

Physiology and Agronomy

Physiology and *agronomy* received less attention than several other botanical specialties during the first half of the nineteenth century, though Henri Dutrochet showed that plant respiration and animal respiration are essentially the same. In the second half of the century, Julius von Sachs and John Bennet Lawes made these specialties more conspicuous. Sachs was a brilliant experimentalist, teacher, and author of textbooks, making him the founder of modern plant physiology. Lawes used private resources to found modern agricultural research in Britain at a time when the U.S. Congress was establishing land grant colleges and state agricultural and forestry research stations. By the end of the century, American scientists were doing as much or more agricultural research as the rest of the world combined. Vasily Vasilievich Dokuchaev developed soil science (agronomy) as an aid to Russian agriculture.

Twentieth Century

All of the specialties from the 1800's continued throughout the 1900's. In addition, *genetics*, *ecology*, and *molecular biology* became important specialties. Plant sciences advanced at an unprecedented rate and in more countries than ever before.

Evolution became the organizing theory for all of biology. However, *evolutionary biology* retained a close relationship with taxonomy and phytogeography. Bessey, and later John Hutchinson, advanced the understanding of the evolution of vascular plants as a whole, while Marie Stopes contributed paleobotanical evidence. Two Russians took the lead in their subspecialties: Nikolai Ivanovich Vavilov used genetics and cytological evidence to clarify the history and phytogeography of domesticated plants, and Aleksandr Ivanovich Oparin used physiology and biochemistry to investigate the origin of life.

Genetics did not develop within a strong evolutionary context during its first four decades, though de Vries had an evolutionary motive to study heredity and Wilhelm Ludwig Johannsen's studies on breeding homozygous versus heterozygous strains of peas had evolutionary implications. Genetics was advanced by both botanists and zoologists. The three re-discoverers of Mendel's laws and article were botanists. Thomas Hunt Morgan studied gene linkage on chromosomes using fruit flies, and later Barbara McClintock continued these studies using maize. Albert Francis Blakeslee initially studied sexual fusion in fungi but is remembered more for discovering that colchicine produces polyploidy in plant chromosomes. A new specialty, molecular biology, arose out of James Watson's and Francis Crick's struggle to understand the structure and function of the gene, as represented by deoxyribonucleic acid (DNA).

Four English botanists advanced plant anatomy, particularly at the level of cellular biology. Ethel Sargent studied intracellular structures relating to cell division and vascular bundles as clues to evolution. Vernon Herbert Blackman studied plant cytology and alternation of generations in rust fungi. Agnes Robertson Arber wrote monographs on monocotyledons as a whole and on particular groups of them. Irene Manton used an electron microscope to study chromosomes and cell organelles. An Italian animal histologist, Camillo Golgi, discovered the "Golgi body" within an owl's brain cell (1898), but explanation of its function came much later. Christian De Duve was a Belgian cytologist and biochemist who used a centrifuge and electron microscope in his research to discover new organelles: lysosomes and peroxisomes.

Physiology flourished during the 1900's, beginning with Frederick Frost Blackman's studies on respiration, Jagadis Chandra Bose's on biophysics, and Mikhail Semenovich Tsvet's on cytophysiology. In the 1930's Paul Jackson Kramer began investigating water usage, and Hans Adolf Krebs began investigating cyclic metabolic pathways. After World War II, François Jacob studied the functioning of DNA and RNA, the genetic control of enzymes, and helped develop the concept of the operon in cellular physiology. Melvin Calvin took advantage of availability of radioactive tracers, particularly carbon 14, to clarify biochemical steps in photosynthesis.

Ecology arose simultaneously with genetics but at a slower pace. Johannes Warming, Gottlieb Haberlandt, and Andreas Franz Wilhelm Schimper were botanists who laid a foundation for plant ecology shortly before 1900, and the self-consciously ecological researches by Christen Raunkiaer, Felix Eugen Fritsch, Frederic Edward Clements, and Henry Chandler Cowles built upon their foundation. Fritsch studied periodicity in phytoplankton and helped found the Freshwater Biological Association. Andrew Ellicott Douglass was interested in sunspot cycles, and to document their occurrence he developed *dendrochronology*, which also was used to clarify vegetation cycles. Clements was an enthusiastic theoretician; Cowles was more cautious, and Henry Allan Gleason and Arthur George Tansley attacked Clements's concepts of climatic climax and plant communities as overinterpretations of the evidence. Gleason preferred the concept of association, which John Thomas Curtis modified into the continuum. Tansley, who helped found the British Ecological Society and the *Journal of Ecology*, preferred his own ecosystem concept, which became extremely important after World War II. Early examples of the use of ecological concepts for environmental protection are Paul Bigelow Sears's *Deserts on the March* (1935) and Rachel Carson's *Silent Spring* (1962).

Microbiology expanded beyond what can be indicated here. Five virologists illustrate the involvement of plant scientists in microbiology. Dmitri Iosifovich Ivanovsky investigated tobacco mosaic disease in the 1890's and early 1900's and found evidence that the causative pathogen passed through a porcelain filter. His microscopic observations were excellent, yet he concluded that the pathogen was a bacterium, whereas it was later determined to be a virus. Martinus Willem Beijerinck investigated the puzzle and found the pathogen is not a toxin and could not be cultivated in vitro; he concluded it must be a molecular pathogen. Three other filterable pathogens were also identified in the same period. Later, Louis Otto Kunkel studied viral diseases in potatoes and sugarcane in order to inhibit their transmission. Frederick Charles Bawden and N. W. Pirie discovered that plant viruses are nucleoproteins.

Agronomy benefited enormously from the advance of many sciences, as indicated by the work of four plant scientists. George Washington Carver drew upon chemistry to find new uses for peanuts and sweet potatoes. Rowland Harry Biffen used the new genetics to improve crops, including rust-resistant wheat. Vavilov used genetic variability in wild plant populations to modify closely related domesticates to achieve varieties best suited to the Soviet Union's diverse environments. Norman E. Borlaug, known as the father of the Green Revolution, bred varieties of rice, corn, and wheat that greatly increased yields in tropical countries.

Frank N. Egerton

See also: Agricultural revolution; Biotechnology; Botany; Cell theory; Dendrochronology; DNA: historical overview; Ecology: concept; Ecology: history; Environmental biotechnology; Evolution: historical perspective; Genetics: Mendelian; Genetics: post-Mendelian; Green Revolution; Paleobotany; Paleoecology; Plant science.

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HORMONES

Categories: Cellular biology; physiology

Plant hormones are the major group of chemical messengers by which most plant activities are controlled. The five different groups of hormones regulate virtually every aspect of plant growth and development.

The majority of higher plants begin life as seeds. When seeds germinate, the embryonic tissues begin to grow and undergo differentiation until, ultimately, the various parts of the mature plant are formed. Every aspect of this growth and development is regulated by a group of chemical messengers called hormones. These plant hormones, or *phytohormones*, function as *plant regulators*. A plant regulator is an organic compound, other than a nutrient, which in small amounts promotes, inhibits, or otherwise modifies a basic plant process. Hormones are produced in one area of the plant and transported to another area, where their effects are exerted. There are five major classes of identifiable plant hormones, and others will surely be identified in the future: *auxins*, *cytokinins*, *gibberellins*, *ethylene*, and *abscisic acid*.

Auxins

Although there are numerous plant responses to the auxins, one of the primary functions of this group of hormones is to cause increases in cell length by loosening cell walls and increasing the synthesis of cell-wall material and protein. In order for plants to grow, cells produced at the stem or root *meristems* must undergo this process of elongation. No cell elongation can take place in the absence of auxin.

The cell elongation promoted by auxins results in regular growth, and it is also responsible for various *tropisms*. For example, *phototropism* causes plants

Plant Hormones and Their Functions

Hormone	*Responsible For*
Abscisic acid	Leaf abscission
Auxins	Cell elongation, tropisms, root growth
Brassinolides	Cell division, cell elongation
Cytokinins	Cell division, increased metabolism, chlorophyll synthesis
Ethylene	Fruit ripening, fruit abscission, dehiscence
Gibberellins	Stem elongation, breaking dormancy
Jasmonates	Seed germination, root growth, accumulation of storage and defense proteins
Salicylic acid	Pathogen defense activator
Systemin	Stimulates defense genes after tissue wounding

to grow toward a source of light. *Gravitropism* is a response to gravity and causes the roots to grow downward.

Besides cell elongation, auxins will initiate root growth at the base of the stem. Auxins inhibit growth of the lateral buds; as long as auxins are being transported down the stem from the apical bud, the lateral buds will not develop. This phenomenon, known as *apical dominance*, accounts for the fact that plants will not bush out until the apical buds are removed. While there are a number of natural and synthetic compounds that exhibit auxin activity, the major, naturally occurring auxin is a compound called indole acetic acid (IAA).

Cytokinins

Cytokinins are referred to as the cell division hormones, and while cell division will take place only in the presence of one of these hormones, the cytokinins stimulate a number of other plant responses as well. These hormones have been shown to retard senescence in detached leaves and to create *metabolic sinks*, areas within a tissue where increased metabolism takes place. As a result, there is an increase in transport of metabolites to the area. For example, amino acids will be transported to a site where the presence of cytokinins has increased protein synthesis.

In many plants, these hormones stimulate the production of larger, greener leaves by causing leaf cells to expand and by promoting both chloroplast development and chlorophyll synthesis. A number of naturally occurring substances that exhibit cytokinin activity have been identified. Of these, *ribosyl zeatin* is one of the most abundant in plants.

Gibberellins

Many dwarf plants exhibit a decrease in height because they contain low levels of the stem elongation hormones called gibberellins. These hormones, of which more than thirty have been identified, increase the amount of water taken up by the cells of stems. As the individual cells swell from the increased water content, the stem grows longer. In addition to stem elongation, the gibberellins elicit a number of other plant responses.

The seeds of numerous plant species exhibit *dormancy*, which can be broken by gibberellins. The length of the daylight period (*photoperiod*) is crucial to the flowering response in many plants. Fall- and winter-flowering plants require short days, while the plants that flower in the spring and summer must be exposed to long days. Some plants must also be subjected to a prolonged period of cold before flowering can occur. The gibberellins can substitute for the long day or the cold requirement in many plants. Additionally, the gibberellins can produce thicker stem growth in certain woody plants and increase the number of fruits that develop in some species.

Ethylene

One of the most important functions of ethylene is fruit ripening. Some fruits produce almost no ethylene until a few days before ripening and then release large amounts. Such fruits are said to be *climacteric*. *Nonclimacteric* fruits continuously produce more moderate amounts of the hormone throughout the ripening period. In all types of fruit, ethylene must be present before ripening can occur.

Ethylene also causes ripened fruit to *abscise* (separate from the parent plant) and is even involved in *dehiscence* (removal of the husk) of some types of fruit, such as pecans and walnuts. In addition to its role in fruiting, ethylene can initiate root development, cause leaves to droop, inhibit plant motion, and increase metabolic activity in some plants. Because ethylene inhibits auxin transport, it will also release apical dominance.

Abscisic Acid

The name "abscisic acid" was chosen because one of the major activities of this compound is to promote *leaf abscission*. During the autumn of the year, the concentration of this hormone increases in many plants. This high concentration causes the leaves to senesce, turn yellow, and abscise. Abscisic acid also inhibits growth and promotes both bud and seed dormancy.

Hormone Mechanisms

In the vast majority of hormone responses, *enzyme activation* or *gene induction* (the turning on of genes that produce new enzymes or other proteins) can be detected. This suggests that the hormones are initially acting as "first messengers." These first messengers react with the cellular membranes, and as a result of these reactions, the membranes activate "second messengers" within the cell. The second messengers then activate a group of substances referred to as *inducers*.

One group of inducers is the protein kinases, a


PhotoDisc

The plant hormone ethylene has been applied in commercial operations to husk walnuts.

class of enzymes that add phosphate to other proteins. Protein kinases activate various enzymes or induce DNA (deoxyribonucleic acid) regulatory proteins to control genes responsible for cell elongation, cell division, flowering, fruit ripening, or one of the many other responses to the hormones. Each class of hormones activates a different set of protein kinases to produce a different set of responses. Most of the information concerning protein kinases is based on studies of animal systems, but it is highly likely that a similar type of mechanism is also present in plants.

Hormone Uses

Horticultural and agricultural applications of hormone technology are widespread. A dilute solution of auxin is used to promote the root development necessary to propagate stem cuttings vegetatively. The cytokinins have been used to enhance sex ratios among the plants in the cucumber family, producing more female plants and thus more fruit. For years, ethylene has been used to enhance flowering and, in turn, increase yields in pineapples. Ethylene has also been used to promote root formation in stem cuttings and has been applied in commercial operations to husk walnuts.

Because gibberellins increase growth in the cellular layer that produces thicker stems in pines, seedlings can be sprayed with the hormone and be made ready for transport in two years rather than the normal three or four. The action of gibberellins on the production of amylase (an enzyme that breaks down starch to glucose) has proved to be useful in the brewing industry. The malting process can be accelerated because barley seeds treated with a gibberellin exhibit an increased rate of starch digestion.

One of the most economically important uses of the gibberellins has been in the grape industry. Yields have been increased by as much as one-third in grape vineyards sprayed with gibberellins. Gibberellins have also been used to increase length and water content in celery and sugar content in Hawaiian sugarcane.

Normally, hormone action is associated with the promotion of, enhancement of, or increase in some plant activity. This is the case, however, only when the concentration of the hormone is extremely low. At high concentrations, hormones actually have detrimental effects and can cause plant death. The knowledge of this has led to the development of a number of hormone-type *herbicides*. The most effective, by far, are the auxin-type herbicides such as 2,4-dichlorophenoxy acetic acid and picloram. These herbicides have provided excellent control of broadleaf weeds in grasses and food grains, because grasses are unaffected by them, while broadleaf weeds die as a result of overgrowth. There are probably a number of plant hormones that have not yet been identified. As these are discovered, and as those currently known are better understood, it will become possible to control even more aspects of plant growth and development.

D. R. Gossett

See also: Dormancy; Flowering regulation; Germination and seedling development; Growth and growth control; Leaf abscission; Pheromones; Roots; Stems; Tropisms.

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HORNWORTS

Categories: Nonvascular plants; paleobotany; *Plantae*; taxonomic groups; water-related life

Hornworts are small, short, nonflowering, nonvascular plants which live both on land and in water. They represent an early land plant group and belong to three hundred species in the order Bryophyta. *Related to mosses and liverworts, hornworts are sometimes called horned liverworts.*

Evolutionary biologists have found a few fossils that could be the first known hornwort specimens. Fossilized spores dating from the late Cretaceous period, about 100 million years ago, are considered to be from hornworts. Other fossils dated earlier in that period resemble hornworts but might actually have been liverworts. Spores from the Miocene epoch, approximately twenty-six million years ago, are the most common hornwort fossils.

Botanists theorize that hornworts first appeared with earliest land plants prior to the Devonian period, 395 million years ago, and that fossil evidence is limited because the plants were so fragile. Many taxonomists consider hornworts to be more primitive than mosses and not as closely related to those plants as previously classified. A separate phylum, *Anthocerophyta*, was designated for hornworts, to separate them from mosses and liverworts.

A common and widely distributed plant, hornworts are blue-green members of six genera in two families, *Notothylales* and *Anthocerotales*, in the class *Anthocerotopsida*, derived from Greek words meaning "horn flower." Sometimes hornworts are classified in the subclass *Anthocerotidae* of the class *Hepaticae* as horned liverworts.

Found globally, usually in moist, shady, and sometimes rocky environments, most hornworts belong to the genus *Anthoceros*. Species in the genera *Dendroceros* and *Megaceros* live primarily in tropical regions. Hornworts are found in forests, fields, ponds, streams, and riverbanks in small clumps or large patches and sometimes grow on tree trunks. They are nonvascular and do not have vessels to transport nourishment and moisture. In 1989 scientists reported they had detected a chemical compound with a structural and antimicrobial function in a hornworts species which was also found in the alga *Coleochaete*. This discovery suggested that green algae and hornworts were more closely related than previously thought.

Life Cycle

Hornworts' reproductive cycle occurs in an alternation of generations, in which a gametophyte creates a plant body (thallus) in the sexual generation, and the sporophyte produces a spore-containing capsule in the asexual generation. In the sexual generation, hornworts' gametophytes are flat and as small as 1 to 2 centimeters (0.4 to 0.8 inch) in diameter.

The thallus has hornworts' sexual organs, the male antheridium and female archegonium, on its top surface (whether the male and female organs occur on the same plant varies by species) and rhizoids on the bottom, which secure plants to soils. The hornworts' gametophytes resemble a clump of small leaves. Occasionally, the cyanobacteria *Nostoc* can be found in holes in the thallus, where it fixes nitrogen to exchange for carbohydrates. Hornworts differ from liverworts in that hornworts lack cellular oil bodies and have mucilage instead of air chambers.

During the asexual generation, the sporophyte relies on the gametophyte for food and moisture, remaining connected to it during its life. Water is essential for the transport of sperm from the antheridium to the archegonium, where fertilized eggs become sporangia. From a basal sheath on the thallus, the sporophyte creates a slender, hornlike cylinder, which can be as high as 12 centimeters (4.75 inches) and gives the hornwort its common name.

Filled with spores, the sporangium elongates and gradually splits open from top to base, scattering spores. Internally, horn tissue continues to divide to produce thousands of spores. Other cells, called *pseudoelaters*, help spread spores, which germinate to begin the cycle again. Hornwort spores can survive as long as one decade in soil. Hornwort reproduction can also be achieved vegetatively if the thallus is fragmented.

Physically, hornworts resemble liverworts. They subtly differ from liverworts by having a place on the sporophyte's base, a near-basal meristem, where cells continue to divide and grow during the sporophyte's life. Hornworts also have a tissue column on the capsule, called a columella.

Hornwort gametophytes can be differentiated from those of liverworts and ferns by examination under a microscope to detect one large chloroplast in each hornwort cell. This chloroplast sometimes surrounds the nucleus and contributes to the color and translucency of hornworts. Magnification also reveals the mucilage between cells, instead of air, where cyanobacteria thrive. Hornwort sporophytes also deviate from those found in mosses and liverworts because they exist even after the gametophyte dies.

Taxonomy

In the late 1990's some botanists, deviating from the Linnean system, pursued new classification methodology in which molecular data was used to evaluate plants' taxonomical descriptions. This evidence was used to investigate and hypothesize about the origins and diversification of land plants. Such studies led some scientists to theorize that although hornworts, liverworts, and mosses physically resemble and grow near one another, liverworts and mosses are more closely related to each

Classification of Hornworts

Subdivision *Anthocerotae*
- Class *Anthocerotopsida*
  - Order *Anthocerotales*
    - Family *Anthocerotaceae*
      - Genus *Anthoceros*
      - Genus *Phaeoceros*
    - Family *Dendrocerotaceae*
      - Genus *Megaceros*
    - Family *Notothyladaceae*
      - Genus *Notothylas*

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

other than they are related to hornworts and should be assigned to different divisions.

Plant evolutionary biologists seek to determine terrestrial plants' primary lineages and phylogenetic relationships to one another. Botanists are especially interested in how the three bryophyte groups are genetically connected and their relationships to land plant lineages. Scientists disagree on whether hornworts or liverworts comprise land plants' sister group and whether mosses and liverworts are descended from the same lineage. Researchers want to determine which plant is the most primitive and whether one group is an ancestor of the others. Based on phylogenetic studies, botanists have developed hypotheses regarding hornworts. They suggest that hornworts are bryophytes derived from the earliest land plant lineages and that hornworts have developed specializations which differentiate them from other bryophytes and terrestrial plants.

In the early 1980's B. D. Mishler and S. P. Churchill presented phylogenetic trees which placed the three bryophyte lineages in the sequence of liverworts, hornworts, and mosses at the base of land plants, indicating that liverworts are a sister group to all land plants, and mosses are the vascular plants' sister group. Although many botanists accepted this interpretation, others developed dissenting theories. David J. Garbary and his colleagues examined male gametogenesis in the sperm of bryophytes, which share similar development characteristics. They determined that bryophytes collectively are a sister group to vascular plants and that mosses and liverworts are more closely related to each other than to hornworts.

Additional molecular sequence analysis of morphological characteristics reinforces the concept that hornworts are the basal lineage for terrestrial plants and that mosses and liverworts are the monophyletic sister group to vascular plants. Other botanists are convinced by molecular examination of chloroplast genetic sequences that hornworts are vascular plants' sister group. Scientists continue to test theories to prove that hornworts represent the oldest surviving land plant lineage.

Uses

The name hornwort is also used to describe an aquatic flowering plant, *Ceratophyllum demersum*, often called the coontail, from the family *Ceratophyllaceae*. Usually considered a weed or herb, this plant has many rigid, toothed, horn-shaped leaves, produced in groups of five. Sometimes looking like a raccoon's tail, it has no roots and lives beneath or floats upon the water surface, occasionally in colonies. This plant can grow as long as 4.6 meters (15 feet) and has branches. For pollination, both tiny male and female flowers are located on plants, which produce fruits with seeds. Most reproduction occurs vegetatively by plant fragments.

These hornworts are popular aquarium plants. Cuttings and shoots grow from placement of rhizoids in gravel-covered tank bottoms and quickly reach water surfaces in thick clumps, which need to be thinned. These hornworts provide cover for fish fry and also oxygenate bodies of water in which they are submerged.

Elizabeth D. Schafer

See also: *Archaea*; Bryophytes; Chloroplasts and other plastids; Cladistics; Evolution: historical perspective; Evolution of plants; Forests; Liverworts; Mosses; Oil bodies; Paleobotany; Systematics and taxonomy; Systematics: overview.

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HORSETAILS

Categories: *Plantae*; seedless vascular plants; taxonomic groups

The plants known as horsetails or scouring rushes belong to the genus Equisetum, *the only remaining genus in the phylum* Sphenophyta, *a group of seedless vascular plants.*

Members of the phylum *Sphenophyta*, the horsetails, reached their maximum diversity during the Late Devonian and Carboniferous periods. One fossil group of the *Sphenophyta*, the calamites, grew from 12 to 18 meters (24 to 60 feet) in height, with trunks as much as 45 centimeters (more than 3 feet) in diameter. Today these ancient plants survive in the single genus *Equisetum*. *Equisetum* is found throughout the world and, depending on the classification scheme, comprises between fifteen and twenty-five species. Species that have branching forms are commonly called horsetails; *scouring rushes* are the unbranched species. *Equisetum* prefers moist or wet habitats, although some species do grow in drier areas. They can often be found growing along streams and the edges of woodlands.

Appearance

The stems of *Equisetum* are distinctly ribbed, with obvious nodes and internodes; there are numerous stomata in the grooves beneath the ribs. While it is the stems that carry out photosynthesis, *Equisetum* does have true leaves. The scalelike leaves are found at the nodes and form a collarlike structure just above the node. They are fused into a sheath around the stem.

Within the stems, especially of the scouring rushes, one can find significant deposits of silica,

Classification of Horsetails

Class *Equisetopsida*
- Order *Equisetales*
  - Family *Equisetaceae*
    - Genus *Equisetum*, U.S. living species:
      - *Equisetum arvense* (field horsetail)
      - *Equisetum fluviatile* (water horsetail)
      - *Equisetum hyemale* (scouring rush)
      - *Equisetum palustre* (marsh horsetail)
      - *Equisetum pratense* (meadow horsetail)
      - *Equisetum laevigatum* (smooth horsetail)
      - *Equisetum sylvaticum* (woodland horsetail)
      - *Equisetum telmateia* (giant horsetail)

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

which gives the stems a rough, gritty texture. The name "scouring rush" indicates that, in a pinch, campers, like their pioneer forebears, can scrub dishes clean with stems of *Equisetum*. American Indians used the abrasive stems to smooth and polish bows and arrows. Stems of some species have often been used in the manner of sandpaper to polish wood.

A cross-section of a stem of *Equisetum* will show that the pith in the stem breaks down as the plant matures, leaving a hollow central canal in the stem. Two cylinders of smaller canals are located outside the pith. The inner cylinders, called carinal canals, are associated with strands of xylem tissue, which conducts water, and strands of phloem tissue, which conducts the products of photosynthesis to places of storage. The outer cylinder contains vallecular canals, which contain air.


PhotoDisc

The extant representatives of the ancient plants known as horsetails survive in the single genus Equisetum.

Reproduction

Asexual reproduction in *Equisetum* can take place through fragmentation of the stems, although sexual reproduction is the more common process. In the spring, some species produce, from the rhizomes, special cream- to buff-colored, nonphotosynthetic stems. Small, conelike strobili develop at the tips of these special stems or, in other species, at the tips of regular photosynthetic stems.

The strobili are usually about 2 to 4 centimeters (1 to 2 inches) long and look somewhat like little cones on top of the stems, with each conelike tip covered with hexagon-shaped plates. Each hexagon marks the top of a sporangiophore, which has five to ten elongate sporangia connected to the rim. When the sporangiophores separate slightly at maturity, the spores are released.

When the spore mother cells in the sporangia undergo meiosis, distinctive green spores are produced. The outer spore wall differentiates from the inside of the spore, forming coiled bands called *elaters*. Elaters uncoil when they dry out, functioning like wings to carry the spore along in the wind. If the spores are blown into a moist habitat, the elaters coil up, allowing the spore to drop and land in habitat suitable for germination.

After germination, spores produce lobed, cushionlike, photosynthetic green gametophytes that are seldom more than 8 millimeters in diameter but may range in size from a few millimeters up to 3.5 centimeters (about 1.5 inches) in diameter. Rhizoids anchor the gametophytes to the surface of the earth. The optimum habitats for gametophyte germination are recently flooded, nutrient-rich mudflats.

At first, about half of the gametophytes are male, with antheridia, and the other half are female, with archegonia. After a month or two, however, the female gametophytes of most species become bisexual, producing only antheridia. When water contacts mature antheridia, sudden changes in water pressure cause the sperm cells produced within the antheridia to be explosively ejected. Sperm have several flagella, which aid them in swimming to the archegonia to fertilize the eggs. Several eggs on a female or bisexual gametophyte may be fertilized, and the development of more than one sporophyte is common.

Toxic Properties

Aerial stems develop from horizontal rhizomes, which are highly branched and perennial. Because the rhizomes can grow quite rapidly, *Equisetum* is often invasive. If livestock pastures are invaded by *Equisetum*, it can cause problems for farmers and ranchers, as the aerial stems of *Equisetum* are poisonous. *Equisetum arvense*, a species found in the United States and southern Canada, is especially toxic in dry hay. Horses, sheep, and cows are all susceptible to *Equisetum* poisoning. Symptoms include trembling, rapid pulse, weakness, excitability, diarrhea, staggering, and cold in the extremities. The major toxic substance is called *thiaminase*, which interferes with thiamine metabolism.

Medicinal Uses

Some members of the genus *Equisetum* have been found useful in folk and herbal medicine. Both *Equisetum arvense* and *Equisetum robustum* are known to exert diuretic effects. Poultices of crushed sterile stems can be applied to wounds to stop bleeding. In Ukraine, decoctions of *Equisetum heleocharis* have been used for this purpose. Boiling the stems yields a liquid extract that can be used as a mouthwash. There is a possibility that horsetail has some antibiotic properties. Roots were often given to teething babies, and *Equisetum* tea was often used to treat tubercular lung lesions.

Carol S. Radford

See also: Ferns; Fossil plants; Paleobotany; Seedless vascular plants.

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HORTICULTURE

Categories: Agriculture; disciplines; economic botany and plant uses; gardening

Horticulture is the branch of agriculture that is connected with the production of plants that are directly used by people for food, medicine, and aesthetic purposes.

The ability to produce crops, particularly those crops associated with food and fiber, is the multidisciplinary science of intensively cultivating plants to be used by humans for food, medicinal purposes, or aesthetic satisfaction. Crop production is largely determined by a variety of environmental conditions, including soil, water, light, temperature, and atmosphere. Therefore, horticulture science is primarily concerned with the study of how to manipulate the plants or these environmental factors to achieve maximum yield.

Because there is tremendous diversity in horticultural plants, the field is subdivided into *pomology*, the growth and production of fruit crops; *olericulture*, the growth and production of vegetable crops; *landscape horticulture*, the growth and production of trees and shrubs; and *floriculture*, the growth and production of flower and foliage plants. Each of these subdivisions is based on a fundamental knowledge of plant-soil interactions, soil science, plant physiology, and plant morphology.

Propagation

Horticulture science is concerned with all aspects of crop production, from the collection and germination of seed to the final marketing of the products. Plant propagation, protection, and harvesting are three areas of particular interest to horticulturists.

Generally, *propagation from seed* is the most common and least expensive way of propagating plants. In order to prevent cross-pollination from undesirable varieties, plants to be used for seed production are grown in genetic isolation from other, similar plants. At maturity, the seed is collected and is usually stored at low temperatures and less than 50 to 65 percent relative humidity to maintain full viability. The seed is often tested for viability prior to planting to determine the percentage of seed that should germinate. At the appropriate time, the seed is usually treated with a fungicide to ensure an adequate crop stand and planted under proper temperature, water, and light conditions. For most crops, the seed is germinated in small containers, and the seedlings are then transplanted to the field or greenhouse.

For many horticultural crops it is not feasible to produce plants from seed. For some, the growth from seed may require too much time to be economically practical. In other cases, the parent plants may produce little or no viable seed, and in still others, there may be a desire to avoid hybridization in order to maintain a pure strain. For some plants, almost any part of the root, stem, or leaf can be *vegetatively propagated*, but chemical treatment of the detached portion to ensure regeneration of the missing tissue is often required.

For other plants, a variety of specific vegetative plant tissues, including the roots, bulbs, corms, rhizomes, tubers, and runners, must be used for propagation. Individual runners are used for propagation purposes, but a number of cuttings can be propagated from one rhizome. Tubers are propagated by slicing the organ into several pieces, each of which must contain an "eye," or bud. Corms and bulbs are propagated by planting the entire structure.

A relatively new process of generating plants from cell cultures grown in the laboratory, called *tissue culture*, is a method often used to propagate pure lines of crops with a very high economic value. *Grafting*, a specialized form of vegetative propagation, is particularly useful in tree farming. The shoot from one plant with a desirable fruit quality can be grafted onto the root stock of another, more vigorous plant with a less desirable fruit quality.

Pest Control

Because plants are besieged by a panoply of biological agents that use plant tissues as a food source, protecting plants from pests is a major concern in the horticulture industry. Microbial organisms, nematodes, insects, and weeds are the major plant pests. Weeds are defined as unwanted plants and are considered to be pests because they compete with crop plants for water, sunlight, and nutrients. If left unchecked, weeds will drastically reduce crop yields because they tend to produce a large amount of seed and grow rapidly. Weed control is generally accomplished either by physically removing the weed or by use of a variety of herbicides that have been developed to chemically control weeds. Herbicides are selected on the basis of their ability to control weeds and, at the same time, cause little or no damage to the desired plant.

Plant protection from microbes, nematodes, and insects generally involves either preventing or restricting pest invasion of the plant, developing plant varieties that will resist or at least tolerate the invasion, or a combination of both methods. The application of chemicals, use of biological agents, isolation of an infected crop by quarantine, and cultural practices that routinely remove infected plants or plant tissues are examples of control methods. A large number of different bactericides, fungicides, nematocides, and insecticides has been developed in recent years. Because many of these chemicals are harmful to other animals, including humans, the use of pesticides, and insecticides in particular, requires extreme caution. There is an increasing interest in the use of biological control methods because many of the chemical pesticides pose a threat to the environment. The development and use of pest-resistant crop varieties and the introduction of natural enemies that will not only reduce the pest population but also live harmoniously in the existing environment are two of the more promising biological measures being employed.

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Harvest

A crop must be harvested once it has grown to maturity. Harvesting is one of the most expensive aspects of crop production because it is usually very labor-intensive. For almost all crops, there is a narrow window between the time the plants are ready to harvest and the time when the plants are too ripe to be of economic value. Hence, the harvesting process requires considerable planning to ensure that the appropriate equipment and an adequate labor supply are available when the crop is ready to be harvested. Predicting the harvest date is of paramount importance in the planning process. The length of the harvest window, the length of the growing season that is necessary for a given plant to mature under normal environmental conditions at a given geographic location, and the influence of unexpected weather changes on the growing season all have to be considered in the planning process. Because nature is unpredictable, even the best planning schedules sometimes have to be readjusted in midseason.

Some crops are picked from the plant by hand and then mechanically conveyed from the field, while other crops are harvested entirely by hand. New mechanical harvesting equipment is continually being developed by agricultural engineers, and crops that lend themselves to mechanical harvesting are growing in importance as the manual labor force continues to shrink. After harvest, most crops are generally stored for varying lengths of time, from a few days to several months. Because post-harvest storage can affect both the quality and appearance of the product, considerable care is given as to how the crop is stored. Sometimes storage improves the quality and appearance, while in other cases, it causes them to deteriorate. The ideal storage conditions are those that maintain the product as close to harvest condition as possible.

Genetic Engineering

In order for horticulture to remain a viable resource in the future, advances in horticulture technology will have to continue to keep pace with the needs of an increasing population. However, horticulturists will also have to be mindful of the fragile nature of the environment. New technologies must be developed with the environment in mind, and much of this new technology will center on advances in genetic engineering. New crop varieties that will both provide higher yields and reduce the dependency on chemical pesticides by exhibiting greater resistance to a variety of pests will have to be developed. The future development of higher-yielding crops that can be harvested mechanically and the production of new types of equipment to facilitate the harvesting process will also be important improvements in the horticulture industry.

D. R. Gossett

See also: Agriculture: experimental; Biopesticides; Biotechnology; Genetically modified foods; High-yield crops; Hydroponics; Plant biotechnology; Plants with potential.

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HUMAN POPULATION GROWTH

Categories: Animal-plant interactions; environmental issues

Since the Industrial Revolution of the nineteenth century, human populations have experienced a period of explosive growth. Overpopulation now poses a real threat to plant lives, ecosystems, and the long-term sustainability of the earth's current ecological balance.

Just eleven thousand years ago, there were only about five million humans who lived on the planet Earth. The initial population growth was slow, largely because of the way humans lived—by hunting. Such a mobile lifestyle limited the size of families for practical reasons. When simple means of birth control, often abstention from sex, failed, a woman would elect abortion or, more commonly, infanticide to limit her family size. Furthermore, a high mortality rate among the very young, the old, the ill, and the disabled acted as a natural barrier to rapid population growth.

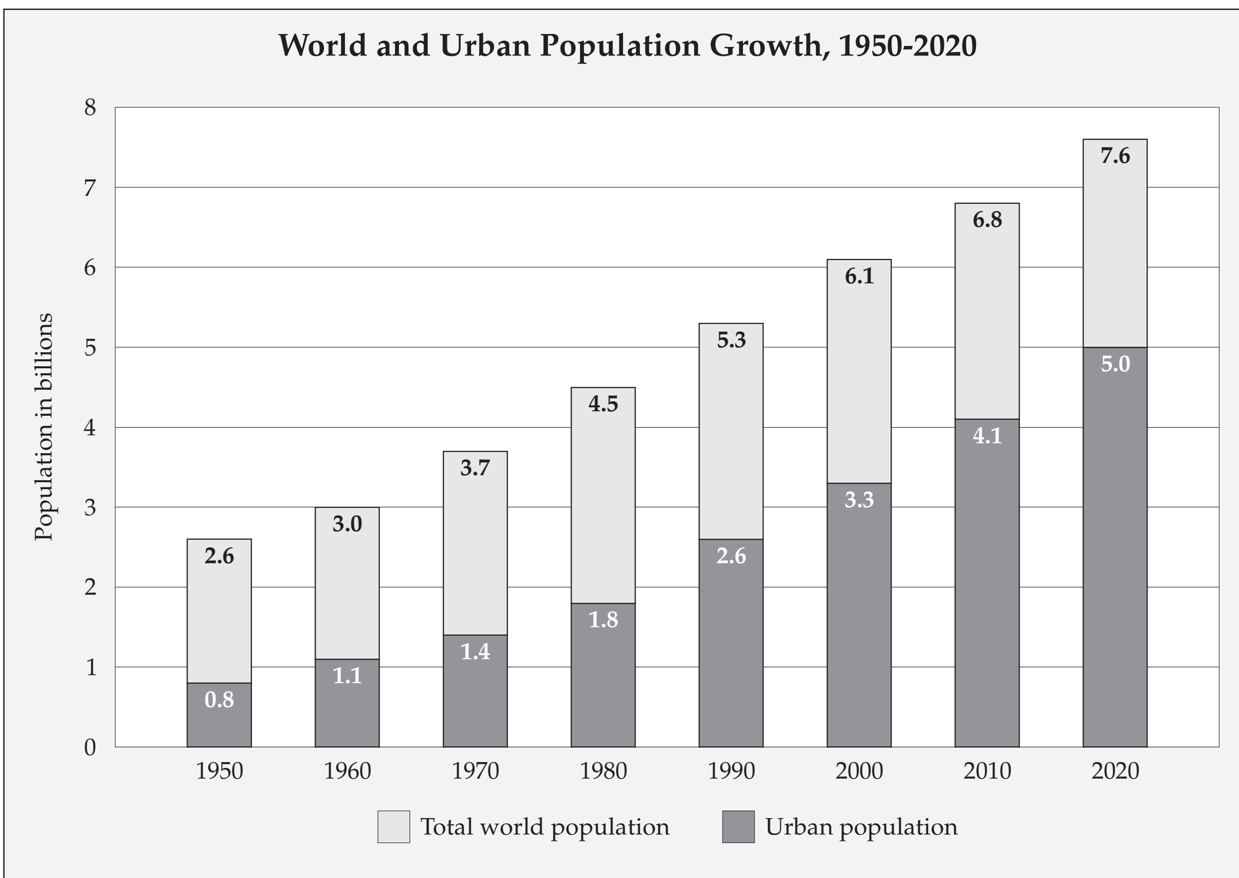
Thus, it took more than one million years for the world's population to reach one billion. The second billion was added in about one hundred years, the third billion in fifty years, the fourth in fifteen years, and the fifth billion in twelve years. When humans became sedentary, some limits on the family size were lifted. With the development of agriculture, children became an asset to their families by helping with farming and other chores.

By the beginning of the common era (1 C.E.), human population had grown to about 130 million, distributed all over the earth. By 1650, the world population had reached 500 million. The process of industrialization had begun, bringing about profound changes in the lives of humans and their interactions with the natural world. With improved living standards, lower death rates, and prolonged life expectancies, human population grew exponentially. By 1999, there were about 6 billion people, compared with 2.5 billion in 1950. By 2002, the world population was well on its way to 7 billion, with an annual growth rate of nearly 100 million.

Plants, Agriculture, and Human Population

Starting about eleven thousand years ago (five million people), humans began to cultivate such plants as barley, lentils, wheat, and peas in the Middle East—an area that extends from Lebanon and Syria in the northwest eastward through Iraq to Iran. In cultivating and caring for these crops, early farmers changed the characteristics of these plants, making them higher yielding, more nutritious, and easier to harvest. Agriculture spread and first reached Europe by approximately six thousand years ago.

Agriculture might also have originated independently in Africa in one or more centers. Many crops were domesticated there, including yams, okra, coffee, and cotton. In Asia, agriculture based on staples such as rice and soybeans and many other crops such as citrus, mangos, taro, and bananas was developed. Agriculture was developed independently in the New World. It began as early as nine thousand years ago in Mexico and Peru.



Note: The world's population passed 6 billion in the year 2000.

Sources: Data are from U.S. Bureau of the Census International Data Base and John Clarke, "Population and the Environment: Complex Interrelationships," in *Population and the Environment* (Oxford, England: Oxford University Press, 1995), edited by Bryan Cartledge.

Christopher Columbus and his followers found many new crops to bring back to the Old World, including corn, kidney beans, lima beans, tomatoes, tobacco, chili peppers, potatoes, sweet potatoes, pumpkins and squashes, avocados, cacao, and the major cultivated species of cotton.

For the last five to six centuries, important staple crops have been cultivated throughout the world. Wheat, rice, and corn, which provide 60 percent of the calories people consume, are cultivated wherever they will grow. Other crops, including spices and herbs, have also been brought under cultivation.

The growing population has changed the landscape, distribution, and diversity of plants dramatically. *Clear-cutting* and *deforestation* have driven many species (both plant and animal) to extinction. Relatively little has been done to develop agricultural practices suitable for tropical regions. As a result, the tropics are being devastated ecologically, with an estimated 20 percent of the world's species likely to be lost by the mid-twenty-first century.

A Threat to Sustainability

Without effective measures of control, the human population could exceed the earth's carrying capacity. Humans are, at present, estimated to consume about 40 percent of the total net products generated via photosynthesis by plants. Human activities have reduced the productivity of earth's forests and grasslands by 12 percent. Each year, millions of acres of once-productive land are turned into desert through *overgrazing* and deforestation, especially in developing countries. Due to overfertilization and aggressive practices in agriculture, loss of topsoil occurs at an annual rate of 24 billion metric tons. Collectively, these practices caused the destruction of 40 million acres of rain forest each year during the 1960's and 1970's and the extinction of enormous numbers of species.

Through technological innovation and aggressive practices in agriculture, a 2.6-fold increase in world grain production has been achieved since 1950. However, this increase in food output is not nearly enough to feed the population. Based upon

PhotoDisc

A busy street in Barcelona, Spain, photographed in 2002, as the world's human population passed 6.1 billion, with an annual growth rate of nearly 100 million.

an estimate by the World Bank and the Food and Agriculture Organization of the United Nations, one out of every five people is living in absolute poverty, unable to obtain food, shelter, or clothing dependably. About one out of every ten people receives less than 80 percent of the daily caloric intake recommended by the United Nations. In countries such as Bangladesh and Haiti and in regions such as East Africa, humans are dying in increasing numbers because of the lack of food. This lack of food may stem from drought, soil depletion, or soil loss; more often, famine results from inequitable distribution of resources among populations. Situations exacerbated by a growing population also pose threats to the environment, aggravating the problems of acid rains, toxic and hazardous wastes, water shortages, topsoil erosion, ozone layer punctuation, greenhouse effects and groundwater contamination.

Ming Y. Zheng

See also: Acid precipitation; Agricultural revolution; Agriculture: modern problems; Agriculture: traditional; Agriculture: world food supplies; Erosion and erosion control; Green Revolution; Plant domestication and breeding; Rain forests and the atmosphere; Sustainable agriculture; Sustainable forestry.

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HYBRID ZONES

Categories: Ecosystems; genetics; reproduction and life cycles

Hybrids are offspring of parents from different species. Hybrid zones are areas where such different species overlap and crossbreed. Hybridization and hybrid zones have played a major role in the formation of new species in a number of plant groups and represent major factors in the evolutionary process.

A *hybrid* individual is produced from successful matings (cross-pollination) between individuals from different species or between individuals from different populations that differ markedly in one or more heritable traits. The mating process by which hybrid offspring are produced is *hybridization*. A distinction needs to be made between natural and artificial hybrids. An artificial hybrid typically involves direct human intervention in an effort to obtain plants with agricultural or horticultural properties superior to those of either parent. Natural hybrids do not involve human intervention; they occur naturally.

In many cases hybridization between individuals that belong to different species is prevented by barriers or impediments to cross-pollination, known as *reproductive isolating mechanisms*. These mechanisms can be either prezygotic, preventing the formation of hybrid zygotes, or postzygotic, preventing or greatly reducing gamete exchange after a hybrid zygote has been formed. Hybridization typically occurs between species in which reproductive barriers (such as impediments to cross-pollination between members of different species) are not fully formed or are incomplete.

A hybrid zone is a geographic location in which two or more populations of individuals that differ in one or more heritable traits (either of the same or of different species) overlap, cross-breed, and produce viable and sometimes fertile offspring. The formation of hybrid zones involves *sympatric species*, that is, species whose geographic ranges overlap. Typically, *allopatric species* (those whose geographic ranges do not overlap) do not form hybrid zones unless some event, such as wind dispersal of seeds, brings individuals of the two species together.

Hybrid zones can be either continuous zones or a mosaic of scattered groups across a geographic range. They can also differ markedly in size. For example, the common herb *Gaillardia pulchella* (*Asteraceae* family) forms narrow hybrid zones in Texas, where transition progeny formed with neighboring *Gaillardia* species occurs over a few meters. In contrast, individuals found in hybrid zones involving the Bishop pine, *Pinus muricata*, in California can be several kilometers wide

In many cases hybrid zones are the result of human disturbance of the natural landscape. Such disturbance can lead to unique and novel habitat conditions in which the hybrid species might have a selective advantage over the parental species. One example occurs in Washington and Idaho, where certain hybrid zones are incubators for the speciation of *Tragopogon mirus* and *T. miscellus*.

Speciation Dynamics of Hybrid Zones

If natural selection eliminates hybrid offspring in the hybrid zone, then the reproductive barriers present in the parental species will be reinforced. If, however, the environment within the hybrid zone allows for persistence and reproduction of hybrid taxa, then these hybrids can persist through time, with several possible results. One result is the eventual establishment of reproductive barriers between the hybrid offspring and the parental species, with the formation of a new species from the hybrid lineage.

In some hybrid zones *allopolyploidy* can lead to the formation of a sterile hybrid. This occurs when two chromosome sets from different parents are present within one hybrid individual. The sterility is due to irregularities at meiosis, as there is only one chromosome of each type leading to irregular segregation at meiosis. However, if the chromosome set is doubled through *autopolyploidy*, meiotic regularity is restored because each chromosome then has a homolog, which allows for successful chromosome segregation and gamete formation. Because of the difference in chromosome number between the polyploid hybrid derivative and the parental species, a reproductive barrier is established, and a new species will be established. This is the case with two species of goat's beard, *Tragopogon mirus* and *T. miscellus*, from southeastern Washington and adjacent Idaho. The progenitors of the polyploid *T. mirus* are the diploid species *T. dubius* and *T. porrifolius*, and of the polyploid *T. miscellus* are *T. dubius* and the diploid *T. pratensis*.

Another mechanism responsible for the formation of species within a hybrid zone is *recombination speciation*. In this process the parental genomes present within the semisterile hybrid offspring undergo rearrangement and recombination events over several generations, eventually producing mixed genomes in hybrid individuals. Over time, fertility is restored in the hybrid individuals, which are then reproductively isolated from the parental species. A prime example of recombination speciation occurs within a group of sunflowers found in the western United States. *Helianthus anomalus* arose as a consequence of hybridization between two sympatric parental species, *H. annuus* and *H. petiolaris*. Because of genome incompatibilities, the immediate hybrid offspring were reproductively isolated from either parental species and were semisterile. The genome arrangements that occurred over time within hybrids and their offspring resulted in increased fertility within the hybrid individual and breeding incompatibility between the hybrids and either parental species.

Introgression and Hybrid Swarms

Introgression occurs when the hybrid offspring engage in *backcrossing* with either one or both of the parental species. A *hybrid swarm* is usually a complex mixture of parental forms, F1 hybrids, and backcross individuals. The Louisiana irises provide a striking example of an introgressive swarm. Two parental species, *Iris fulva* and *I. hexagona*, have produced numerous hybrid populations in southern Louisiana. The hybrid individuals found in the hybrid zones are not true F1 hybrids but are the progeny resulting from numerous backcrosses to the parental species. A mixture of phenotypes is present in the hybrid swarm, with differing levels of similarity to the parental species among hybrid offspring.

Pat Calie

See also: Animal-plant interactions; Flower structure; Gene flow; Hybridization; Pollination; Polyploidy and aneuploidy; Population genetics; Reproductive isolating mechanisms; Species and speciation.

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HYBRIDIZATION

Categories: Agriculture; genetics

Hybridization is the process of crossing two genetically different individuals to result in a third individual with a different, often preferred, set of traits. Plants of the same species cross easily and produce fertile progeny. Wide crosses are difficult to make and generally produce sterile progeny because of chromosome-pairing difficulties during meiosis.

Hybridization is the process of crossing two genetically different individuals to create new genotypes. For example, a cross between a parent 1, with the genetic makeup (genotype) *BB*, and parent 2, with *bb*, produces progeny with the genetic makeup *Bb*, which is a hybrid (the first filial generation or F_1). Hybridization was the basis of Gregor Mendel's historic experiments with garden peas. Inheritance studies require crossing plants with contrasting or complementary traits.

Hybridization of plants occurs in nature through various mechanisms. Some plants (such as the oil palm) are insect-pollinated, and others (such as maize, or corn) are wind-pollinated. Such plants are referred to as *cross-pollinated plants*. Natural hybridization has played a significant role in producing new genetic combinations and is the norm in cross-pollinated plants. It is a common way of generating genetic variability.

In plants with perfect flowers (*autogamous*, having flowers with both stamens and pistils), cross-pollination rarely occurs. Such plants (such as wheat and rice) are called *self-pollinated plants*. Flowers bearing only pistils or stamens are said to be imperfect flowers. Plants that have separate pistillate and staminate flowers on the same plant (such as maize) are called *monoecious*. Plants that have male and female flowers on separate plants (such as asparagus) are called *dioecious*.

Through artificial means (controlled pollination), hybridization of both cross-pollinated and self-pollinated plants can be accomplished. Artifi-

Image Not Available

cial hybridization is an important aspect of improving both cross-pollinated and self-pollinated plants. The breeder must know the time of development of reproductive structures of the species, treatments to promote and synchronize flowering, and pollinating techniques.

Applications to Agriculture

The concept of *hybrid vigor*, or *heterosis*, resulted from hybridization. Heterosis (or heterozygosis) occurs when the hybrid outperforms its parents for a certain trait. Around 1761 Joseph Gottlieb Kölreuter was the first to report on hybrid vigor in interspecific crosses of various species of *Nicotiana*. He concluded that cross-fertilization was generally beneficial and self-fertilization was not. In 1799 T. A. Knight conjectured that because of widespread existence of cross-pollination in nature, it must be the norm. Charles Darwin reported the results of his experiments with maize. He indicated that in twenty-four crosses, there was an increase in plant height, which was attributed to hybridization, and that decrease in plant height was associated with self-pollination (or selfing). He also noted that crossing of inbred plants could reverse the deleterious effects of selfing or *inbreeding*. In 1862 Darwin wrote, "Nature tells us, in the most emphatic manner, that she abhors perpetual self-fertilization." In the late 1800's William J. Beal evaluated hybrids between maize varieties. He observed that some hybrids yielded 50 percent more than the mean of their parents. S. W. Johnson provided an explanation for hybrid vigor in 1891. G. W. McClure reported in 1892 that hybrids between maize varieties were superior to the mean of the two parents.

Exploitation of Heterosis

The phenomenon of heterosis has been exploited in crop plants, such as maize, sorghum, sunflower, onion, and tomato. Maize (corn) was the first crop in the United States in which hybrids were produced from *inbred lines*. It was George Shull who, following the rediscovery of Mendel's laws of inheritance in 1900, conducted the first experiments on inbreeding and crossing, or hybridizing, of inbred lines. Shull suggested that inbreeding within a maize variety resulted in pure (*homozygous*) lines and that hybrid vigor resulted from crossing of pure lines because *heterozygosity* was created at many allelic sites. Hybrid maize was introduced in the United States in the late 1920's and early 1930's, after which U.S. maize production increased dramatically from the use of hybrids.

Heterosis now drives a multibillion-dollar business in agriculture. Yield improvement made in various crops in which heterosis was detected has been tremendous. In 1932 in the United States, 44.8 million hectares (111 million acres) were required to produce 51 million metric tons of maize grain, with a mean yield of 1.66 metric tons per hectare. In 1994 it took only 32 million hectares (79 million acres) to produce 280 million metric tons of grain, with a mean yield of 8.69 metric tons per hectare. In the United States in 1996, twenty-one vegetable crops occupied 1,576,494 hectares (3.9 million acres), with a mean of 63 percent of the crop in hybrids. Heterosis saved an estimated 220,337 hectares (544,459 acres) of agricultural land per year, feeding 18 percent more people without an increase in land use. From 1986 to 1995, the best rice hybrids showed a 17 percent yield advantage over the best inbred-rice varieties at the International Rice Research Institute.

Despite the impact that heterosis has had on crop production, its molecular genetic basis is still not clear. It is hoped that with the progress being made in the genetic sequencing of various plant species, a better understanding of heterosis will emerge. Plant breeding entails hybridization within a species as well as hybridization between species or even genera, called *wide crosses*. The latter are important for generating genetic variability or for incorporating a desirable gene not available within a species. There are barriers, however, for accomplishing *interspecific* and *intergeneric* crosses. Plants of the same species cross easily and produce fertile progeny. Wide crosses are difficult to make and generally produce sterile progeny because of chromosome-pairing difficulties during meiosis.

Triticale is the only human-made cereal crop, which is a cross between the genus *Triticum* (wheat) and the genus *Secale* (rye). The first fertile triticale was produced in 1891. Some of the interspecific and intergeneric barriers should be overcome via the newer techniques of gene transfer. It is expected that genes from wild relatives of cultivated plants will continue to be sought to correct defects in otherwise high-yielding varieties.

Manjit S. Kang

See also: Agriculture: traditional; Alternative grains; Corn; Genetics: Mendelian; Grains; Green Revolution; Hybrid zones; Pollination; Species and speciation; Wheat.

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HYDROLOGIC CYCLE

Categories: Biogeochemical cycles; ecology

The hydrologic cycle is a continuous system through which water circulates through vegetation, in the atmosphere, in the ground, on land, and in surface water such as rivers and oceans.

The sun and the force of gravity provide the energy to drive the cycle that provides clean, pure water at the earth's surface. The total amount of water on earth is an estimated 1.36 billion cubic kilometers. Of this water, 97.2 percent is found in the earth's oceans. The ice caps and glaciers contain 2.15 percent of the earth's water. The remainder, 0.65 percent, is divided among rivers (0.0001 percent), freshwater and saline lakes (0.017 percent), groundwater (0.61 percent), soil moisture (0.005

percent), the atmosphere (0.001 percent), and the biosphere and groundwater below 4,000 meters (0.0169 percent). While the percentages of water appear to be small for these water reservoirs, the total volume of water contained in each is immense.

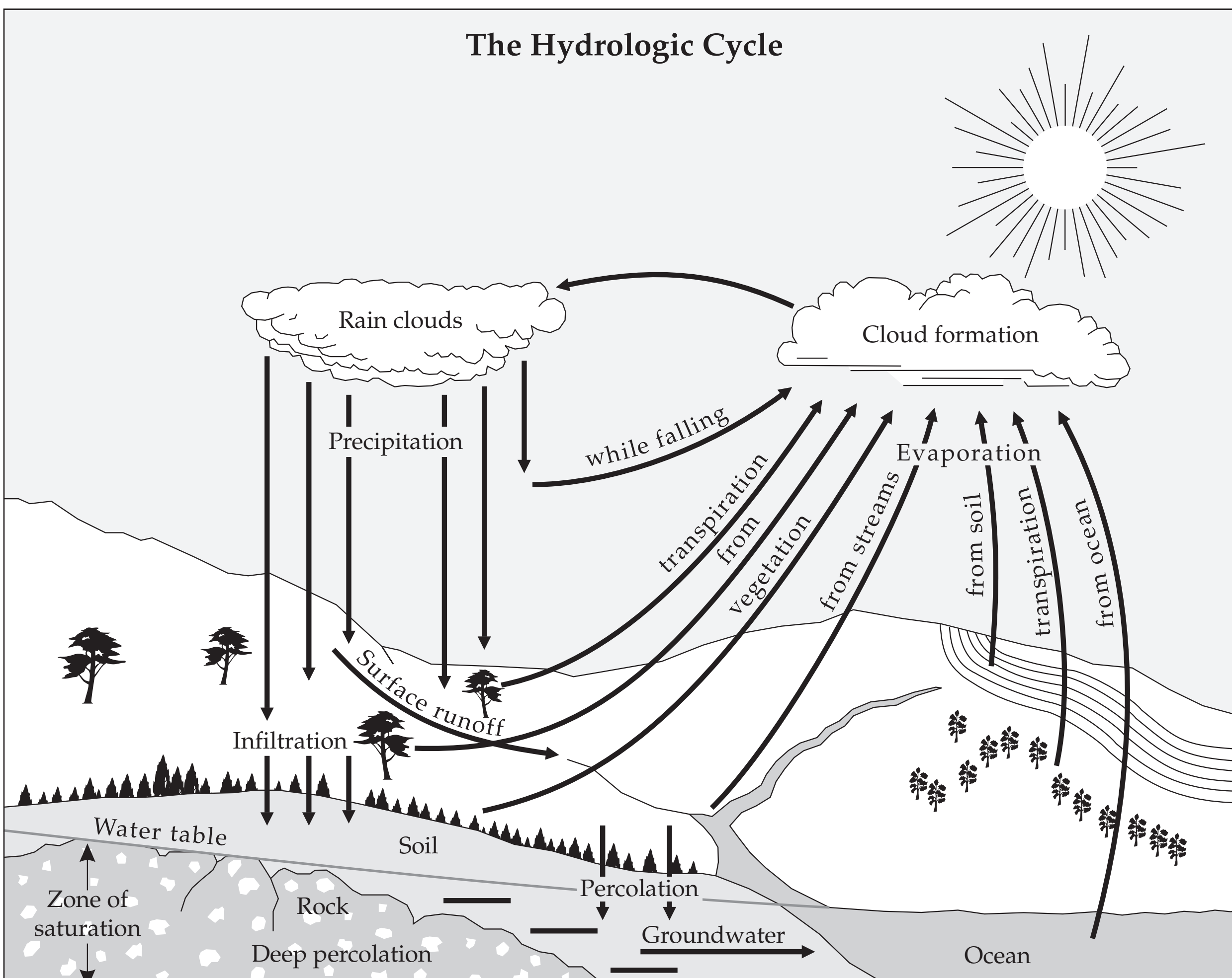
Evaporation

Evaporation is the process whereby a liquid or solid is changed to a gas. Heat causes water molecules to become increasingly energized and to move more rapidly, weakening the chemical force that binds them together. Eventually, as the temperature increases, water molecules move from the ocean's surface into the overlying air. The rate of evaporation is influenced by radiation, temperature, humidity, and wind velocity.

Each year about 320,000 cubic kilometers of water evaporate from these oceans. It is estimated that an additional 60,000 cubic kilometers of water evaporate from rivers, streams, and lakes or are *transpired* by plants each year. A total of about 380,000 cubic kilometers of water is *evapotranspired* from the earth's surface every year.

Condensation and Precipitation

Wind may transport the moisture-laden air long distances. The amount of water vapor the air can hold depends upon the temperature: The higher the temperature, the more vapor the air can hold. As air is lifted and cooled at higher altitudes, the vapor in it condenses to form droplets of water. *Condensation* is aided by small dust and other particles in the atmosphere. As droplets collide and coalesce, raindrops begin to form, and *precipitation* begins.



Source: U.S. Department of Agriculture, *Yearbook of Agriculture* (Washington, D.C.: Government Printing Office, 1955).

AP/Wide World Photos

A wall of fog blows into the bay in Grand Portage, Minnesota. Wind may transport the moisture-laden air long distances. The amount of water vapor the air can hold depends upon the temperature: The higher the temperature, the more vapor the air can hold.

Most precipitation events are the result of three causal factors: frontal precipitation, or the lifting of an air mass over a moving weather front; convectional precipitation related to the uneven heating of the earth's surface, causing warm air masses to rise and cool; and orographic precipitation, resulting from a moving air mass being forced to move upward over a mountain range, cooling the air as it rises.

Each year, about 284,000 cubic kilometers of precipitation fall on the world's oceans. This water has completed its cycle and is ready to begin a new cycle. Approximately 96,000 cubic kilometers of precipitation fall upon the land surface each year. This precipitation follows a number of different pathways in the hydrologic cycle. It is estimated that 60,000 cubic kilometers evaporate from the surface of lakes or streams or transpire directly back into the atmosphere. The remainder, about 36,000 cubic kilometers, is intercepted by human structures or vegetation, infiltrates the soil or bedrock, or becomes surface runoff.

Interception

In cities, the amount of water intercepted by human structures may approach 100 percent. However, much urban water is collected in storm sewers or drains that lead to a surface drainage system or is spread over the land surface to infiltrate the subsoil. *Interception* loss from vegetation depends upon interception capacity (the ability of the vegetation to collect and retain falling precipitation), wind speed (the higher the wind speed, the greater the rate of evaporation), and rainfall duration (the interception loss will decrease with the duration of rainfall, as the vegetative canopy will become saturated with water after a period of time). Broad-leaf forests may intercept 15 to 25 percent of annual precipitation, and a bluegrass lawn may intercept 15 to 20 percent of precipitation during a growing season.

Transpiration

Plants are continuously extracting soil moisture and passing it into the atmosphere through a process called *transpiration*. Moisture is drawn into the plant rootlet through osmotic pressure. The water moves through the plant to the leaves, where it is passed into the atmosphere through the leaf openings, or stomata. The plant uses less than 1 percent of the soil moisture in its metabolism; thus, transpiration is responsible for most water vapor loss from the land in the hydrologic cycle. For example, an oak tree may transpire 151,200 liters per year.

Overland Flow and Infiltration

When the amount of rainfall is greater than the earth's ability to absorb it, excess water begins to run off, a process termed *overland flow*. Overland flow begins only if the precipitation rate exceeds the infiltration capacity of the soil. *Infiltration* occurs when water sinks into the soil surface or into fractures of rocks; the amount varies according to the characteristics of the soil or rock and the nature of the vegetative cover. Sandy soils have higher infiltration rates than clay rock soils. Nonporous rock has an infiltration rate of zero, and all precipitation that reaches it becomes runoff. The presence of vegetation impedes surface runoff and increases the potential for infiltration to occur.

Water infiltrating the soil or bedrock encounters two forces: capillary force and gravitational force. A capillary force is the tendency of the water in the subsurface to adhere to the surface of soil or sediment particles. Capillary forces are responsible for the soil moisture a few inches below the land surface.

The water that continues to move downward under the force of gravity through the pores, cracks, and fissures of rocks or sediments will eventually enter a zone of water saturation. This source of underground water is called an aquifer—a rock or soil layer that is porous and permeable enough to hold and transport water. The top of this aquifer, or saturated zone, is the *water table*. This water is moving slowly toward a point where it is discharged to a lake, spring, or stream. Groundwater that augments the flow of a stream is called *base flow*. Base flow enables streams to continue to flow during droughts and winter months. Groundwater may flow directly into the oceans along coastlines.

When the infiltration capacity of the earth's surface is exceeded, overland flow begins. Broad, thin sheets of water a few millimeters thick are called *sheet flow*. After flowing a few meters, the sheets break up into threads of current that flow in tiny channels called rills. The rills coalesce into gullies and, finally, into streams and rivers. Some evaporation losses occur from the stream surface, but much of the water is returned to the oceans, thus completing the hydrologic cycle.

Residence Time

Residence time refers to how long a molecule of water will remain in various components of the hydrologic cycle. The average length of time that a water molecule stays in the atmosphere is about one week. Two weeks is the average residence time for a water molecule in a river, and ten years in a lake. It would take four thousand years for all the water molecules in the oceans to be recycled. Groundwater may require anywhere from a few weeks to thousands of years to move through the cycle. This time period suggests that every water molecule has been recycled millions of times.

Methods of Study

Several techniques are used to gather data on water in the hydrologic cycle. These data help scientists determine the water budget for different geographic areas. Together, these data enable scientists to estimate the total water budget of the earth's hydrologic cycle.

Scientists have developed a vast array of mathematical equations and instruments to collect data on the hydrologic cycle. Variations in temperature, precipitation, evapotranspiration, solar radiation, vegetative cover, soil and bedrock type, and other factors must be evaluated to understand the local or global hydrologic cycle.

Precipitation is an extremely variable phenomenon. The United States has some thirteen thousand precipitation stations equipped with rain gauges, placed strategically to compensate for wind and splash losses. Precipitation falling on a given area is determined using a rain-gauge network of uniform density to determine the arithmetic mean for rainfall in the area. The amount of water in a *snowpack* is estimated by snow surveys. The depth and water content of the snowpack are measured and the extent of the snow cover mapped using satellite photography.

The amount of precipitation lost by interception can be measured and evaluated. Most often, interception is determined by measuring the amount above the vegetative canopy and at the earth's surface. The difference is what is lost to interception.

The volume of water flowing by a given point at a given time in an open stream channel is called discharge. Discharge is determined by measuring the velocity of water in the stream channel, using a current meter. The cross-sectional area of the stream channel is determined at a specific point and multiplied by the stream velocity. Automated stream-gauging stations are located on most streams to supply data for various hydrologic investigations.

The U.S. National Weather Service maintains about five hundred stations using metal pans, mimicking reservoirs, to measure free-water evaporation. Water depths of 17 to 20 centimeters are maintained in the pans. Errors may result from splashing by raindrops or birds. Because the pans will heat and cool more rapidly than will a natural reservoir, a pan coefficient is employed to compensate for this phenomenon. The wind velocity is also determined. A lake evaporation nomograph determines daily lake evaporation. The mean daily temperature, wind velocity, solar radiation, and mean daily dew point are all used in the calculation.

The amount of evapotranspiration can be measured using a lysimeter, a large container holding soil and living plants. The lysimeter is set outside, and the initial soil moisture is determined. All precipitation or irrigation is measured accurately. Changes in the soil moisture storage determine the amount of evapotranspiration.

Samuel F. Huffman

See also: Calvin cycle; Carbon cycle; Leaf anatomy; Nitrogen cycle; Phosphorus cycle; Plant tissues; Water and solute movement in plants.

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HYDROPONICS

Categories: Agriculture; disciplines; economic botany and plant uses; gardening; water-related life

Literally "water culture," hydroponics originally referred to the growth of plants in a liquid medium. It now applies to all systems used to grow plants in nutrient solutions with or without the addition of synthetic soil for mechanical support.

Hydroponics has become an important method of crop production with the increase in the number of commercial greenhouse operations. Greenhouses are utilized in the production of a wide array of bedding plants, flowers, trees, and shrubs for commercial as well as home and garden use. Cash receipts from greenhouse and nursery crops total more than $4 billion annually. In some arid regions, the majority of vegetable crops are produced in greenhouses.

Image Not Available

Types of Systems

The four most commonly used hydroponic systems are *sand-culture systems*, *aggregate systems*, *nutrient film techniques*, and *floating systems*. While these systems are similar in their use of nutrient solutions, they vary in both the presence and type of supporting medium and in the frequency of nutrient application. In sand culture, coarse sand is used in containers or spread over a greenhouse floor or bed, on top of a recirculating drain system. A drip irrigation system is used to apply nutrient solution periodically, and a drainage system is used to collect the excess solution as it drains through the sand.

In an aggregate open system, plants are transplanted into plastic troughs filled with an inert supporting material, and nutrient solution is supplied via drip irrigation. The aggregate system and the sand culture are open systems because the nutrient solution is not recycled.

In the nutrient film technique, there is no supporting material. Seedlings are transplanted into troughs through which the nutrient solution is channeled, and the plants are in direct contact with the nutrient solution. In this closed system, the nutrient solution is channeled past the plant, collected, and reused. The floating hydroponic system involves the floating of plants over a pool of nutrient solution.

While the nutrient film technique and floating hydroponic systems are primarily used in research applications, the sand culture and aggregate systems are commonly used in commercial plant production. These two systems require the use of a nutrient solution and synthetic soil for mechanical support. A variety of nutrient solutions have been formulated since the first was developed in 1950.

Mechanical Support Materials

A large variety of both *organic* and *inorganic* materials have been used to formulate the synthetic soils used for mechanical support in hydroponic systems. Commonly used organic materials include sphagnum moss, peat, manure, wood, and other plant residues. Sphagnum moss, the shredded, dehydrated remains of several species of moss in the genus *Sphagnum*, is harvested for the purpose of producing synthetic soil. "Peat" is a term normally used to describe partially decomposed remains of wetlands vegetation that has been preserved under water. Peat moss is the only type of peat suitable for synthetic soil mixes. Peat moss is harvested from peat bogs, dried, compressed into bales, and sold. Animal manures are almost never used in commercial synthetic soil mixtures because they require costly handling and sterilization procedures.

Wood residues such as tree bark, wood chips, shavings, and sawdust are generally produced as by-products of the timber industry. A variety of other plant residues, including corn cobs, sugarcane stems, straw, and peanut and rice hulls have been substituted for peat in synthetic soil mixtures where there is a supply of these materials.

Commonly used inorganic materials include vermiculite, sand, pumice, perlite, cinders, and calcined clay. Vermiculite is a very lightweight material produced by heating mica to temperatures above 1,090 degrees Celsius (nearly 2,000 degrees Fahrenheit). Sand is a preferred material for formulating synthetic soils because it is inert and inexpensive but very heavy compared to other commonly used materials. Pumice, a natural, glasslike material produced by volcanic action, provides a good inert supporting material when ground into small particles. Perlite, a porous material that will hold three to four times its weight in water, is produced by heating lava at temperatures above 760 degrees Celsius (1,400 degrees Fahrenheit). Cinders are derived from coal residues that have been thoroughly rinsed to remove harmful sulfates. Calcined clay is derived from the mineral montmorillonite baked at temperatures above 100 degrees Celsius.

D. R. Gossett

See also: Fertilizers; Horticulture; Nutrients; Nutrition in agriculture.

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INFLORESCENCES

Categories: Anatomy; angiosperms; gardening

The term "inflorescence" refers to the arrangement of flowers on a floral axis. Most schemes that define inflorescence types separate solitary flowers from flower clusters and stipulate that an inflorescence is a cluster of two or more flowers.

It is not always easy to distinguish between *solitary flowers* and an inflorescence. An examination of the evolutionary development of the flower and the inflorescence provides some insight into the problem. It generally is accepted that the flower arose as a modified stem tip that bore male and female reproductive structures at its apex. These reproductive structures became the pistils and stamen of the flower. Leaves that immediately subtended the reproductive structures became the sterile parts of the flower (petals and sepals) and are typically more leaflike as distance from the apex increases.

If leaves subtending the flower are much smaller or distinctly different from regular leaves, they are referred to as bracts. If a second, considerably smaller set is present, its component parts are termed *bracteoles*. The determination of whether subtending leaflike structures are leaves or bracts may establish a flower as solitary or as part of an inflorescence.

Sometimes woody branches that support flowers are modified. They may grow much more slowly than branches that support only vegetative structures. The latter pattern is observed in many fruit tree species, such as apples and pears, where the fruit is supported by short, modified branches called *spurs*. Clusters of flowers issuing from such spurs may resemble inflorescence types, although the flowers are solitary.

Flowers may be *complete*, possessing all four sets of floral appendages, or they may be reduced to as little as one set of reproductive structures (stamen or pistils). If clusters of many reduced flowers are borne on very short stems, the resulting aggregation may superficially resemble a single flower. This type of inflorescence is associated with daisies and asters (*Asteraceae*) and is often mistaken for a single flower by those unfamiliar with flower and inflorescence structure. In spite of these confusing elements, most common inflorescence patterns can easily be recognized.

Parts of an Inflorescence

The following terms, some of which already have been introduced, are features or structures that are used to classify inflorescences. An *axillary bud* occurs in the angles between a stem and a leaf petiole. A *bract* is a small or modified leaf immediately beneath a flower or inflorescence. A bracteole is a bract that is much smaller in size.

An *involucre* is a series of bracts or bracteoles subtending a flower or inflorescence. A *pedicel* is a stalk supporting a single flower of an inflorescence. A *peduncle* is a stalk of a solitary flower or of an inflorescence. A *rachis* is the main branch or axis within a complex inflorescence.

Inflorescence Types

Parameters used to classify basic inflorescence types include

(1) number and position of flowers

(2) sequence of flower development, and

(3) the nature of inflorescence branching.

Because the inflorescence type of a given species may result from evolutionary reduction, classification schemes are typically artificial and do not reflect evolutionary significance. The form of an inflorescence, however, is determined largely by two patterns of development.

If the growing tip of the stem (*apical meristem*) continues to grow and produce new flowers as it elongates, the inflorescence is said to be *indeterminate*. A raceme (defined below) is a typical indeterminate inflorescence. If the apical meristem quickly matures into a flower, it can no longer grow in length, and the inflorescence exhibits a limited growth pattern. This type of inflorescence is said to be *determinate* and is best represented by a cyme (defined below). The following descriptions of inflorescence types represent most of the basic types. Any vascular plant taxonomy text will provide a more comprehensive list.

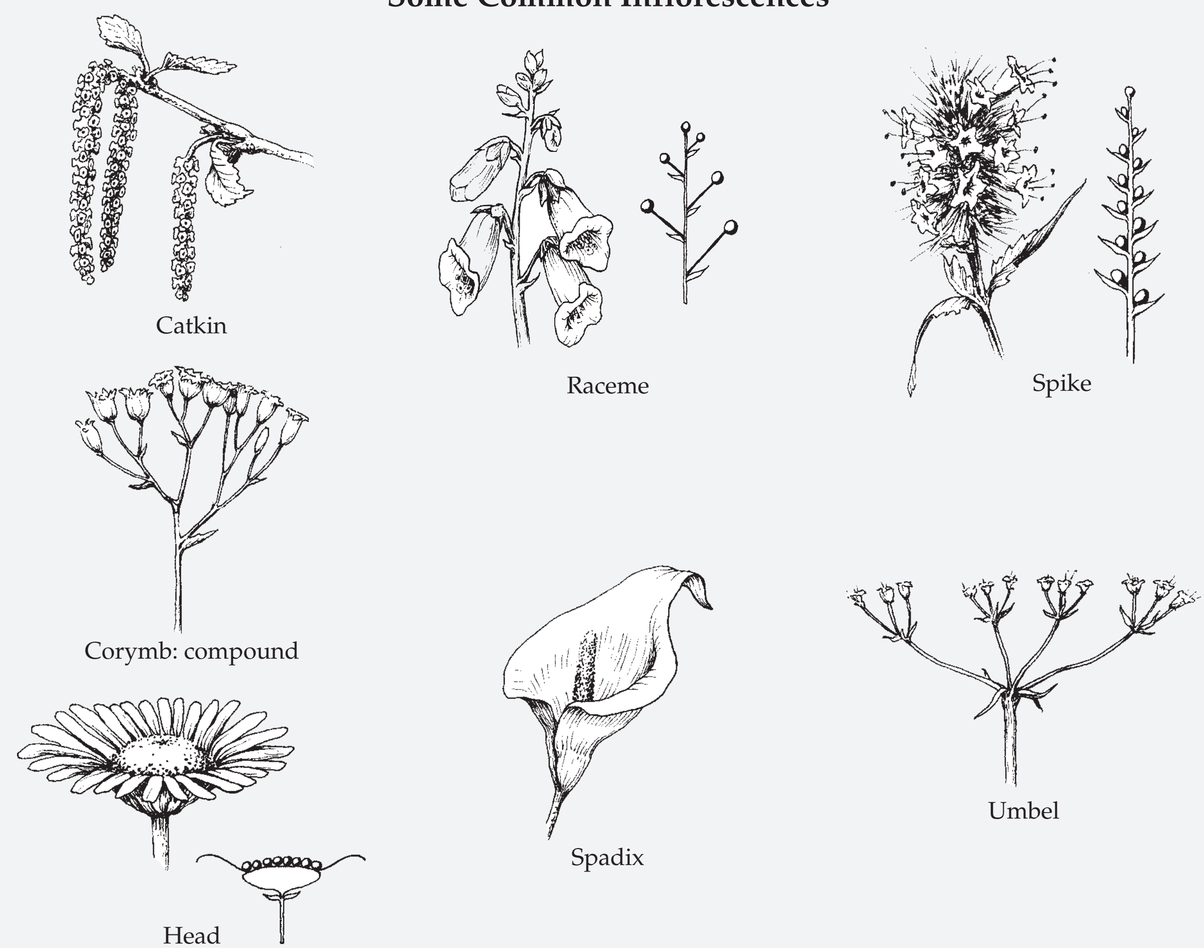
Indeterminate Inflorescences

A *catkin* (also known as an *ament*) is a spikelike inflorescence. Dissection may reveal the presence of minute, and possibly branched, pedicels. The flowers are typically unisexual and are hidden by bracts. This inflorescence is typical of trees such as oaks, hickories, and birches.

A *corymb* is a flat- or rounded-top inflorescence. The pedicels of flowers are attached along the length of the peduncle. Corymbs may be simple or compound. Examples include hydrangea and hawthorn.

A *head*, or *capitulum*, is a tight cluster of sessile flowers (flowers with no pedicel) borne on a flattened or short stem tip (receptacle). Heads are a diagnostic feature of the sunflower family (*Asteraceae*),

Some Common Inflorescences



Kimberly L. Dawson Kurnizki

The variety of arrangements flowers may take on a floral axis, called the "inflorescence," is far greater than those examples displayed here, also including cyme, panicle, cluster, cyathium, mono-, di-, and pleiochasium, thyrse, and verticillaster inflorescences and variations on these. Solitary flowers are technically not inflorescences because they are not clusters of flowers.

examples of which are daisies, chrysanthemums, and sunflowers.

A *panicle* has a branched floral axis (rachis), which may re-branch prior to bearing flower pedicels (described sometimes as a compound raceme).

A *raceme* has pedicellate flowers borne on an elongate rachis. It is often confused with a spike when the pedicels are small and inconspicuous. Examples include foxglove and lupine.

A *spike* has sessile flowers borne on a single rachis. Examples are ladies' tresses (a type of orchid) and plantain. A *spikelet* is a small spike. The flowers are inconspicuous and often hidden by a series of modified bracts. This is the basic inflorescence unit of grasses and sedges.

A *spadix* is a spike with flowers embedded in a fleshy rachis. Typically, the spadix is subtended and surrounded by a large modified bract termed a spathe. The spadix is characteristic of the arum family (*Araceae*), examples of which are jack-in-the-pulpit and elephant ear.

Determinate Inflorescences

An *umbel* can be determinate or indeterminate, with a flat or rounded top. The pedicels of flowers are attached to a common point on the peduncle. Umbels may be simple or compound. Compound umbels are the typical inflorescence of most members of the carrot family (*Apiaceae*). Examples include onion, carrot, and dill.

A *cyme* is a branching inflorescence with individual flowers at the end of each branch. A simple cyme is determinate, with a grouping of three flowers on a peduncle. The central flower matures first. Examples include champions and some of the anemones. A compound cyme is composed of two or more cymes together. Examples include chickweed and phacelia.

John F. Logue

See also: Angiosperm cells and tissues; Angiosperm evolution; Angiosperms; Flower structure; Flower types; Flowering regulation; Garden plants: flowering; Pollination; Shoots; Stems.

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INTEGRATED PEST MANAGEMENT

Categories: Agriculture; environmental issues; pests and pest control

Integrated pest management (IPM) is the practice of integrating insect, animal, or plant management tactics, such as chemical control, cultural control, biological control, and plant resistance, to maintain pest populations below damaging levels in the most economical and environmentally responsible manner.

In the past, pest management strategies in agriculture focused primarily on eliminating all of a particular pest organism from a given field or area. These strategies depended on the use of chemical pesticides to kill all of the pest organisms. Prior to the twentieth century, farmers used naturally occurring compounds such as kerosine or pyrethrum for this purpose. During the second half of the twentieth century, synthetic pesticides began playing a prominent role in controlling crop pests.

Chemical Effects

After 1939 the use of pesticides such as dichlorodiphenyl-trichloroethane (DDT) was so successful in terms of controlling pest populations that farmers began to substitute a heavy dependence on pesticides for sound pest management strategies. Soon pests in high-value crops became resistant to one pesticide after another. In addition, outbreaks of secondary pests occurred because either they developed resistance to the pesticides or the pesticides killed their natural enemies. This supplied the impetus for chemical companies to develop new pesticides, to which the pests also eventually developed resistance.

Rationale for IPM

Certain pests have developed resistance to all federally registered materials designed to control them. In addition, many pesticides are toxic to humans, wildlife, and other nontarget organisms and therefore contribute to environmental pollution. For these reasons, and because it is very expensive for chemical companies to put a new pesticide on the market, many producers began looking at alternative strategies such as IPM for managing pests. The driving forces behind the development of IPM programs are concern about the contamination of groundwater and other nontarget sites, adverse effects on nontarget organisms, and development of pesticide resistance. Pesticides will probably continue to play a vital role in pest management, even in IPM, but it is believed that their role will be greatly diminished over time.

An agricultural ecosystem consists of the crop environment and its surrounding habitat. The interactions among soil, water, weather, plants, and animals in this ecosystem are rarely constant enough to provide the ecological stability of nonagricultural ecosystems. Nevertheless, it is possible to use IPM to manage most pests in an economically efficient and environmentally friendly manner. IPM programs have been successfully implemented in the cropping of cotton and potatoes, and they are being developed for other crops.

Developing IPM Programs

There are generally three stages of development associated with IPM programs, and the speed at which a program progresses through these stages is dependent on the existing knowledge of the agricultural ecosystem and the level of sophistication desired. The first phase is referred to as the *pesticide management phase*. The implementation of this phase requires that the farmer know the relationship between pest densities and the resulting damage to crops so that the pesticide is not applied excessively. In other words, farmers do not have to kill all of the pests all of the time. They must use pesticides only when the economic damage caused by a number of pest organisms present on a given crop exceeds the cost of using a pesticide. This practice alone can reduce the number of chemical applications by as much as half.

The second phase is called the *cultural management phase*. Implementation of this phase requires knowledge of the pest's biology and its relationship to the cropping system. Cultural management includes such practices as delaying planting times, rotating crops, altering harvest dates, and planting resistance cultivars. It is necessary to understand pest responses to other species as well as abiotic factors, such as temperature and humidity, in the environment. If farmers know the factors that control population growth of a particular pest, they may be able to reduce the impact of that pest on a crop. For example, if a particular pest requires short days to complete development, farmers might be able to harvest the crop before the pest has a chance to develop.

The third phase is the *biological control phase*, which involves the use of biological organisms rather than chemicals to control pests. This is the most difficult phase to implement because farmers must understand not only the pest's biology but also the biology of the pest's natural enemies and the degree of effectiveness with which these agents control the pest.

In general, it is not possible to rely completely on biological control methods. A major requirement in using biological agents is to have sufficient numbers of the control agent present at the same time that the pest population is at its peak. It is sometimes possible to change the planting dates so that the populations of the pests and the biological control agents are synchronized. Also, there is often more than one pest species present at the same time within the same crop, and it is extremely difficult to control simultaneously two pests with biological agents.

D. R. Gossett

See also: Agriculture: modern problems; Biopesticides; Pesticides; Sustainable agriculture.

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INVASIVE PLANTS

Categories: Environmental issues; poisonous, toxic, and invasive plants; water-related life

Nonnative (also termed "exotic") fungi and plants that can outcompete native species are called invasive plants. Invasive plants cause irreversible changes to ecosystems, threaten plant and animal species, and cost billions of dollars to control.

Between the damage they cause and the cost of control efforts, invasive plants cost the United States more than $140 billion every year. Nearly half of the threatened and endangered plant species listed for the United States in 1999, 400 of 958, are in peril because of competition from invasive species. Thus, invasive plants are capable of causing irreparable changes in ecosystems.

Most invasive species invading the United States originated in Asia or Europe. A key factor in this problem is that seeds or spores of these plants are accidentally transported into new habitats by humans, but the plants' natural enemies and competitors are left behind. Without natural biological controls, the alien species can thrive and outcompete the native flora, driving the native plants toward extinction and creating a near monoculture of the invader.

Invasive plants are weedy species that grow rapidly, produce large numbers of long-lived seeds, and frequently have perennial roots, or rhizomes, that enhance asexual propagation. Invasive plants have a variety of effects on invaded ecosystems. Many invasive species deplete soil moisture and nutrient levels, either by growing more vigorously than native plants early in the growing season or by being more tolerant of reduced levels of water and nutrients than are natives. Some invasive species produce toxic chemicals (*allelopathy*) that are released into the soil and inhibit the growth of competitors. By outcompeting native plants, the invader decreases species diversity as it replaces many native species. As a result, animal species dependent on native flora are also affected. Fungi and seed plants are among the most disruptive invasive plants in the United States today.

Control Methods

Invasive species are carried to new habitats, either in or on machinery or organisms, and are usually transported by humans, so prevention is the most cost-effective method of control. Once an invasive species has entered an area, plant quarantine is an effective first line of defense. For example, living plants and animals brought into the United States must pass inspection by the U.S. Department of Agriculture Animal and Plant Health Inspection Service (APHIS) to ensure that they are not carrying

Most plant species invading the United States originated in Asia or Europe, such as this Scotch broom. In Oregon and Washington, complete Douglas fir plantation failures have been attributed to Scotch broom.

potentially invasive species. Particular care is taken to ensure that imports from known areas of infestation are clean of seeds, spores, or propagules.

The next most effective strategy is detection and control of small infestations. When there is a known threat of invasion, the affected area should be surveyed periodically and individual plants removed by hand or, in extreme cases, by "spot-spraying" herbicide. Eradication is possible when the infestation is small.

Once an invasive species becomes established, the only means of management are expensive chemical or biological controls which, at best, will only minimize damage. A variety of chemicals may be used to kill invasive plants. Most chemicals, however, affect a broad spectrum of plants, including native species. Biological controls, including natural enemies from the invasive plant's native ecosystem, can be more specific but may also be capable of displacing native species and becoming "invaders."

Fungi

Many of the most serious plant pathogens are invasive species introduced into the Americas since the beginning of European settlement. Two classic examples are Dutch elm disease, caused by the fungi *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* and chestnut blight, caused by the fungus *Cryphonectria parasitica*. At the beginning of the twentieth century, the most common street tree growing in the cities of the eastern United States was the American elm. About 1910, the European bark beetle was introduced into the United States. It was not until the 1930's that Dutch elm disease was observed in Ohio and a few eastern states. The fungal spores are carried by the beetles, which burrow under the elm bark. The native elm has little resistance to this fungus, whose spores rapidly germinate and form extensive mycelia within the phloem of the host tree, killing it within a few years. After its initial contact, the fungus spread throughout the cities and forests of the East and gradually westward, so that by 1990 nearly all of the native American elm trees in the United States had been killed.

American chestnut was also one of the early dominant trees of the eastern U.S. forest. In addition to providing edible fruit, the chestnut became a commercially important timber tree. Chestnut blight fungus was first reported in 1904 on chestnut trees in the New York Zoological Garden and quickly began to spread. This infestation led directly to passage of the Plant Quarantine Act of 1912, the forerunner of APHIS. By 1950 most native chestnut trees were reduced to minor understory shrubs. Biological control using virus strains first isolated in Italy show promise for controlling the blight.

Terrestrial Green Plants

Virtually all of the plants commonly called "weeds" are foreign invaders that are difficult, if not impossible, to control. Some of the most severe include Canada thistle (*Circium arvense*), leafy spurge (*Euphorbia esula*), and purple loosestrife (*Lythrum salicaria*). Canada thistle is the most widespread and difficult species of thistle to control. It was introduced to Canada from Europe in the 1600's and in 1795 was listed as a noxious weed in Vermont. It is now found in most of the United States as well as in Canada. Single herbicide applications do not provide long-term control, and there are no effective biological controls that do not also attack native species.

Leafy spurge was first reported in Newbury, Massachusetts, in 1827, where it arrived in ship ballast. By 1900 it had reached the West Coast, and it now thrives in more than half the states and in Canada. Thirteen species of insects are approved for biological control, and several herbicides can be used to control infestations effectively. Sheep and goats will browse on spurge.

Purple loosestrife was introduced into the United States as an ornamental plant in the early 1800's and became established in New England by 1830. Its early spread into the Great Lakes region was by barge and other canal traffic. Rapid expansion of the pest, particularly in the West, occurred after 1940, primarily due to the plant's "escape" from ornamental cultivation into irrigation projects. It is now found in all the lower forty-eight states except Florida. At present, there are no effective controls.

Aquatic Green Plants

Invasive plants are not limited to the terrestrial habitat or to vascular plants. One dramatic example is the alga *Caulerpa taxifolia*, the so-called killer alga. This attractive tropical alga was found to be easy to grow in saltwater aquaria and useful as a secondary food source for herbivorous tropical fish. It began to be used this way at the Oceanographic Museum of Monaco in 1982. Two years later, a meter-square patch was found growing in the Mediterranean Sea, visible from a win-

Backyard Solutions

Public understanding is fundamental to successful control of invasive plant species. Gardeners and landscapers have a personal role to play. Many reputable garden suppliers offer problem plants. Additionally, government agencies will recommend these plants for specific purposes, presuming they will be maintained and controlled in the landscape.

When considering new plants for gardens or landscapes, check references for warnings about high seed production, rank growth, or other invasive characteristics. The Web site http://plants.usda.gov/ is a database of standardized information about plants including identification, distribution, and growth information; a list of plants considered invasive can be searched by common or scientific name.

If the plant being considered has been known to pose a problem, avoid it or be vigilant in keeping it under control, particularly if cultivating an area near natural and unmaintained habitats. Horticulturalists should remember that their industry can be a source of invasive escapes. Additional ways gardeners can help are by eradicating invasive weeds on their property and volunteering for local groups that monitor or eradicate invasive plants.

According to the National Tropical Botanical Garden, botanic gardens, museums, herbaria, and protected areas should take responsibility for publicizing threats from invasive species. Garden clubs, the horticultural and forestry industries, and botanic gardens should have policies and activities to prevent inadvertant introduction of invasive plants.

dow of the museum. By 1990 the alga had reached France, and by 1995 it could be found from Spain to Croatia. *Caulerpa* produces a number of toxins that inhibit foraging by native fish, and it is a prolific vegetative reproducer. Fragments of the alga, stuck on an anchor for example, can start a new infestation wherever the anchor is next dropped. This species has been discovered in Southern California, and a related species has become dominant in Sydney Harbor, Australia. Other aquatic invasive plants in the United States include the mosquito fern (*Azolla*), the Eurasian water milfoil (*Myriophyllum*), and the water hyacinth (*Eichhornia crassipes*).

Marshall D. Sundberg

See also: Algae; Allelopathy; Animal-plant interactions; Aquatic plants; Biopesticides; Biological invasions; Community-ecosystem interactions; Competition; Dinoflagellates; Endangered species; Eutrophication; Fungi; Herbicides; Pesticides.

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IRRIGATION

Category: Agriculture

Irrigation techniques supply additional water to arid and semiarid horticulture or farming regions where few, if any, crops could otherwise be grown.

Approximately 350 million acres (142 million hectares) of land worldwide are irrigated. In the United States more than 10 percent of the crops, encompassing approximately 50 million acres (20 million hectares), receive water through irrigation techniques; 80 percent of these are west of the Mississippi River. In countries such as India, Israel, North Korea, and South Korea, more than one-half of food production requires irrigation. From 1950 to 1980, the acreage of irrigated cropland doubled worldwide. Increases since then have been more modest.

Imperial Valley and Israel

An often-cited example of irrigation success is that of the Imperial Valley of Southern California. The valley, more than 5,000 square miles (12,900 square kilometers) in size, was originally considered to be a desert wasteland. The low annual rainfall resulted in a typical desert ecosystem with cacti and other arid-adapted plants and animals. In 1940, however, engineers completed the construction of the All-American Canal, which carries water 80 miles (130 kilometers) from the Colorado River to the valley. The project converted the Imperial Valley into a fertile, highly productive area where farmers grow fruits and vegetables all year.

Successful agriculture in Israel also requires irrigation. As a result of settlement of the area throughout the twentieth century, large amounts of food must be produced. To fulfill this need, a system of canals and pipelines carries water from the northern portion of the Jordan Valley, where the rainfall is heaviest, to the arid south.

Methods and Technology

Irrigation is an expensive operation that requires advanced technology and large investments of capital. In many cases, irrigation systems convey water from sources hundreds of miles distant. Such vast engineering feats are largely financed by taxpayers. Typically, water from a river is diverted into a main canal and from there into lateral canals that supply individual farms. From the lateral canals, various systems are used to supply water to the crop plants in the field.

Image Not Available

Flood irrigation supplies water to fields at the surface level. Using the *sheet irrigation* method, land is prepared so that water flows in a shallow sheet from the higher part of the field to the lower part. This method is especially suitable for hay and pasture crops. Row crops are better supplied by *furrow irrigation*, in which water is diverted into furrows that run between the rows. Both types of flood irrigation cause soil *erosion* and loss of nutrients. However, erosion can be reduced in furrow irrigation by contouring the furrows.

Sprinkler irrigation, though costly to install and operate, is often used in areas where fields are ungraded or steeply sloped. Sprinklers are supplied with water by stationary underground pipes or a center pivot system in which water is sprinkled by a raised horizontal pipe that pivots slowly around a pivot point. A disadvantage of sprinkler irrigation is loss of water by *evaporation*. In *drip irrigation*, water is delivered by perforated pipes at or near the soil surface. Because it is delivered directly to the plants, much less water is wasted by evaporation compared to other methods.

Much of the water used in irrigation never reaches the plants. It is estimated that most practices deliver only about 25 percent of the water to the root systems of crop plants. The remaining water is lost to evaporation, supplies weeds, seeps into the ground, or runs off into nearby waterways.

Soil Salinization

As fresh water evaporates from irrigated fields over time, a residue of salt is left behind. The process, called *salinization*, results in a gradual decline in soil productivity and can eventually render fields unsuitable for agricultural use. Correcting saline soils is not a simple process. In principle, large amounts of water can be used to leach salt away from the soil. In practice, however, the amount of water required is seldom available, and if it is used, it may waterlog the soil. Also, the leached salt usually pollutes groundwater or streams. One way to deal with salinization is to use genetically selected crops adapted to salinized soils.

Water Resources

As the number of acres of farmland requiring irrigation increases, so does the demand for water. When water is taken from surface streams and rivers, the normal flow is often severely reduced, changing the ecosystems downstream and reducing their biodiversity. Less water becomes available for other farmers downstream, and that situation can lead to disputes over water rights.

In other cases water is pumped from deep wells or aquifers. Drilling wells and pumping water from such sources can be expensive and may lead to additional problems, such as the sinking of land over aquifers. Such land subsidence is a major problem in several parts of the southern and western United States. Subsidence in urban areas can cause huge amounts of damage as water and sewer pipes, highways, and buildings are affected. In coastal areas, depletion of aquifers can cause the intrusion of salt water into wells, rendering them unusable. The federal government spends millions of dollars to repair damage to irrigation facilities each year.

Like many modifications to natural ecosystems, the use of water for irrigation achieves some remarkable but temporary advantages that are complicated by long-term environmental problems. Assessments of total financial costs and environmental impacts are continuously weighed against gains in production.

Thomas E. Hemmerly

See also: Agriculture: modern problems; Erosion and erosion control; Hydrologic cycle; Soil salinization.

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KREBS CYCLE

Categories: Cellular biology; photosynthesis and respiration; physiology

The Krebs cycle, also called the citric or tricarboxylic acid cycle, is a series of chemical reactions that completes the aerobic breakdown of glucose and facilitates the transfer of energy to the electron transport system.

Every living organism must process chemical energy to survive. The series of metabolic pathways known as *cellular respiration*, which obtains most of the energy needed for cellular metabolism, consumes both organic fuel and oxygen. Respiratory processes ultimately produce the *adenosine triphosphate* (ATP) that drives metabolic processes. The Krebs cycle, named for biochemist Hans A. Krebs, is a basic chemical process that is found in the mitochondria of all eukaryotic cells.

The Krebs cycle is the crucial second part in the breakdown of glucose to water and carbon dioxide—a part of *cellular respiration*. Cellular respiration begins in the cytoplasm (the fluid within the cell) with the breakdown of glucose to form pyruvic acid, in a process known as *glycolysis*. Pyruvic acid is then transported across the mitochondrial membranes into the matrix, where it loses a molecule of carbon dioxide and is converted into acetyl coenzyme A (acetyl CoA). The Krebs cycle completes the breakdown of glucose by joining the acetyl portion of acetyl CoA to an organic acid which then, through a series of steps, releases the equivalent of what was left of the glucose as carbon dioxide.

Together, these steps supply energized electrons, which are necessary for the final step, *oxidative phosphorylation*, where the bulk of the cell's ATP is produced. In addition to its central role in *catabolism*, or the breakdown of organic molecules, the Krebs cycle plays a central role in *anabolism*, or the synthesis of organic molecules. Many of the intermediate molecules in the Krebs cycle can be used in other biochemical pathways to produce amino acids, carbohydrates, and lipids.

Oxidation and Electron Transfer

The fuel for running the Krebs cycle is the two-carbon fragments known as *acetyl groups*. The overall chemistry of the Krebs cycle involves the *oxidation* of the acetyl group's two carbon atoms to two molecules of carbon dioxide. As oxidation occurs in the Krebs cycle, electrons are released, in the form of hydrogen atoms, and picked up by electron carriers. The release of these electrons, which have a high energy content, is the primary goal of the Krebs cycle. They are used later as the energy source for oxidative phosphorylation.

The electron acceptors are two coenzymes similar to coenzyme A; *nicotinamide adenine dinucleotide* (NAD^+) and *flavin adenine dinucleotide* (FAD). Both NAD^+ and FAD have a ring containing nitrogen that shares four electrons with an adjacent carbon atom. Such arrangements are especially suitable for accepting electrons and protons and then releasing them later. In their oxidized states, NAD^+ and FAD are each capable of accepting two electrons, donated initially as two hydrogen atoms. When NAD^+ reacts with two hydrogen atoms, it keeps one and strips away the electron from the other, releasing what is left as a free proton (H^+). In the process NAD^+ is made into its reduced form, NADH. When FAD reacts with two hydrogen atoms, it accepts them both, along with their two electrons, to become $FADH_2$. Thus, the coenzymes NAD^+ and FAD, as NADH and $FADH_2$, serve as electron transfer agents, connecting the Krebs cycle with the *electron transport system* embedded in the inner mitochondrial membrane.

Principal Steps

After years of research, a detailed picture of the chemistry of the Krebs cycle is available. For each of the eight principal steps, the structure of the reactants and products, as well as the enzymes that catalyze the reactions, has been determined. During one turn of the Krebs cycle, the equivalent of one acetyl group is converted into two carbon dioxide molecules.

The first step of the Krebs cycle occurs when acetyl CoA reacts with oxaloacetate, the ionic form of oxaloacetic acid, to form citrate. (All of the acids in the Krebs cycle occur in their ionic forms.) This first product is tricarboxylic acid; hence, one of the other names of this cycle, the tricarboxylic acid cycle. In addition to citrate, the first step in the Krebs cycle releases a molecule of coenzyme A, which is ready to react with another acetyl group from a pyruvate molecule. While the overall result of the Krebs cycle is degradation, this initial step is one of building up, or synthesis.

In the second step, citrate is made into isocitrate by a complex rearrangement involving the loss of a molecule of water and then the addition of a water molecule. The net effect is to move a hydroxyl or alcohol group from one carbon to an adjacent one. The starting citrate and the product, isocitrate, have the same molecular formula but have different molecular structures. Such molecules are called *isomers*.

In the third step, isocitrate is oxidized. It passes two hydrogen ions to NAD^+, thus reducing it to NADH and releasing a free proton. Isocitrate also loses a molecule of carbon dioxide and becomes alpha-ketoglutarate. With the loss of this carbon dioxide molecule, the equivalent of only one of the two original acetyl carbon atoms remains.

The fourth step involves the loss of another carbon, in the form of carbon dioxide, equivalent to another of the original two acetyle carbon atoms. Alpha-ketogluterate bonds with a molecule of coenzyme A to form succinyl CoA. The remaining steps involve the remaking of oxaloacetate so the cycle can occur again with another acetyl group. In the process, a few more high-energy electrons are passed off to electron carriers.

The fifth step involves splitting succinyl CoA to produce free coenzyme A and succinate. The splitting of this bond releases enough energy to drive a substrate-level phosphorylation reaction which takes place in two steps. First, a molecule of guanosine diphosphate (GDP) reacts with inorganic phosphate to form guanosine triphosphate (GTP). Then GTP transfers its phosphate to adenosine diphosphate (ADP), to produce ATP. These two nucleotides are very similar in having high-energy phosphate bonds, but they differ in their nitrogenous bases; GTP has guanine, and ATP has adenine.

In step six, succinate is oxidized to a fumarate. In the process two hydrogen atoms, with their high-energy electrons, are passed to FAD to form $FADH_2$.

In step seven, fumarate is transformed to malate by the addition of a molecule of water.

In the last step, malate is made into oxaloacetate, which is ready to start the process all over again. A further consequence of this reaction is the release of another two hydrogen atoms, with high-energy electrons, that are picked up by NAD^+, with the consequent production of the usual free proton.

Advantages

Detailed studies of these chemical reactions reveal that the carbon atoms that are actually oxidized and released as carbon dioxide come from the oxaloacetate portion of the citrate ion rather than from the acetyl group. The acetyl group is now one-half of the new oxaloacetate and, after another turn of the Krebs cycle, these acetyl carbons will be released as carbon dioxide.

The mechanics of the Krebs cycle have additional advantages. The cycle's chief function of obtaining energy for the cell's needs is accomplished in small, discrete increments rather than in one large burst. This stepwise process allows finer control of the entire reaction sequence, with a large number of points at which control can be exercised. Finally, as the acetyl group passes through a cycle, a variety of molecules are produced, which can provide raw materials for the synthesis of essential biological molecules.

Bryan Ness

See also: ATP and other energetic molecules; Glycolysis and fermentation; Oxidative phosphorylation; Respiration.

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LEAF ABSCISSION

Categories: Cellular biology; physiology; reproduction and life cycles

In the process of leaf abscission, plants periodically shed their leaves. Leaf abscission involves a number of biochemical and physical changes that are largely controlled by plant hormones.

Plants are primarily categorized as *annuals*, *biennials*, or *perennials*, based on their growth patterns. Annuals are those plants that undergo a complete life cycle from seed to seed in one growing season. Biennials require two growing seasons to complete a life cycle; during the first year, only vegetative growth takes place. The aboveground portion dies through the winter, and in the next growing season the roots send up a reproductive shoot that produces the seeds. Perennials have the capacity to live through many successive growing seasons. In this group, those plants referred to as *deciduous* species shed all their leaves at the same time. The *evergreen* species shed leaves throughout the year, yet never shed the entire complement at any one time.

Preparation and Precursors

Prior to any natural abscission that may take place, leaves (or any other plant organ subject to abscission, such as flowers or fruit) undergo *senescence*. Senescence can be defined as the deterioration that occurs in conjunction with aging, and it results in the death of an organ or organism. Senescence can occur throughout the entire plant, as it does in annuals, or in only the aboveground portion, as it does in perennial herbs. In woody perennials, however, only the leaves senesce, while the bulk of the stem and roots remain alive.

From the time that leaves begin to grow, biochemical activities such as photosynthesis increase. This increase will continue until the leaves expand to maximum size. Soon after they reach maximum size, senescence begins, and photosynthetic rates begin to decrease. As the photosynthetic ability of the leaves declines, there is an accompanying decrease in other metabolic activities. Respiration rates begin to subside dramatically, and leaf protein levels drop sharply because of increased *proteolytic* activity (enzymatic breakdown of proteins). Protein synthesis diminishes, and there is an increase in the enzymatic degradation of ribonucleic acid (RNA). There is also an increase in the hydrolytic breakdown of carbohydrates. Finally, destruction of the green pigment, *chlorophyll*, is accompanied by increased visibility of the yellow or orange pigments called *carotenoids*, which were previously masked by chlorophyll. Most of the protein, carbohydrates, RNA, and chlorophyll degradation products are rapidly transported out of the senescing leaf. The final result is the production of yellowish, dead leaves.

The senescence process is a natural progression of the normal plant life cycle; however, environmental conditions can influence the process. Lack of water will speed the senescence process in most species. Higher-than-normal temperatures also cause an increase in senescence-related reactions. Darkness dramatically hastens senescence: Most leaves will senesce two or three times faster in darkness than if growing under normal light conditions.

Numerous studies strongly suggest that senescence is under hormonal control. Both *ethylene* and *abscisic acid* enhance senescence, but ethylene is the more effective of the two. The *gibberellins*, *cytokinins*, and *auxins* (other types of hormones) have all been shown to delay the process in various plant species. The exact role of each of these hormones in senescence has not yet been determined, but it is apparent that the process involves the interaction of several of these growth-regulating substances.

Onset of Abscission

Following senescence, abscission of the leaves inevitably takes place. This process usually involves the formation of an *abscission layer* at the base of the leaf petiole. During the early life of a leaf, auxin is produced in relatively high concentrations and is steadily transported out of the leaf through the petiole. As long as the auxin level remains high in the leaf and a sufficient amount of the hormone is transported across the petiole, both senescence and abscission are delayed.

In addition, gibberellins and cytokinins are produced elsewhere in the plant and then sent to the leaves to help retard the destructive processes. As the leaf matures, however, the level of the senescence-retarding hormones, especially auxin, decreases.

With the decrease in auxin levels, the catabolic (breakdown) reactions begin to outnumber the anabolic (synthetic) processes. In conjunction with the increase in catabolic reactions, there is a rise in the levels of abscisic acid and, especially, ethylene. Ethylene is particularly important in producing the abscission layer.

In most species, the abscission layer is formed from one or perhaps several layers of cells across the base of the petiole. In the earlier stages of abscission, there is a noticeable rise in the respiration rates of the cells of the abscission layer closest to the stem (the proximal cells). As the respiration rates increase to supply additional energy, ethylene stimulates one or more of these cell layers nearest the stem to increase in size. Along with the increase in size of those cells, the cells in the abscission layer farthest from the stem (the distal cells) increase the production of enzymes that break down polysaccharides in the cell walls. With the secretion of these enzymes into the cell walls, digestion of the cell-wall materials begins. The pressure created by the expansion of the cells in the proximal region of the abscission layer (causing them to grow against the weakened senescing cells of the distal region) results in the two layers breaking apart. Thus, the leaf detaches and falls from the plant.

Abscission, like senescence, is a natural order of progression during the life cycle of most plants. Although the process is closely correlated with regular seasonal changes, variations in environmental conditions can enhance abscission. Deficiencies in certain nutrients, such as nitrogen, or lack of water can stimulate abscission. These conditions also hasten senescence, and senescence always precedes abscission. Hence, adverse environmental conditions perhaps trigger only the onset of senescence, and abscission occurs as a secondary result of the aging process.


Digital Stock

Throughout much of the world trees and other plants are subjected to freezing temperatures. Leaves age and fall prior to winter. Without the abscission process to cause the plant to prepare for winter by shedding its leaves, the senescent tissues would shade the new spring growth that appears the following growing season on what are shown here as bare branches.

Function of Abscission

Throughout much of the world, plants are subjected to freezing temperatures. The leaves of most plants are unable to withstand the cold weather and face certain death during the winter. If the leaves did not prepare for the onset of cold weather by undergoing senescence, the first freeze would kill the leaves before materials within them could be salvaged. Without the abscission process to remove the dead leaves, the senescent tissues would shade the new spring growth that appears the following growing season. Hence, senescence and abscission provide a means by which perennials can recycle a major portion of leaf materials as the plants prepare for both the cold weather and the following growing season.

Competition for nutrients from other parts of the plant may initiate the senescence process. The pull of nutrients to another part of the plant such as roots, flowers, or fruit would reduce the amount of these materials bound for the leaves. The reduced supply of nutrients could very well decrease synthetic rates, and the overall result would be a decline in major leaf macromolecules such as proteins, chlorophyll, and nucleic acids.

Competition alone, however, cannot account for the senescence and abscission phenomena, because even in plants that do not produce fruit, the leaves experience aging and the loss of leaves. In addition, numerous studies have shown that leaf senescence will still occur when flowers are removed from the plant soon after being formed. Although competition for nutrients may not be the sole cause of the phenomenon, the mobilization of substances such as amino acids and carbohydrates from the leaves to other metabolic sinks, such as the fruit, is definitely linked to the initiation of senescence. Several of the plant hormones or other factors that stimulate mobilization also hasten senescence. Hence, it is possible that the competition for nutrients triggers the production of some unknown senescence hormone by the fruit or some other competing plant part. This theoretical substance would be transported to the leaves, where it would initiate mobilization of leaf contents. This mobilization might enhance senescence, which, in turn, might trigger the metabolic reactions that lead to abscission of the leaves.

D. R. Gossett

See also: Angiosperm life cycle; Hormones; Leaf anatomy; Plant life spans.

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LEAF ANATOMY

Categories: Anatomy; photosynthesis and respiration

The leaf has evolved as the chief part of the plant for gathering light energy from the sun and conducting photosynthesis to transform that light energy into biochemical energy. Hence, its structure is adapted to that function.

Leaves are formed by a plant to manufacture food. *Photosynthesis*—a complicated chemical reaction in which carbon dioxide from the air and water from the soil, in the presence of light, produce sugar—is carried out in the *chloroplasts* found packed within the leaf cells. Because energy is derived from light by chlorophyll, either the leaf must be thin enough for light to penetrate all the cell layers or, in the case of plants with succulent leaves, chloroplasts must be most concentrated near the surface of the leaves.

Orientation to Light

No matter how many leaves a plant has, each is arranged in respect to light. Although some plants that are adapted to hot, dry conditions may orient their leaves to minimize exposure to the sun, most arrange their leaves to maximize exposure to the sun. Some are exposed to direct rays of the sun; others may face only a portion of the sky. A plant may be forced into various growing patterns to allow the leaves to be exposed to light. Some species germinate their seeds high above the ground, in the cracks of bark on tree trunks and branches. Plants that climb wind their way around larger plants until they gain a place in the sun. Therefore, leaf shape may be determined by where a plant species is best adapted to grow.

The leaves of plants that grow mostly in shade, called *shade plants*, have a larger surface area, tend to be thinner, and have a higher concentration of chlorophyll. The leaves of plants growing mostly in the sun, called *sun plants*, have a smaller surface area, tend to be thicker, and have a lower concentration of chlorophyll. Even leaves on the same plant can vary in structure depending on whether they spend most of their time in the sun or the shade, showing similar traits as seen in sun and shade plants. Taxonomists use leaf pattern, leaf arrangement, and leaf shape to help identify and classify plants.

Leaf Margins

As leaves vary in size and shape, so do their edges, or *margins*. Many plants, such as holly and thistles, have prickly margins; prickles are the outgrowths of the leaf's vein endings. The prickly boundary acts as a defense against grazing animals. Some margins have razor-sharp, sawlike teeth that cut anything that brushes across them. The margins of many tropical leaves terminate in finely pointed tips, called *drip tips*. When rainwater accumulates on the leaf's surface, the tip helps the water to drain off the leaf so that accumulated water will not weigh down the leaf to the point of breakage. Many leaves, however, have no distinctive margins; when the margin is even all around, it is called an "entire" margin.

Leaf Parts

Normally, a mature leaf has three parts: the *petiole*, a stemlike portion that grows from a node on the stem and supports the leaf; the *blade*; and, at the base of the petiole, a *sheath*, which attaches the petiole to the stem. If the blade has no petiole, it is attached directly to the stem and is referred to as being *sessile*. Petioles are able to move to some extent, so that leaves can be arranged to receive sufficient light.

Vascular tissue that makes up *leaf veins* is composed of *xylem*, which brings water up from the roots, and *phloem*, which is responsible for transporting the products of photosynthesis. Xylem and phloem extend from the branch or stem into the leaf by a *leaf trace*. This strand is continuous through the petiole into the leaf veins that intersect the entire leaf. The veins are the point of contact between root and chloroplasts, ensuring that water can be continually furnished during the photosynthetic process. The veins may also act as a structural support within the leaves. If a blade has a *midrib*, it appears that the petiole extends onward to the tip of the leaf. Often, secondary veins branch off from this central vein, forming a reticulate pattern; other times, many of the same-sized veins branch out from the base of the blade in a fan-shaped pattern.

The upper surface of a leaf is covered by a continuous, transparent sheet of cells called the *cuticle*. The cuticle may perform three functions: to help prevent excess water loss, to protect against physical damage or damaging organisms, and to aid in reflecting intense sunlight. Cuticle cells are generally thin-walled, except, perhaps, on the margin, where thicker cells reinforce the leaf and aid in preventing tearing of the leaf by wind currents.

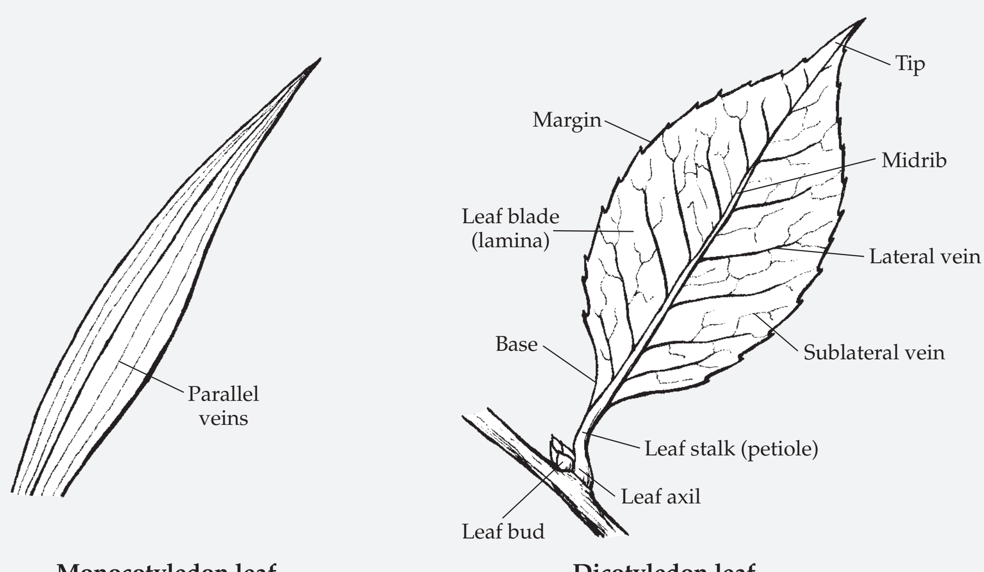
The cell layer immediately beneath the cuticle layers is the *epidermis*. Cells between the upper and lower epidermis form *mesophyll* tissues (from the Greek *mesos*, "middle," and *phyll*, "leaf"). Mesophyll in dicot leaves forms two observable layers; the upper layer is the *palisade mesophyll*, composed of cells that are columnar and closely packed; they are also rich in chloroplasts. Below this layer is the *spongy mesophyll*, so named because of numerous air spaces surrounding the small, oval cells. The air spaces are important in circulating carbon dioxide and oxygen that enters and leaves from *stomata*, small openings, generally confined to the underside of the leaf, where gas exchange is regulated.

Transpiration Organs

The stomata are bounded and controlled by two kidney-shaped cells called *guard cells*. Water evaporates from the leaf cells and goes into the air through these ventilation sites by a process referred to as *transpiration*. Normally, during light hours, the stomata are open (and losing water). At nighttime, the cells close, and water is retained. To open, potassium ions (K^+) are pumped into the guard cells, and water follows by osmosis, which causes an increase in internal pressure, called *turgor pressure*. As pressure increases, the water pushes against and stretches the guard-cell walls, bowing the cells outward. The filling and stretching of the guard cells opens the stoma.

Stomata close when *water stress* (lack of water in the plant) occurs, which can result from insufficient water in the soil or excessive transpiration rates. The most likely physiological mechanism for stomatal closing involves the hormone *abscisic acid* (ABA). The effects of water stress seem directly to trigger the release of ABA. The exact mechanism is unclear, but in some way ABA causes K^+ ions to move out of the guard cells and, again, water pas-

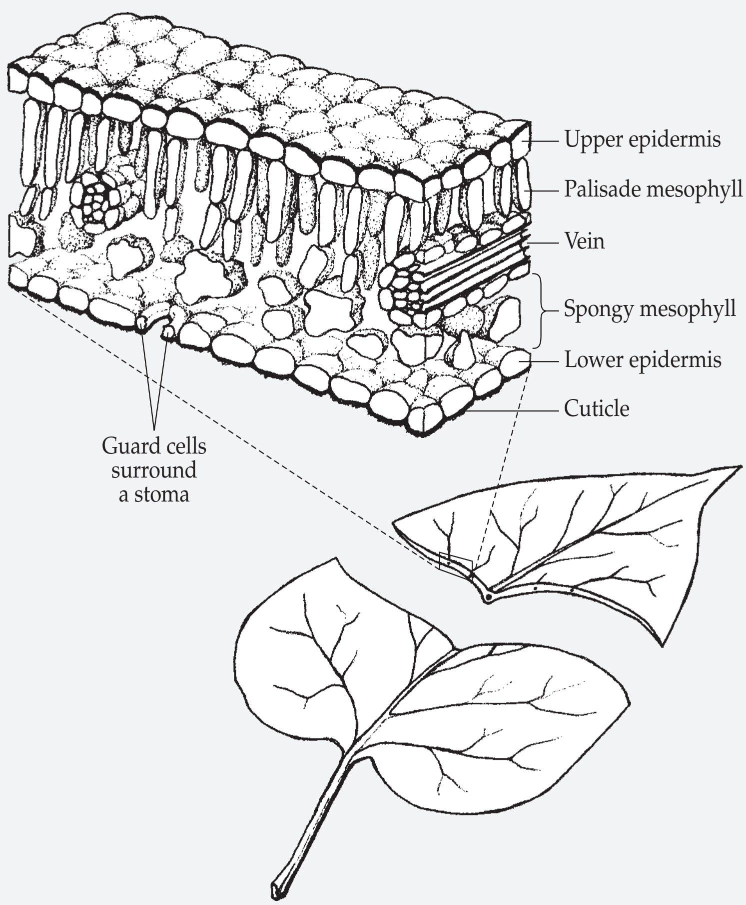
Parts of a Leaf



Monocotyledon leaf **Dicotyledon leaf**

Kimberly L. Dawson Kurnizki

Cross-Section of Leaf Tissue



Kimberly L. Dawson Kurnizki

sively follows. When the guard cells lose their water, they become limp and close, sealing the stomatal opening, thus greatly reducing transpiration.

Transpiration of water at the leaf surface may be affected by several factors. Wind blowing across the surface carries off water molecules, leaving room for more water molecules to take their place; an increase in temperature does the same thing. Loss of water may be slowed by opposite conditions. In rainy or foggy conditions when the air is already saturated with water, water loss from leaves is lower. Water loss also occurs slowly in cool conditions, such as those prevailing at night. An average-sized birch tree will typically lose 17,260 liters of water through transpiration in a single growing season. One acre of grass lawn may lose 102,200 liters of water in a single week.

Water transpired into the air can affect rainfall patterns: It is likely that 50 percent of rainfall in the Brazilian rain forest originates from transpired water. Plants that grow in arid conditions have developed specialized leaves to decrease the amount of water lost by transpiration. Many of these plants have leaves that are small and thick, so that surface area is reduced. The stomata may be housed in deep pits, away from wind's evaporative force. During especially dry periods, some plants even shed their leaves to reduce water loss. Others carry on an alternate form of photosynthesis that allows the stomata to remain closed during all or part of the day.

Kranz Anatomy

In certain plants known as C_4 plants, the leaves have adapted a particular way of fixing carbon; this has resulted in a ringlike arrangement of photosynthetic cells around the leaves' veins, called *Kranz anatomy*. This term (*Kranz* in German means "wreath") refers to the fact that in C_4 plants the cells that surround the water- and carbohydrate-conducting system (known as the *vascular system*) are packed very tightly together and are called *bundle sheath cells*. Surrounding the bundle sheath is a densely packed layer of mesophyll cells. The densely packed mesophyll cells are in contact with air spaces in the leaf, and because of their dense packing they keep the bundle sheath cells from contact with air. This Kranz anatomy plays a major role in C_4 photosynthesis.

In C_4 plants the initial fixation of carbon dioxide from the atmosphere takes place in the densely packed mesophyll cells. After the carbon dioxide is fixed into a four-carbon organic acid, the malate is transferred through tiny tubes from these cells to the specialized bundle sheath cells. Inside the bundle sheath cells, the malate is chemically broken down into a smaller organic molecule, and carbon dioxide is released. This carbon dioxide then enters the chloroplast of the bundle sheath cell and is fixed a second time with the enzyme Rubisco and continues, as in non-C_4 plants, through the C_3 pathway.

Iona C. Baldridge, updated by Bryan Ness

See also: C_4 and CAM photosynthesis; Cacti and succulents; Gas exchange in plants; Leaf lobing and division; Leaf arrangements; Leaf abscission; Leaf margins, tips, and bases; Leaf shapes; Liquid transport systems; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Plant tissues; Shoots; Stems; Water and solute movement in plants.

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Prance, Ghillean Tolmie. *Leaves: The Formation, Characteristics, and Uses of Hundreds of Leaves Found in All Parts of the World*. New York: Crown, 1985. A wonderfully simple but quite complete book taking the reader through every aspect of the leaf. Accompanied by hundreds of beautiful photographs taken from all over the world, this volume is a beautiful addition to every botanist's library.

LEAF ARRANGEMENTS

Category: Anatomy

The study of leaf arrangements, or phyllotaxy, considers not only the descriptive classification of leaf arrangements but also theories regarding the cause of such arrangements.

The function of the arrangement of leaves (*phyllotaxy*) is to increase a plant's ability to carry on photosynthesis by positioning the leaves in such a way as to maximize the surface area available to intercept sunlight. Leaves may be either *caulescent* (on obvious stems) or *acaulescent* (with no obvious stems). Flowering plants have three basic types of arrangements: *alternate spiral*; *opposite*; and *whorled* or *verticillate*. The alternate spiral arrangement is generally considered to be the most primitive condition, with the opposite and whorled conditions being derived by suppression of internode development.

There are two major hypotheses regarding the processes governing these basic arrangements. The *field hypothesis* of phyllotaxy posits that, as leaf primordia (new leaf cells) are created by the plant, a zone that inhibits the growth of other primordia is laid down around it, and not until the shoot tip has grown beyond that zone can a new leaf primordium be laid down. The *first available space hypothesis* posits that new leaves grow as soon as the plant shoot has grown out far enough to allow space for them.

The various types of leaf arrangements are usually one of the easiest vegetative characteristics to use in helping to identify vascular plants. This is especially true when leaf arrangement is combined with other characteristics, such as the presence or absence of petioles or the quality of being sessile or nonsessile. Other characteristics include the shape of the leaves and the appearance of the margins, bases, and apices types.

Alternate

Alternately arranged leaves produce one leaf per node. These leaves may be on alternate sides of the stem (2-ranked or *distichous*), on one side of the stem (*1-ranked* or *secund*), or in a spiral around the stem. If 2-ranked leaves overlap, as in some oncidium orchids and iris species, then they are referred to as *equitant*.

Leaves of members of the grass family (*Poaceae*) are distichous and alternate. Their leaves differ from most other vascular plant leaves in that they normally consist of a split tubular sheath that surrounds the stem and more or less linear blades held at right angles to the stem. They also have a small, tongue-like structure (*ligule*) at the junction of the sheath and blade, although in some species it may be obsolete.

Spiral

Spiral arrangements involve alternately arranged leaves in which each succeeding stem node and attached leaf is rotated slightly from the nodes below and above it. If the spiral is to the right, it is referred to as *dextrorse*; if to the left, it is referred to as *sinistrorse*.

Opposite

When two leaves occur at one node, the arrangement is called opposite. Oppositely arranged leaves may be either 2-ranked, as in Mexican heather (*Cuphea hyssopifolia*) in the henna family (*Lythraceae*), or 4-ranked or *decussate*, in which each succeeding pair of leaves is at right angles to the pairs above and below them. Decussate arrangement of leaves is characteristic of the mint family (*Lamiaceae*), the maple family (*Aceraceae*), and some members of the milkweed family (*Asclepiadaceae*), such as *Asclepias viridis*.

Whorled or Verticillate

When three or more leaves occur at one node, a whorled or verticillate arrangement is produced. The genera *Galium* and *Sherardia* in the madder family (*Rubiaceae*) are characterized by whorled leaves, as is also *Isotria* in the orchid family (*Orchidaceae*).

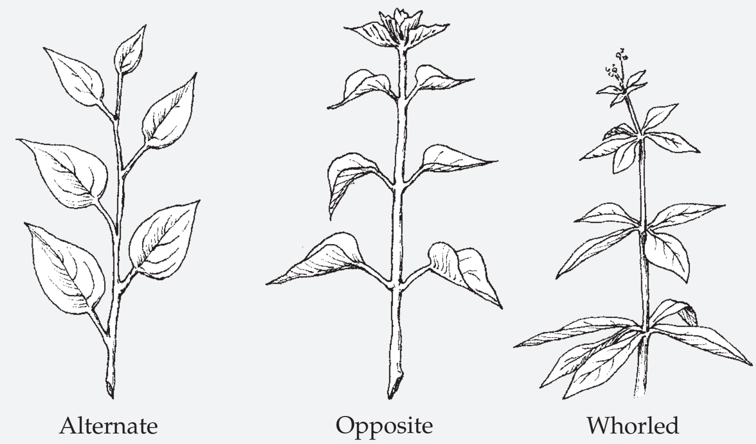
Rosette

Rosettes, often referred to as basal rosettes, occur in acaulescent plants, such as the common dandelion (*Taraxacum officinalis*) in the sunflower/aster family (*Asteraceae*). Acaulescent plants do have a stem, but the internodes are greatly contracted, and the leaves have a spiral alternate arrangement. Many biennial plants, such as carrots (*Daucus carota*) and poison hemlock (*Conium maculatum*) in the carrot family (*Apiaceae*), will produce a basal rosette during the first year of growth, followed by the production of a flowering stem with alternate leaves the second year.

Perfoliate

A leaf or a pair of connately fused leaves with the stem going through the center are referred to as *perfoliate*. *Montia perfoliata* and *Bupleurum rotundifolium* are examples of the perfoliate condition derived from a single leaf. *Silphium perfoliatum* is a good example of the basal connate fusion of leaves to achieve the perfoliate condition. The upper cauline leaves of henbit (*Lamium amplexicaule*) in the mint family (*Lamiaceae*) are sessile and clasping the stem but are not actually fused.

Common Leaf Arrangements



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Coniferous Leaves

The leaves of most conifers have developed with the need to minimize water loss while maximizing photosynthesis under relatively cold and dry (physiological drought) conditions where water is often not easily obtained. Needle-like leaves arranged in close, regularly spaced secund (one-sided, like a comb) divisions are referred to as *pectinate* or *comb-like*. *Acicular* leaves arranged in bundles or fascicles are typical of pines and spruces. In pines each fascicle is composed of two, three, four, five, six, seven, or eight divisions of needles, which form a more or less cylindrical shape if pushed together. The fascicles are spirally arranged on the tree branches.

In eastern red cedar (*Juniperus virginiana*), the leaves are reduced to minute *scales*, which have an opposite decussate arrangement, giving the appearance of 4-ranks. The scales are imbricate or overlapping, much like shingles on a roof. The leaves of the yew (*Taxus*) are sharp-pointed, flattened, and narrowly lance-shaped. They are spirally arranged on the branches but almost always give the appearance of being 2-ranked. This is also true for the dawn redwood (*Metasequoia*) and bald cypress (*Taxodium distichum*), both of which are deciduous in the fall, dropping entire branchlets with the attached leaves. Yew podocarpus (*Podocarpus macrophylla*) in the podocarpus family (*Podocarpaceae*), on the other hand, has a obvious spiral arrangement of the leaves.

Lawrence K. Magrath

See also: Leaf anatomy; Leaf lobing and division; Leaf margins, tips, and bases; Leaf shapes.

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LEAF LOBING AND DIVISION

Category: Anatomy

The pattern of leaf lobes (projections) or divisions, leaf arrangement, the number, and the shape of leaflets composing compound leaves are often useful characteristics for identification of plants.

Leaves, the main photosynthetic organs of plants, are usually green, flattened structures that are formed as lateral outgrowths at stem nodes. Simple leaves are composed of a single *lamina*, or blade, which may be attached to the stem via a cylindrical structure called a petiole. Leaves lacking a petiole are called *sessile*. Laminae of simple leaves may exhibit various patterns and degrees of lobing, which are often characteristic of individual species of plants and, together with reproductive features, are used in plant identification. Other species have *compound* leaves, in which the leaf laminae are subdivided into smaller leaflets. The pattern of arrangement, the number, and the shape of leaflets comprising compound leaves are often useful characteristics for identification of plants.

Some species of plants exhibit either gradual or abrupt changes in leaf lobing and division during development and are called *heterophyllous*. For example, some species exhibit a mixture of *pinnatifid* (pinnately lobed) and *pinnatisect* (pinnately compound) leaves on the same stem. Heterophylly is often observed in water plants, with one form of leaf being produced where the plant stem is submerged and another being produced where the stem is above water. Light periodicity, intensity, and quality, as well as oxygen and carbon dioxide concentrations, are known to influence leaf form in some species. In other species, different portions of a single leaf lamina can be pinnatifid or pinnatisect. The developmental mechanism for leaves of this type is not completely understood.

Lobing

Lobes typically extend greater than one-eighth of the distance from the margin to the midrib of the leaf or leaflet. The margin is the edge of the leaf lamina lying between the apex and base. The midrib is the prominent vein that subdivides the leaf or leaflet into two halves from base to apex. *Palmately lobed* margins are indented toward the base of the leaf lamina, creating a pattern like fingers extending from a hand, or a digitate pattern.

Pinnately lobed margins are indented one-quarter to one-half of the distance to the midrib, with the indentions oriented toward the midrib in a featherlike pattern. *Pinnately cleft* margins are indented a little more than half of the distance to the midrib. *Pinnately incised*, or pinnatifid, margins are deeply indented toward the midrib, extending well over half to almost completely to the midrib. The term "pinnately lobed" is sometimes used in reference to lobed, cleft, and incised leaves, collectively.

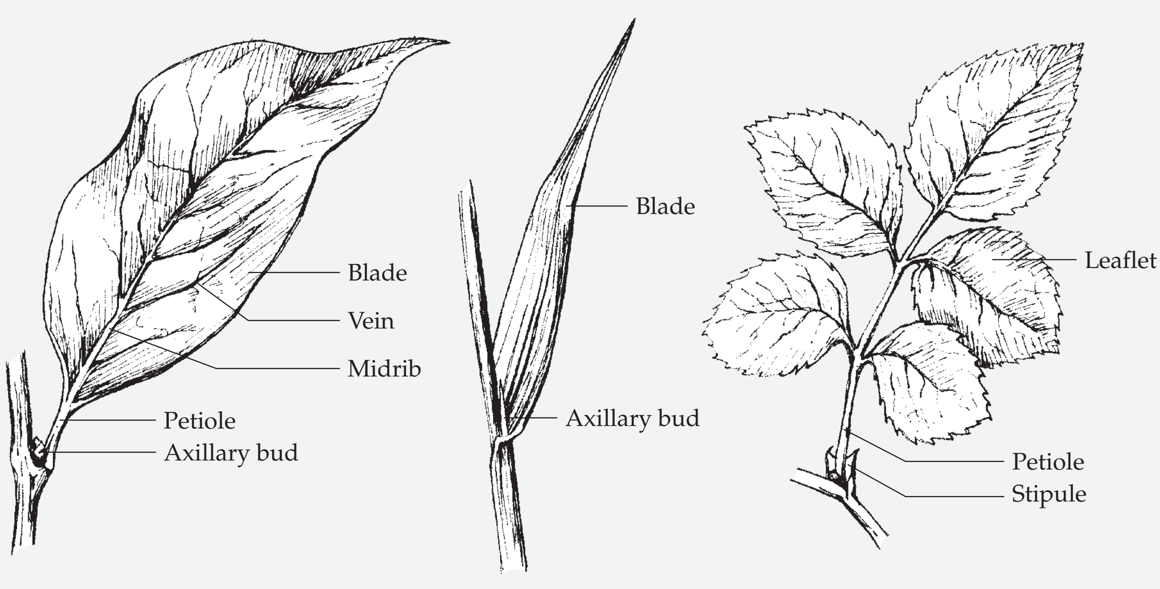
Simple and Compound Leaves

To discriminate between *simple* and *compound* leaves, one may locate the axillary bud at the base of a leaf petiole in the node region of the stem. This area signifies the basal end of the entire leaf in both simple and compound leaves.

A simple leaf has only one blade, or lamina, associated with it. There are no leaflets. In *singly compound* leaves, the leaf is sudivided into leaflets, which attach to a central *rachis* (axis). The rachis is continuous with the petiole, which attaches to the node region of the stem, where the axillary bud will be found. In doubly, or *bipinnately*, *compound* leaves, the primary leaflet lamina is subdivided into smaller secondary leaflets, which attach to a secondary rachis, or *rachilla*. The secondary rachis attaches to the primary or central rachis. The primary rachis is continuous with the petiole, which attaches to the node region of the stem where the axillary bud will be found.

The number of leaflets in a compound leaf is often constant in many plant species. In *even pinnately compound* leaves, all of the leaflets are paired. There is no terminal leaflet; thus, the total number of leaf-

Types of Leaves



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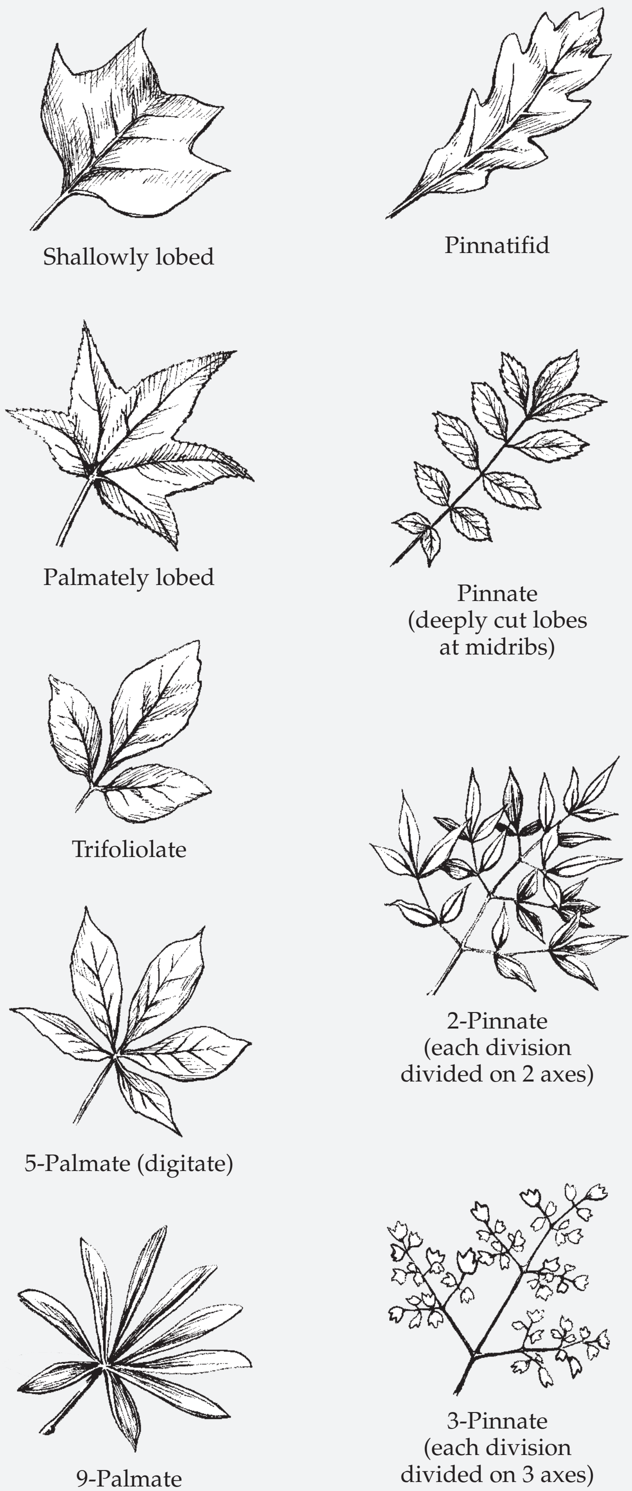
Common Patterns of Leaf Lobing and Division



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lets per leaf is an even number. In *odd pinnately compound* leaves, there is one terminal, unpaired leaflet at the end of the leaf, making the total number of leaflets an odd number. *Trifoliolate* leaves have three leaflets, which may have petiolules or be sessile. The term *ternate* denotes groups of threes.

Leaf blade length is measured from where the blade joins the petiole straight to the tip of the leaf and perpendicular to the width. Width is measured at the widest part of the leaf perpendicular to the length. The petiole is the more or less round stalk that connects the leaf blade to the node region of the stem. Petiole length is measured from the point of attachment of the leaf blade to the node region of the stem. Some species lack petioles or have very short petioles.

The singly compound leaf blade is subdivided into leaflets which attach to a central rachis. The leaflet blade, or lamina, is the flat part of the leaflet. The *petiolule* is the stalk extending from the base of the leaflet lamina to the rachis. The rachis is continuous with the petiole, which attaches to the node region of the stem, where the axillary bud will be found. Leaflet length is measured from where the leaflet blade joins the petiolule straight to the tip of the leaflet perpendicular to the width. Width is measured at the widest part of the leaflet perpendicular to the length.

In the doubly or bipinnately compound leaf, the primary leaflets are themselves subdivided into still smaller secondary leaflets. The leaflet lamina is attached to a secondary rachis, or rachilla. The petiolule extends from the base of the leaflet lamina to the rachilla. The rachilla attaches to the primary or central rachis.

Roger D. Meicenheimer

See also: Leaf anatomy; Leaf arrangements; Leaf margins, tips, and bases; Leaf shapes; Shoots.

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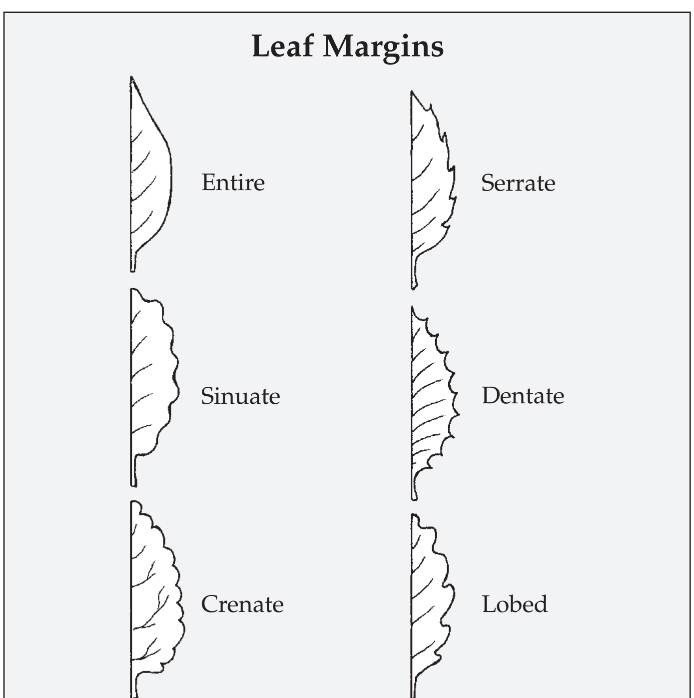
LEAF MARGINS, TIPS, AND BASES

Category: Anatomy

The flattened part of the leaf is the leaf blade or lamina, which can be subdivided into three discrete regions: The tip or apex is the part of the lamina farthest removed from the point of attachment of the leaf to the stem. The base of the leaf is the part of the lamina that is closest to the point of attachment of the leaf to the stem. The margin is the perimeter of the leaf between the apex and base.

The form, or morphology, of leaves is often characteristic of individual species of plants and, like the reproductive features, is an important base of plant identification. Some plants have a more or less cylindrical *petiole* that joins the base of the leaf to the stem, while others lack a petiole and are called *sessile*. The *midrib* is the prominent vein that subdivides the leaf into two halves from base to apex.



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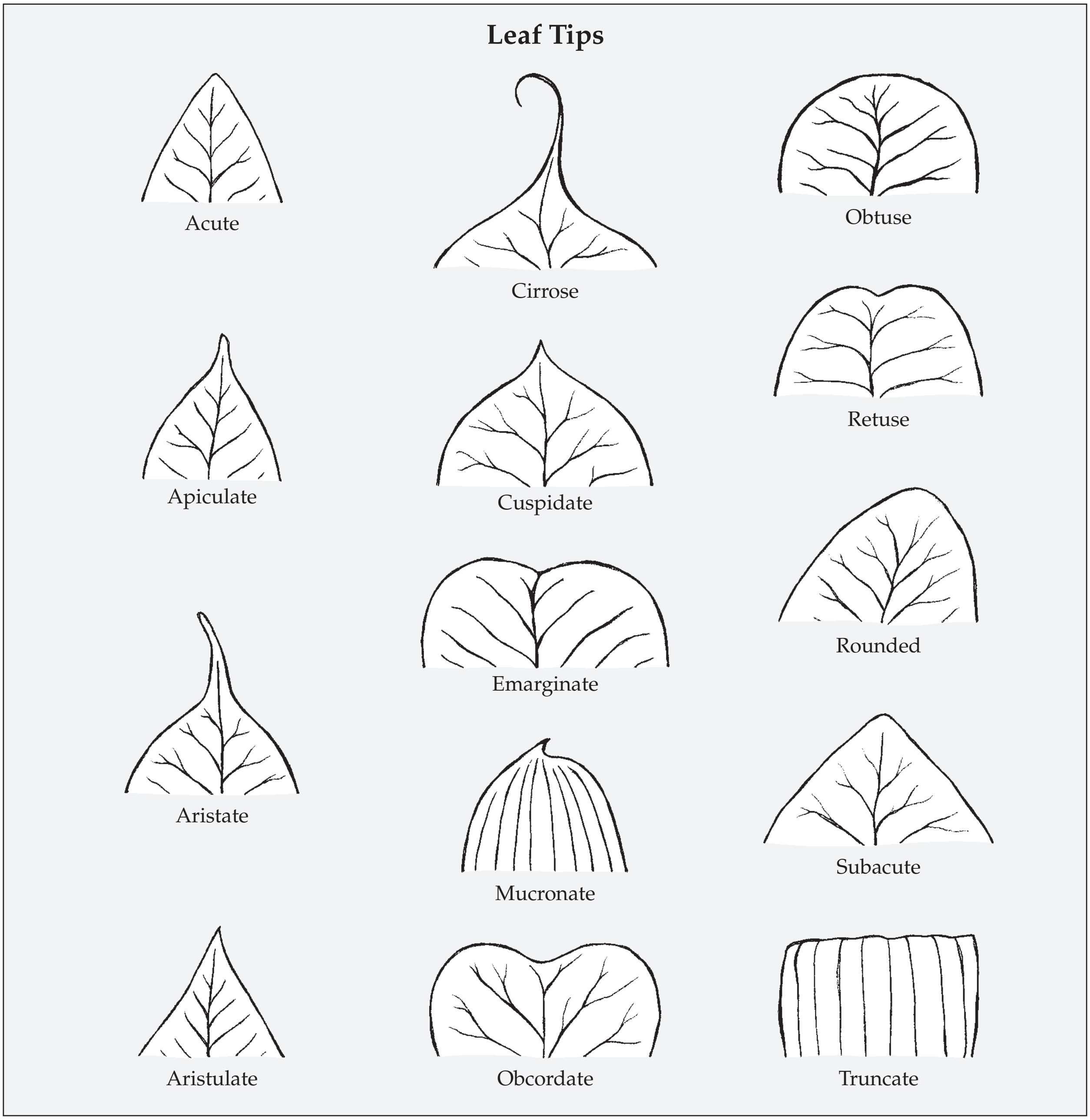
Leaf Margins

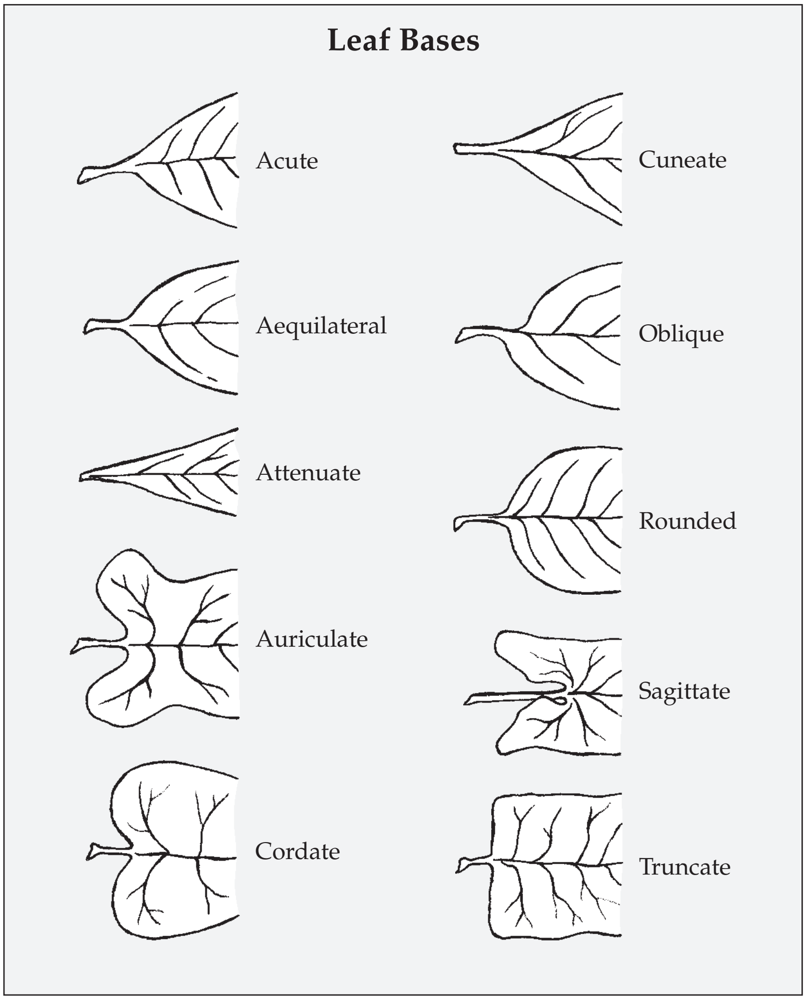
The margin is the edge of the leaf lamina lying between the apex and base. *Entire* margins are smooth, without indentations or incisions. *Revolute* margins are rolled downward, toward the lower surface of the leaf. *Involute* margins are rolled upward, or toward the upper surface of the leaf. *Repand* margins are slightly and irregularly wavy, with the lamina surface undulating in a downward and upward direction. *Sinuate* leaf margins are shallowly indented and strongly wavy in the horizontal plane.

Teeth

"Teeth" are commonly seen in leaf margins and typically extend less than one-eighth of the distance from the margin to the midrib of the leaf. Various shapes and sizes of teeth are associated with leaf mar-



gins. *Crenate* margins have shallowly ascending round or obtuse teeth. *Crenulate* (minutely crenate) margins have minute, shallowly ascending round or obtuse teeth. *Serrate* margins have sharp, saw-toothed teeth pointing forward or toward the apex. *Serrulate* (minutely serrate) margins have very fine, sharp, saw-toothed teeth pointing forward or toward the apex. *Doubly serrate* margins have coarse, saw-toothed teeth bearing smaller teeth on the basipetal part of their edges. *Dentate* margins have sharp teeth, or indentions, pointing outward at right angles to the midrib. *Denticulate* (minutely dentate) margins have fine, sharp teeth, or indentions, pointing outward at right angles to the midrib. *Aculeate* margins have spiny or prickly projections along their edges. *Bristle tips* refer to teeth or lobes that are terminated by a sharp, flexible, elongated point.



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Glands

Glands are small, protruding bumps on the leaf margin that are typically different in color from the surrounding lamina tissue. Often they occur at the apices of teeth or lobes or on leaf petioles. Use of a hand magnifying lens helps in observing the small glands of some species.

Tips or Apices

The apex is the tip of the leaf blade. *Acuminate* apices have a long, slender, sharp point, with a terminal angle less than 45 degrees, and straight to convex sides. *Acute* apices have a sharp-pointed tip, with a terminal angle between 45 and 90 degrees, and straight to convex sides. *Mucronate* apices have a tip that is terminated by a short, sharp, abrupt point. *Cuspidate* apices have a tip that is abruptly and sharply constricted into an elongated, sharp-pointed tip or cusp (a sharp, rigid point). *Obtuse* apices have a blunt or rounded tip, with the sides forming an angle of more than 90 degrees, and straight to convex sides. *Rounded* apices have a tip that is curved to form a full, sweeping arc. *Truncate* apices have a tip that looks as though it was cut off at almost a right angle to the midrib, forming a flat-topped or squared-off shape. *Retuse* apices have a shallow notch in a rounded or obtuse apex. *Emarginate* tips have a shallow and broad notch at the apex. These are only a few of the many forms leaf apices can take.

Bases

The base of a leaf is the lower part of the lamina, where it is attached to the petiole or stem. *Cuneate* bases are sharp-pointed, with an angle less than 45 degrees between opposite sides which form a wedge or triangular shape that tapers to a narrow region at the point of attachment of lamina with petiole. *Acute* bases have a sharp-pointed base, with opposite sides forming an angle between 45 and 90 degrees at the position where the lamina joins the petiole. *Obtuse* bases have a blunt or narrowly rounded base with opposite sides forming an angle greater than 90 degrees at the position where the lamina joins the petiole. *Rounded* bases are curved to form a full, sweeping arc. *Truncate* bases look as though they were cut off at nearly a right angle to the midrib, forming a flat-topped or squared-off shape. *Cordate* bases are valentine-shaped, with both right and left margins forming broad arcs that meet in the middle of the junction between lamina and petiole. *Inequilateral* bases have asymmetrical left and right sides of different sizes or shapes. *Auriculate* bases have earlike lobes where the lamina joins the petiole.

Roger D. Meicenheimer

See also: Leaf anatomy; Leaf arrangements; Leaf lobing and division; Leaf shapes; Shoots.

Sources for Further Study

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LEAF SHAPES

Category: Anatomy

The overall shapes of leaves and leaflets are often characteristic of individual species of plants and, together with reproductive features, are used in plant identification.

To assess the shape of a leaf, one examines the outline formed by the apex, margin, and base of the leaf or leaflet. If the leaf has teeth or lobes along its margin, one imagines a smooth curve interconnecting the tips of the teeth or lobes to assess the overall shape. The shapes of compound leaves can likewise be assessed by imagining a smooth curve connecting the tips of the leaflets that form the compound leaf blade. The terminology below is used to describe the shape of laminae of simple and compound leaves as well as the laminae of the leaflets of compound leaves.

Elongated Leaves

Linear leaves have a long and very narrow leaf shape, with sides that are almost parallel with one another and are usually more than four times longer than broad. *Oblong* leaves have a rectangular leaf blade two to four times longer than it is wide, with sides that are almost parallel to each other. *Ensiform* leaves resemble the shape of a broad sword. *Ligulate* leaves are straplike, resembling a tongue. *Falcate* leaves are elongated and recurved, resembling the shape of a sickle blade. *Lanceolate* leaves have a lance-shaped leaf, with the widest part of the leaf near the base and the narrowest part near the apex. The prefix *ob* means that the shape is inverted or upside down. Thus, *oblanceolate* leaves have a lance-shaped leaf, with the widest part of the leaf near the apex and the narrowest part near the base.

Circular to Elliptical Leaves

Orbicular leaves have a more or less circular leaf shape in which the width and length of the lamina are equal, or nearly so. *Elliptical* leaves have a shape that looks like an ellipse, twice as long as broad, with the widest part of the leaf near the middle. *Oval* leaves are broadly elliptical, with the blade width being more than half the length and the widest part of the leaf near the middle. Oval leaves are wider than elliptical leaves of the same length. *Ovate* leaves are egg-shaped, with the widest part of the leaf below the middle toward the base, while *obovate* leaves are egg-shaped, with the widest part of the leaf above the middle toward the apex.

Other Shapes

Reniform leaves have a shape like a kidney. *Cordate* leaves are shaped like a valentine or heart, with the lobes of the valentine at the base of the leaf and the pointed portion at the apex. *Obcordate* leaves are also valentine-shaped, but the lobes are at the apex, and the basal lamina tapers into the petiole. *Sagittate* leaves have a shape like an arrowhead. *Hastate* leaves are also shaped like an arrowhead, but the basal lobes diverge or extend away from the midrib, giving an outline that resembles a halberd. *Rhombic* leaves have a more or less diamond shape, with straight margins and with the widest part of the leaf lamina near the middle. *Spatulate* leaves have a spoon-shaped or spatula-shaped leaf where the lamina is widest near the rounded apex. *Flabellate* leaves are fan-shaped or broadly wedge-shaped, with the broadest part of the lamina at the apex. *Deltoid* leaves are delta-shaped, resembling an equiangular triangle. Often the sides of the deltoid leaves are slightly curved toward the apex.

Conifer Leaf Shapes

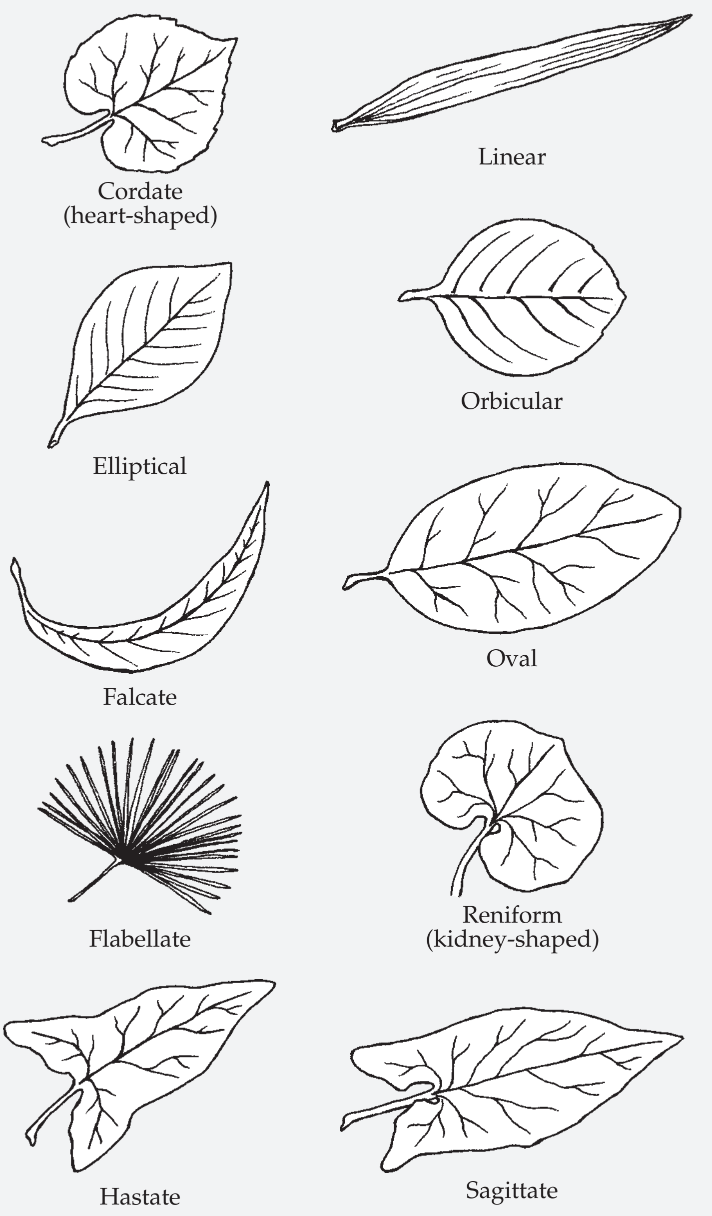
Needlelike, or *acicular*, leaves have a long and very narrow leaf shape, with sides that are almost parallel to each other and are usually more than ten times longer than broad. Acicular leaves are often borne on short lateral branches called *fascicles*. The number of acicular leaves per fascicle is constant within a species. *Linear* leaves have a long, narrow leaf shape, with sides that are almost parallel with each other and usually are more than four times longer than broad. Linear leaves can be flat, triangular, or square in cross section. They may also exhibit a distinct twist along their vertical axes.

Subulate leaves are short, narrow, flat, stiff, awl-shaped leaves that taper to a sharp point. *Scale* leaves are small, inconspicuous leaves that are typically appressed tightly to the stem and have overlapping margins. Scale leaves may or may not be photosynthetic (green). *Decurrent* leaves have an extension of tissue running down the stem below the point of junction of the leaf, with a stem that forms a wing or ridge of tissue. Some species have leaves that are borne on a semiwoody *peg* that extends away from the twig surface. These pegs do not abscise with leaves and remain visible on the twig for many years after leaf abscission.

Roger D. Meicenheimer

See also: Leaf anatomy; Leaf arrangements; Leaf lobing and division; Leaf margins, tips, and bases; Shoots.

Common Leaf Shapes



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LEGUMES

Categories: Agriculture; economic botany and plant uses; food

Legumes, including peas and beans, are among the most important staple food crops worldwide. Legumes are also planted among other crops because of their ability to enrich soil nitrogen content.

Legumes are plants of the pea or bean family classed in the family *Leguminosae*, which is referred to as the family *Fabaceae* in North America. With 18,000 species and 650 genera, the legumes are one of the largest families of plants in the world. The vast majority of legumes are herbaceous plants, but family members range in size from dwarf willowlike herbs of Arctic and alpine habitats to massive tropical trees. Most are flowering plants, but the family also includes a number of shrubs and trees, some quite tall and many bearing thorns or spines.

Legumes can be recognized by their distinctive fruits, which are typically elongated pods that contain and protect the seeds. The fruit is an ovary that splits along two sides at maturity. The legume family includes three subfamilies, each with a distinctive type of flower.

Subfamilies

The largest of the subfamilies is the *Papilonoidae*, named for the distinctive, butterfly-shaped wings of the flower petals. This subfamily includes the most familiar and economically important legumes, such as beans, peas, peanuts, lentils, and soybeans, the vetches and other ground covers, and animal forage crops, such as clovers, sweet clovers, lupines, and alfalfa.

Most members of the subfamily *Caesalpinioidae* are tropical and subtropical trees and shrubs, many of which are widely planted as ornamentals, including the honey-locust (*Gledtsia*) and redbud (*Cercis* species)—both very popular ornamentals—along with a number of subtropical shrubs and small trees, notably the mesquite and palo verde of the American Southwest. The subfamily also includes a number of vines, such as wisteria (*Wisteria floribunda*) and wait-a-minute vine. An extract of the wild senna (*Senna alexandrina*) is an important purgative medicine. The flowers of *Caesalpinioidae* have five uneven petals.

The subfamily *Mimosoidae* also consists mostly of tropical and subtropical trees and shrubs, such as mimosa and the Kentucky coffee tree, *Gymnocladus dioica*. Legumes of this subfamily typically have a cluster of small flowers on a single stem, the whole covered by long stamens.

Nitrogen Fertilizer from Legumes

The importance of legumes as a green fertilizer has been recognized for centuries. As early as the third century B.C.E., the Greek philosopher and scientist Theophrastus recommended that beans should be planted to enrich farm soils. Then, as now, a common agricultural practice was to rotate cereal crops, such as corn or wheat, with leguminous crops, such as clover or alfalfa (*Medicago sativa*). The legumes used as green fertilizer not only contribute nitrogen to the soil but also can be harvested as animal feed.

The ability of legumes to enrich soil nitrogen content stems from their symbiotic relationship with *Rhizobium* and other nitrogen-fixing bacteria, which enter and colonize the root hairs of certain legume seedlings. The cell walls of the root hairs respond by curling to form a nodule that houses and protects the colony of nitrogen-fixing bacteria. The bacteria fix molecular nitrogen of the atmosphere into nitrogen-containing compounds useful to the plant, which in turn provides the bacteria with water, minerals, and carbon-based products of photosynthesis.

Legumes as Crops

For centuries, people around the world have depended on a combination of grains and legumes for a healthy and sustaining diet. Legumes were among the earliest of crops cultivated in the Fertile Crescent of the Middle East (the region between the Tigris and Euphrates Rivers) some eleven thousand years ago, where farmers supplemented their wheat and barley crops with lentils and peas.

Legumes still rank among the most important of all staple food crops, especially the *pulses* (edible seeds), such as peas and beans, chickpeas, and lentils. Legumes are also important as cover plants to hold and stabilize soils, as nutrient-rich feed for livestock, as timber products, and as green fertilizer. Some species are also valuable because they can be grown in poor soils or in areas of low rainfall. Other derivatives include medicines, food flavorings, tannins, gums, resins, and dyes. An extract from *Lonchocarpus* and *Derris* called rotonene is the active ingredient in fish poisons, molluscicides, and insecticides.

Nutritionally, legumes are especially good sources of proteins, carbohydrates, minerals, vitamins, and fiber. Especially important as protein sources in areas where animal protein is scarce, legumes contribute about 18 percent of the total plant protein consumed by humans. Legume proteins contain large amounts of some essential amino acids, such as lysine, but are low in the sulfur-containing amino acids methionine and cystine. Legumes' carbohydrate content varies from 13 to 65 percent, of which half or more is starch. Many legumes are also sources of iron, calcium, phosphorus, zinc, copper, and magnesium. They are particularly high in B vitamins, such as thiamin, riboflavin, niacin, folic acid, and pantothenic acid, as well as vitamins C and E. Legumes are also valued for their low fat content.

Among the most common legumes found in the human diet are the following:

Garden pea. Native to Asia, the garden pea (*Psum sativum*) is a cool-season crop that is widely cultivated throughout the world, with China and Russia being the most important producers of dried peas and the United States and Great Britain leading the production of green peas. The garden pea also deserves mention as the plant used by Gregor Mendel in his experiments that defined the science of genetics. The garden pea is marketed as frozen, canned, dried peas, or

PhotoDisc

Legumes can be recognized by their distinctive fruits, which are typically elongated pods that contain and protect the seeds. The fruit is an ovary that is dehiscent, splitting along two sides at maturity, as do these green beans.

as snow peas and sugar peas, which represent the harvested pods.

Common bean. Another extremely important legume crop, the common bean (*Phaseolus vulgaris*) is a warm-season crop native to South America but is now one of the most widely cultivated legumes in the world, thanks to its introduction into Europe and Africa by Spanish and Portuguese during the sixteenth century. The common bean remains the most important pulse crop in tropical Africa and America, especially in Brazil. Common beans are harvested in the podded stage (snap beans or string beans) or as shell beans. Shell beans are by far the largest crop and include various types such as navy, kidney, French, string, pinto, and yellow-eye beans. Common beans are the primary ingredient in many staple and well-known foods, including Boston baked beans and chili con carne. Because of their relatively high pectin content, common beans must be soaked in water prior to consumption.

Lima bean. Also known as the butter bean or Madagascar bean, the lima bean (*Phaseolus lunatus*) is native to Central America, where it was cultivated at least seven thousand years ago. Like the common bean, the lima bean has been introduced throughout the world and is now grown in the warmer regions of Africa, Asia, and North America. The seeds are harvested and marketed canned or frozen in North America, as a bean paste in Japan, and ground into bread flour in the Philippines. Although rich in proteins and carbohydrates, lima beans contain glycosides, which can produce toxic prussic acid, and must therefore be thoroughly prepared by soaking and boiling in frequent changes of water.

Peanut. One of the most nutritious legumes, the peanut (*Arachis hypogaea*) is native to Brazil but has been widely introduced, particularly in the United States, where it has long been an important cash crop along the southern tier of states. The plant initially pushes a flowering stalk above ground, but following fertilization the stalk is pushed into the ground, where it matures, giving rise to the name ground peanut.

Soybean. Soybeans (*Glycine max*) are an important food crop that have been cultivated in the Far East for thousands of years, often in combination with rice crops. The high protein content of about 45 percent is a major reason for their importance as a food crop. An oil extracted from soybean seed is used in the manufacture of cooking oils and some margarine. Other important soybean products include tempeh, miso, tamari, and tofu.

Lentil. One of the oldest of crops, lentils (*Lens culinaris*) were domesticated as early as 8000 B.C.E. in the Fertile Crescent region of the Middle East, between the Tigris and Euphrates Rivers. Lentils are still cultivated widely in the Old World; their highest production rates are in India, but lentils also remain the most important pulse crop in Nepal and Bangladesh. Harvested lentil seeds are used in the production of flour, soups, and as a dried snack food, while the plant is used as high quality straw feed for livestock in the Middle East. Lentils are considered an excellent pulse crop because of their high protein content as well as being excellent sources of vitamins A and B, potassium, and iron. Nutritionally, they are also valuable because they lack fat content and cholesterol.

Toxic Substances

Toxic or antinutritional substances found in some legumes include alkaloids, cyanide poisons, enzyme inhibitors, saponin, and goitrogen, the last causing an enlargement of the thyroid gland. More serious still are the lectins or haemagglutinins (blood clotting agents) that may cause vomiting, diarrhea and severe abdominal pain, and lathyrism, which can produce mild to severe neurological disorders. Unpleasant but nontoxic substances that occur in certain legumes include stachyose and raffinose carbohydrates, which cause flatulence. Most of these unwanted substances can be removed by appropriate washing and cooking methods prior to consumption.

Dwight G. Smith

See also: Agriculture: traditional; Fruit crops; Fruit: structure and types; Nitrogen fixation; Organic gardening and farming; Sustainable agriculture; Vegetable crops.

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LICHENS

Categories: Algae; fungi; taxonomic groups

Lichens are composed of two distinct species, a fungus and a photosynthetic alga (or bacterium) that have coevolved to live in a symbiotic relationship with each other as a single life-form that grows on rocks, trees, and other substrates. Lichens are classified as members of the kingdom Fungi*, with most being placed under the phyla* Ascomycota *and* Basidiomycota*. It is estimated there are seventeen thousand species of lichen, representatives of which have been found nearly everywhere in the world.*

Symbiosis

Symbiosis is an extreme form of an ecological relationship known as mutualism between members of different species, in which each partner in the union derives benefits from the other. In symbiotic unions, the partners are so dependent on each other they can no longer independently survive.

In lichens, the fungal (mycobiont) symbiont provides protection, while the green-algal or bacterial (photobiont) symbiont provides sugars, created by photosynthesis. It is often suggested that the fungus in lichen species might also pass water and nutrients to the photobiont, but this function is less well documented. This special relationship allows lichens to survive in many environments, such as hot deserts and frozen Arctic tundra, that are inhospitable to most other life-forms. As a result, the lichen whole is greater than the sum of its parts. While in nature lichen partners always exist together, under laboratory conditions it is possible to take the lichen apart and grow the two partners separately.

Anatomy

Whereas in most plant species the anatomy of the organism is identified with structures associated with a single vegetative body, the "lichen body" is more aptly described as a colony of cells that share a variety of associations with one another that vary from one species of lichen to the next. In some species of lichen, fungal and algal cells merely coexist. *Coenogonium leprieurii*, for example, is a lichen that lives in low-light tropical and subtropical forests in which the filamentous green algal partner (*Trebouxia*) is dominant.

In most lichen species, however, the relationship between the symbiotic partners is more intimate, with the lichen body appearing to be a single entity.

Image Not Available

In these species the algal symbiont has no cell walls and is penetrated by filaments from the fungal symbiont called *haustoria*, which pass sugars from the algal cell to the fungal cell and may have a role in the transportation of water and nutrients from the fungal cell. This integration is so complete that many naturalists prior to the nineteenth century mistakenly classified lichens as mosses.

In most lichen species it is nevertheless possible, with a good magnifying device, to identify several distinct regions of the thallus or lichen body. The outermost region is the *cortex*, a compacted layer composed of short, thick *hyphae* (widely dilated filaments) of the fungal symbionts that protect the lichen from abiotic factors in its environment. These hyphae extend downward into a second region, the *photobiont layer*, where they surround the algal symbionts. Below this is a third region, the *medulla*, composed of a loosely woven network of hyphae.

Underneath this is a fourth region, the *undercortex*, that is similar in appearance and structure to the cortex. The bottom of the lichen body is composed of *rhizines*, rootlike structures composed of bundles of hyphae that attach the lichen to its substrate (the rock, bark, or other support on which it resides). This arrangement of regions into layers serves to prevent water loss. Many species can survive complete desiccation, coming back to life when water becomes available again. The cortex also contains *pseudocyphellae*, which are pores that allow for the exchange of gases necessary for photosynthesis.

Life Cycle

Lichens typically live for ten years or more, and in some species the lichen body can survive for more than a hundred years. Reproduction in most fungal species proceeds by the development of a cup- or saucer-shaped fruiting body called an *apothecium*, which releases fungal spores to its surroundings. Procreation in lichens is more problematic in that the fungal offspring must also receive the right algal symbiont if they are to survive. The most common form of dispersion in lichen is by the accidental breaking off of small pieces of the thallus called *isidia*, which are then spread by wind to new substrates. In some species, small outgrowths of the thallus known as *soralia* arise, composed of both fungi and algae and surrounded by hyphae, to form *soredia*, which after dispersion give rise to a new thallus.

Biological and Agricultural Importance

Lichens are excellent bioindicators of air pollution, as many species are particularly sensitive to certain contaminants in their surroundings, such as sulfur dioxide. They represent a major food source for reindeer in Lapland and are used as cattle fodder there as well. One species of lichen (*Umbilicaria esculenta*) is considered a delicacy in Japan. Historically, lichens have been used as pigments for the dying of wool. The medical properties of some species of lichens for the treatment of lung disease and rabies have led to a renewed interest in them.

David W. Rudge

See also: Algae; Bacteria; Coevolution; Community-ecosystem interactions; Fungi; Green algae; Photosynthesis.

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LIPIDS

Categories: Cellular biology; physiology

Lipids are a diverse group of compounds sharing the common property of being hydrophobic (insoluble in water). Lipids include fatty acids, fats, oils, steroids (sterols), waxes, cutin, suberin, glycerophospholipids (phospholipids), glyceroglycolipids (glycosylglycerides), terpenes, and tochopherols.

Lipids are ubiquitous in plants, serving many important functions, including storage of metabolic energy, protection against dehydration and pathogens, the carrying of electrons, and the absorption of light. Lipids also contribute to the structure of membranes. In addition, plant lipids are agricultural commodities important to the food, medical, and manufacturing industries.

Fatty Acids

Fatty acids, the simplest of the lipids, are highly reduced compounds with a hydrophilic (water-soluble) carboxylic acid group and a hydrophobic hydrocarbon chain. Hundreds of different fatty acids have been isolated from plants. Fatty acids differ from one another in the length of the hydrocarbon chain and degree of saturation (number of carbon-carbon double bonds). The most common fatty acids have chain lengths ranging from sixteen to twenty carbon atoms, but many less common fatty acids are longer or shorter.

Saturated fatty acids have no double bonds, whereas unsaturated fatty acids have one or more double bonds. Naturally occurring *unsaturated* fatty acids have *cis* double bonds, in which the two hydrogen atoms bonded to the carbon atoms of the double bond are on the same side of the fatty acid molecule. Fatty acids with one double bond and two or more double bonds are referred to as *monounsaturated*, *diunsaturated*, and *polyunsaturated*, respectively.

Fats and Oils

Fatty acids rarely occur free in the cell. Instead they are attached by ester linkages to *glycerol*, a three-carbon sugar alcohol, to form *fats* and *oils*, the most abundant lipids. Glycerol molecules with one, two, and three fatty acids attached are referred to as *monoglycerides*, *diglycerides*, and *triglycerides* (often called *triacylglycerols*), respectively. The fatty acids attached to a triglyceride may be the same, in which case it is referred to as a simple triglyceride, or the fatty acids may be different, in which case it is referred to as a mixed triglyceride.

The degree of saturation and hydrocarbon chain length of fatty acids in triglycerides affects their melting point. Common fats, such as those from palms and coconuts, are triglycerides that contain a high proportion of saturated fatty acids and are solid at room temperature (22 degrees Celsius). Common oils, such as those from corn, peanuts, soybeans, sunflowers, and olives, are triglycerides that contain a high proportion of unsaturated fatty acids and are liquid at room temperature.

Because plants cannot control their temperatures, they contain much more oil than fat so their membranes will be fluid at ambient temperatures. The most common monounsaturated fatty acid is *oleic* acid, while the most common polyunsaturated fatty acids are *linoleic acid* and *linolenic acid*. Some plants have a high proportion of saturated fats, containing such fatty acids as *palmitic acid*, the most common saturated fatty acid found in plants. Plants also contain lesser amounts of other saturated fatty acids, such as *lauric* and *myristic acid*. *Phytanic acid*, a product of chlorophyll metabolism, is a saturated, branched chain fatty acid.

Plant oils are a mixture of triglycerides and are used as a storage form of energy in seeds. Because fats are more highly reduced than starch, they provide almost twice the energy on a per-weight basis. When fatty acids are removed from glycerol they can undergo oxidation to yield energy.

Waxes, Cutin, and Suberin

Waxes are long-chain fatty acids attached to long-chain alcohols by ester linkages. *Cutin* is a complex of hydroxylated fatty acids (fatty acids with hydroxyl groups attached to them) cross-linked to one another. Waxes and cutin are found in the cuticle, the outermost layer of plant surfaces exposed to the air, and provide protection from dehydration and pathogens. *Suberin* is a complex compound of unknown structure. It is the major component of the walls of cork cells, the outermost layer of bark. Like cutin and waxes, suberin provides protection from dehydration and pathogens.

Glycerophospholipids

Glycerophospholipids, or phosphoglycerides , contribute substantially to cellular plasma membranes. Thus, they form one of the most important classes of lipids. Glycerophospholipids are composed of glycerol phosphate to which is attached two fatty acids by ester linkages. Molecules, such as ethanolamine, choline, inositol, and serine, may be bonded to the phosphate, resulting in an even greater variety of glycerophospholipids.

Glycerglycolipids

Known as *glyceroglycolipids*, or glycosylglycerides, these lipids are primarily found in chloroplast membranes, are widespread in plants, and consist of glycerol to which is attached one or two sugar molecules and two fatty acids. The sugars attached to the glycerol are either glucose, galactose, or a digalactose unit.

Steroids

Steroids, also called *sterols*, comprise another class of lipids that are important constituents of the plant plasma membrane. They also function as plant hormones. Steroids are formed by a conjugated ring system. Side chains and groups attached to the rings result in a variety of steroids with many biological activities. Stigmasterol, beta-sitosterol, lanosterol, and ergosterol are plant steroids. Cholesterol, a common steroid in the plasma membranes of animal cells, is rarely present in plants.

Terpenes

Terpenes are lipids that are composed of two or more five-carbon isoprene units. More than twenty-two thousand terpenes have been described. The familiar flavor and aroma of many plants are due to their characteristic terpenes. Plant terpenes and terpenoid derivatives include phytol, a constituent of chlorophyll; beta-carotene, a photosynthetic pigment that is a precursor of vitamin A in animals; paclitaxel, an anticancer agent; and rubber. The blue haze often seen in the air on summer afternoons is due, in part, to terpenes emitted from leaves.

Tocopherols

Tocopherols contain an aromatic ring and a long isoprene side chain. Plant tocopherols include vitamin E, a biological antioxidant that protects unsaturated fatty acids from damage from free radical attack; vitamin K, which plays an essential blood clotting role in higher animals; and ubiquinone and plastoquinone, which are essential electron carriers in the reactions leading to the synthesis of adenosine triphosphate (ATP).

Charles L. Vigue

See also: Cell wall; Chloroplasts and other plastids; Cytosol; Membrane structure; Metabolites: primary vs. secondary; Oil bodies; Plant cells: molecular level; Plasma membranes.

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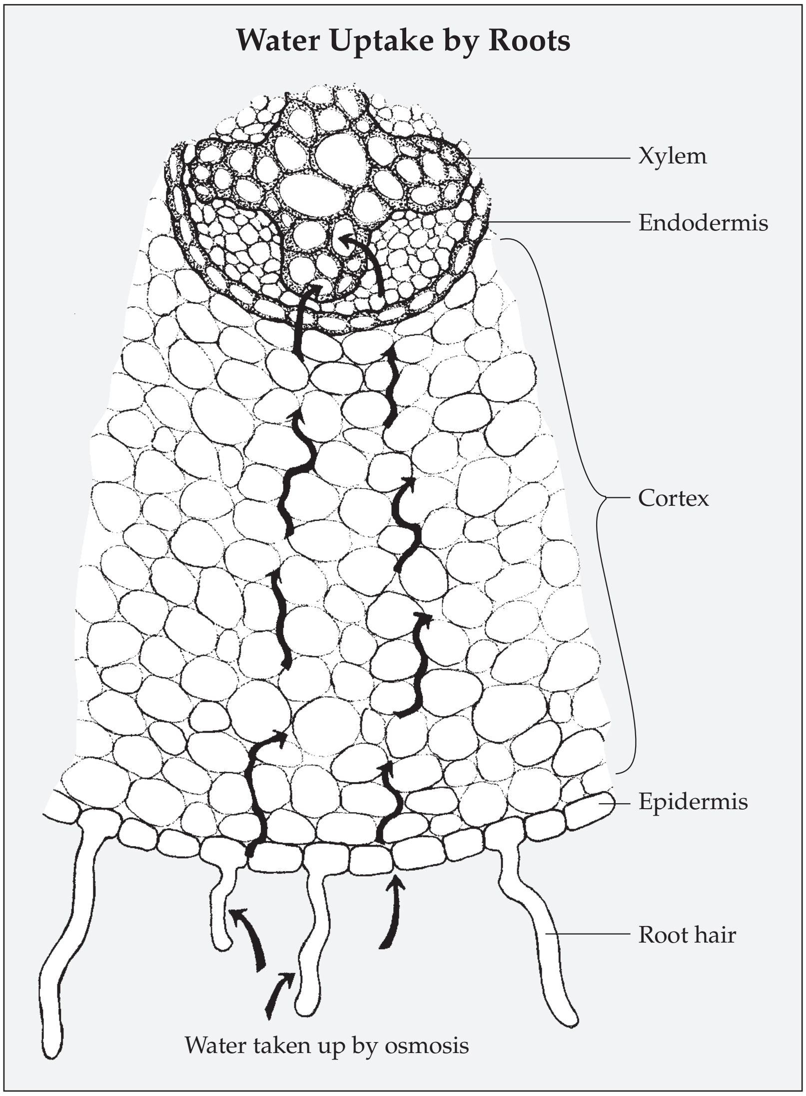
LIQUID TRANSPORT SYSTEMS

Categories: Anatomy; physiology; transport mechanisms

Liquid transport systems are structures that facilitate the movement of water, via the xylem, from a plant's roots to its leaves. Water then evaporates from the leaves through the stomata in the process of transpiration.

Water is the most abundant compound in plant cells. It accounts for 85-95 percent of the weight of most plants. It even makes up 5-10 percent of the weight of "dry" seeds. More than 95 percent of the water gathered by a plant, however, evaporates back into the atmosphere, often within hours after being absorbed. This evaporation of water from a living plant is called *transpiration*. Most transpiration is from leaves.

Plants transpire huge amounts of water. On a warm, dry day, an average-size maple tree transpires more than 200 liters per hour, while herbaceous plants transpire their own weight in water several times per day. A corn plant transpires almost 500 liters of water during its four-month growing season. If humans required an equivalent amount of water, a person would have to drink approximately 40 liters per day.



A cross section of a root: Water moves into the root hairs, across the epidermis, through the cortex, across the endodermis, and into the xylem, from which it is transported up into the plant.

Plant survival depends on the ability to transport water and dissolved materials. Inside individual cells, *diffusion* is usually adequate for this movement. Small molecules can diffuse across a 50-micrometer-wide cell in less than one second. However, diffusion is inadequate for transport from one part of a multicellular plant to another. Multicellular plants must absorb and transport large amounts of water and dissolved minerals from the soil to their leaves, which may be many meters away from the soil. Multicellular plants must also have a system for transporting the sugars produced in leaves to distant sites for storage and use. Thus, the multicellular nature of plants was largely responsible for the evolution of *xylem* and *phloem*, the two long-distance transport systems in plants.

Leaves and Roots

Leaves are the primary photosynthetic organs of most plants. The rate of gas exchange for photosynthesis depends, among other things, on the amount of available surface area. The loose internal arrangement of cells in leaves produces a large internal surface area for transpiration—an area that may be more than two hundred times greater than the leaf's external surface area.

The internal surface area of a leaf is connected with the atmosphere via an extensive system of intercellular spaces, pores called *stomata*, that occupy as much as 70 percent of a leaf's volume. Stomata are so numerous that a typical leaf of a squash plant has more than eighty million of them. Leaves also have an efficient system of *veins* (vascular tissue) for distributing water to their internal evaporative surfaces. One square centimeter of leaf may have as many as six thousand outlets of vascular tissue.

Water lost via transpiration must be replaced by water absorbed from the soil by the plant's roots. The movement of water from the roots to the leaves is very rapid. Water molecules may move as fast as 75 centimeters per minute, which is roughly equivalent to the speed of the tip of a second hand sweeping around a wall clock.

Water and its dissolved minerals move from roots to leaves in xylem. The two kinds of cells in xylem that carry water are *tracheids* and *vessels*. Both of these cell types are hollow and dead at maturity. They have thick cell walls and can therefore withstand the fluctuations in pressure associated with water flow.

Tracheids are usually long (up to 10 millimeters) and thin (10-15 micrometers in diameter) and overlap one another. Their walls have numerous thin areas that link adjacent tracheids into long, water-conducting chains. Vessels are shorter and much wider than tracheids. The walls separating adjacent vessel elements are often wholly or partially dissolved. Because of their larger diameter and dissolved walls, water moves faster in vessels than in tracheids. This increased flow rate in vessels may help explain why angiosperms dominate today's landscapes: Flowering plants, such as grasses, contain tracheids and vessels, while gymnosperms, such as pines, contain only tracheids. In woody plants, the xylem that transports water and dissolved minerals makes up the wood of the trunk.

Water Flow

Water movement through plants requires no metabolic energy; rather, water flows passively from one place to another. Although root pressure, caused by the pumping of dissolved minerals into the roots, can push water up to a few meters, in taller plants water and dissolved minerals are pulled up through the xylem. The driving force for this movement is the transpiration of water from the leaves. The hypothesis that describes the process is known as the *transpiration-cohesion hypothesis of water movement*. It states that solar-driven transpiration of water dries the walls of *mesophyll* cells of leaves; the loss of water from the cell wall then causes water from neighboring cells to enter the leaf cell. Cells bordering tracheids and vessels replace their water with water from the xylem. The loss of water from xylary elements creates a negative pressure, thereby lifting the water column up the plant. The water column does not break, because water molecules cohere strongly.

The negative pressure created in the xylem by transpiration extends all the way down to the tips of roots, even in the tallest trees. The tension in the root xylem causes water to flow passively from the soil, across the root cortex, and into the xylem of the root. This water is then pulled up the xylem to leaves to replace water lost via transpiration.

Transpiration is affected by atmospheric humidity, wind, air temperature, soil, light intensity, and the concentration of carbon dioxide in the leaf. Transpiration is greatest in plants growing in moist soil on a sunny, dry, warm, and windy day. In these conditions, transpiration often exceeds the plant's ability to absorb water. As a result, many plants wilt at midday, even if the soil in which they are growing contains abundant water. Transpiration also moves solutes in plants; for example, most minerals move from roots to shoots in the transpiration stream.

Stomata

Stomata regulate gas exchange between the atmosphere and a plant and are a key adaptation to life on land. Almost all the factors that affect transpiration do so by influencing the opening or closing of stomata. For example, decreasing the internal concentration of carbon dioxide in a leaf causes stomata to open, therefore increasing gas exchange and transpiration.

Stomata occur throughout the plant kingdom. In angiosperms, they occur on all aboveground organs, including leaves, stems, petals, stamens, and carpels. Open stomata occupy less than 2 percent of a leaf's area. In most plants the stomata are confined to the lower surfaces of leaves (away from the sun) to reduce transpiration rates. Stomata on the upper surfaces, where direct sunlight strikes, could cause serious water loss.

A stomatal complex consists of two *guard cells* and adjacent epidermal cells called *subsidiary cells*, all of which surround a *pore*. Guard cells and stomata have several distinguishing features. For example, guard cells of dicotyledons are crescent-shaped, while in most grasses they are shaped like dumbbells. Most leaves have 1,000 to 100,000 stomata per square centimeter of leaf area. Plants in dry, bright environments, such as deserts, often have smaller and more numerous stomata than plants growing in wet, shaded environments. When wide open, stomatal pores are usually 3-12 micrometers wide and 10-40 micrometers long.

Guard cells control the size of a stomatal pore by changing shape—their unusually elastic walls buckle outward when stomata open and sag inward when stomata close. Stomatal opening and closing is controlled by movement of water into and out of the guard cells. The water movement occurs by osmosis, and the direction of movement is determined by the concentrations of ions under a complex set of cellular controls. Stomatal opening is primarily caused by radial micellation of guard cells by cellulose microfibrils arranged much like the belts in a belted tire. These microfibrils are inelastic; they restrict radial expansion of guard cells while allowing increases in length. When the guard cells lengthen because of an influx of water, they bow apart and form the stomatal pore. Closing of stomata occurs when water moves out of the guard cells, causing them to become flaccid.

Sieve Tubes and Sugar

Sugars and other organic substances move in sieve tubes of the phloem. *Sieve tube members* are arranged end-to-end and are associated with files of companion cells. Companion cells and sieve elements function as a single unit. Sieve tube members are tiny cylinders approximately 40 micrometers in diameter and 1,200 micrometers long. The protoplasts of sieve tube members are connected by sievelike areas called *sieve plates*, each of which has numerous sieve pores. In woody plants, the phloem makes up the innermost layers of the bark.

Peak rates of solute transport in phloem may exceed 2 meters per hour. As a result, as much as 20 liters of sugary sap can be collected per day from severed stems of sugar palms. A sieve element 0.5 millimeter long empties and fills every two seconds, thereby delivering approximately 5 to 10 grams of sugar per hour per square centimeter of phloem area to sites of sugar storage or use.

Solutes move through the phloem via pressure flow. In 1926 plant physiologist Ernst Munch proposed the *pressure-flow hypothesis*, which states that a *turgor pressure* gradient drives the unidirectional *mass flow*, or *bulk flow*, of solutes and water through sieve tubes of the phloem. According to this model, solutes move passively through sieve tubes along a pressure gradient in a fashion analogous to the movement of water through a garden hose.

Sucrose produced at a source is actively loaded into a sieve tube. This loading causes water to enter the sieve tube via osmosis from the xylem. The influx of water into sieve tubes carries sucrose to a *sink*, which is an area where sucrose is unloaded for use or storage. Removing sucrose at the sink causes water also to move out of the sieve tube. The influx of water at the source and the efflux of water at the sink create a pressure-driven flow of fluids in the phloem.

Sugars in the cell wall are loaded into sieve tubes by companion cells. These companion cells often have numerous cell-to-cell channels called *plasmodesmata*. Their cell walls and cell membranes also have elaborate infoldings that provide a large surface area for transporting sugars from the cell wall into the sieve tube. The loading of sieve tubes requires metabolic energy in the form of *adenosine triphosphate* (ATP) and is driven indirectly by a proton gradient. Phloem transport is affected by temperature, light, and the nutritional status of the plant.

More than 90 percent of the solutes in sieve tubes are carbohydrates. In most plants, these carbohydrates are transported as sucrose. The concentration of sucrose may be as high as 30 percent, thereby giving the phloem sap a syrupy consistency. A few plant families also transport other sugars, such as raffinose and stachyose. These sugars are similar to sucrose and consist of sucrose attached to one or more molecules of D-galactose. Like sucrose, all these sugars are nonreducing sugars. This is important because nonreducing sugars such as sucrose are less reactive and less prone to enzymatic breakdown than are reducing sugars such as glucose and fructose. Sieve tubes also contain ATP and nitrogen-containing compounds. More than a dozen different amino acids occur in sieve tubes of some plants. Sieve tubes also transport hormones, alkaloids, viruses, and inorganic ions such as potassium ions.

Randy Moore

See also: Gas exchange in plants; Leaf abscission; Leaf anatomy; Nutrients; Osmosis, simple diffusion, and facilitated diffusion; Plant tissues; Roots; Water and solute movement in plants.

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LIVERWORTS

Categories: Medicine and health; nonvascular plants; paleobotany; *Plantae*; taxonomic groups

Liverworts (phylum Hepatophyta*) are one of three ancient lines of bryophytes (liverworts, hornworts, and mosses): low-growing land plants that depend on free water (rain) for fertilization*.

Liverworts, with about six thousand species, generally prefer somewhat cooler, moister, shadier, and more acidic habitats than mosses. Like any bryophyte, a liverwort has a dominant (conspicuous) green gametophyte and a small, attached sporophyte, which is a single-stalked sporangium that developed from a fertilized egg. As in hornworts, liverwort gametophytes are typically dorsiventrally symmetrical (flattened). A unique feature of liverworts is the presence, in the gametophyte, of *oil bodies*, cellular organelles that produce aromatic terpenoids.

Many freshly collected liverworts have a pleasing aroma, which quickly disappears as oil bodies disintegrate. Possibly defending liverworts from herbivores, *terpenoids* (chemically diverse and found in 90 percent of liverworts) have potential medicinal value. Liverwort sporophytes mature while completely enclosed in the gametophyte. Thereby shielded from natural selection, they are far more uniform than moss sporophytes. A typical liverwort sporophyte comprises a foot, a fleshy stalk (*seta*), and a round to cylindrical capsule that splits open to release spores and *elaters*. The seta is green when young but is short-lived and grows only by cell elongation (not by meristematic cells as in other bryophytes). *Elaters*, unique to liverworts, are cells with spirally thickened walls. Their jerky, hygroscopic movements help disperse spores from the capsule.

Leafy Liverworts

Liverwort gametophytes are distinctive. They are either leafy (about two-thirds of the species) or thalloid (straplike), whereas all mosses are leafy. Liverwort leaves are often round and lobed, unlike the pointed leaves of mosses. Liverwort gametophytes are anchored by unicellular rhizoids (hairs), whereas the rhizoids of mosses are multicellular. Leafy liverworts are placed in the class *Jungermanniopsida*, with most species in the order *Jungermanniales*. The leaves are only one cell thick and lack midribs. The rounded cells have numerous chloroplasts and variable numbers of oil bodies; these resemble clusters of grapes in some species.

Stems are creeping or ascending and usually bear three rows of leaves: two rows of dorsal leaves and (in most species) one row of ventral leaves or underleaves. Leaves generally overlap and are attached to the stem at a slanted angle (a transverse angle is less common). The arrangement of the leaves in leafy liverworts can be referred to as being either *succubous* or *incubous*, based on the way the leaves overlap. In succubous species the leaves overlap, as do the shingles of a roof; the upper part of a leaf is covered by the next leaf above it (toward the apex). In incubous species, leaves overlap in the opposite way (away from the apex). Leaves of many species are divided into lobes and filaments, giving the gametophyte a delicate appearance. For example, *Frullania* has two rows of dorsal leaves, one row of bifid underleaves, and two rows of helmet-shaped ventral leaf lobes or "water sacs" (in which "wheel animals," or rotifers, may live). *Trichocolea* has leaves divided into filaments that resemble wool. The external complexity of leafy liverworts makes them well suited for capillary conduction and storage of rainwater. However, like most bryophytes, leafy liverworts have a thin cuticle (or lack one); after a rain, they soon dry out and become inactive. Upon remoistening, they quickly revive.

The archegonia (egg sacs) of leafy liverworts develop at the tips of stems and branches, whereas the antheridia (sperm sacs) are produced behind the apex. These gametangia are protected from drying out by slime hairs (which secrete mucilage) and bracts (specialized leaves). Archegonia may be concealed within an envelope of fused leaves (the *perianth*). After fertilization, the base of the archegonium swells into a calyptra that protects the embryo. The embryo may also be enclosed by a sheath of stem tissue (the *perigynium*). After sporophyte maturation (often in spring or fall) the seta elongates and forces the capsule through the protective layers. The capsule splits open, its four valves resembling a small flower, and releases the spores and elaters. A few days later, the delicate seta collapses and dies.

If a spore lands in a favorable site, it may germinate and develop into a new leafy gametophyte, which grows by means of an apical cell (initial) at the stem tip. Liverworts of moist habitats, such as *Frullania*, often show precocious spore germination, and juvenile gametophytes (rather than spores) are shed from the capsule. Juvenile gametophytes are often globular, rather than threadlike, as in mosses. Liverwort spores that are unusually tolerant of cold, dry conditions may be dispersed over great distances by wind. Many leafy liverworts also produce abundant specialized asexual propagules (gemmae), which may be dispersed by rain, wind, or the feet of animals. Asexual reproduction helps compensate for infrequent sexual reproduction; most leafy liverworts (like most bryophytes) are unisexual, and sometimes male and female plants live far apart.

Leafy liverworts flourish in humid, shaded habitats and are often pioneers on rocks, tree trunks, decaying logs, stumps, and soil by streams, ponds, footpaths, and roads. Habitats range from sunny ridges to deeply shaded gorges. A few species are aquatic, such as *Scapania undulata*, a major producer in mountain streams that is remarkably tolerant of acid mine drainage. Many species are epiphytes, festooning trees as pendent mats in temperate and

Classification of Liverworts

Subclass *Jungermanniae*
- Order *Calobryales*
  - Family:
    - *Haplomitriaceae*
- Order *Jungermanniales*
  - Families:
    - *Acrobolbaceae*
    - *Antheliaceae*
    - *Arnelliaceae*
    - *Calypogeiaceae*
    - *Cephaloziaceae*
    - *Cephaloziellaceae*
    - *Chonecoleaceae*
    - *Geocalycaceae*
    - *Gymnomitriaceae*
    - *Gyrothyraceae*
    - *Herbertaceae*
    - *Jubulaceae*
    - *Jungermanniaceae*
    - *Lejeuneaceae*
    - *Lepidoziaceae*
    - *Mastigophoraceae*
    - *Mesoptychiaceae*
    - *Plagiochilaceae*
    - *Pleuroziaceae*
    - *Porellaceae*
    - *Pseudolepicoleaceae*
    - *Ptilidiaceae*
    - *Radulaceae*
    - *Scapaniaceae*
    - *Trichocoleaceae*
- Order *Metzgeriales*
  - Families:
    - *Allisoniaceae*
    - *Aneuraceae*
    - *Blasiaceae*
    - *Fossombroniaceae*
    - *Metzgeriaceae*
    - *Pallaviciniaceae*
    - *Pelliaceae*
    - *Treubiaceae*

Subclass *Marchantiae*
- Order *Marchantiales*
  - Families:
    - *Aytoniaceae*
    - *Cleveaceae*
    - *Conocephalaceae*
    - *Corsiniaceae*
    - *Lunulariaceae*
    - *Marchantiaceae*
    - *Monosoleniaceae*
    - *Oxymitraceae*
    - *Ricciaceae*
    - *Targioniaceae*
- Order *Sphaerocarpales*
  - Families:
    - *Riellaceae*
    - *Sphaerocarpaceae*

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

tropical rain forests. Although leafy liverworts are (like most bryophytes) typically perennial, their substrata are often "temporary" on a scale of years (fields, flood plains), decades (logs), or centuries (old-growth trees). Propagules (spores and gemmae) enable them to "shuttle" to new substrata as they become available.

Thalloid Liverworts

Thalloid liverworts typically have green cells above, scattered oil cells (one oil body per cell), ventral tissue hosting symbiotic fungi, and rhizoids arising from a central thickened area (which may include a distinct midrib). There are two kinds of thalloid liverworts, classified based on anatomy: simple and complex. Simple thalloid liverworts are placed in the class *Jungermanniopsida*, with most species in the order *Metzgeriales*. The straplike or ribbonlike thalli (bodies) grow by means of "apical initials" in marginal notches. Branching patterns vary, but thalli generally expand outward, forming circular mats. In *Pallavicinia*, a distinct midrib contains "hydroids," elongated cells specialized for water conduction, analogous to tracheids of higher plants. Archegonia and antheridia in the *Metzgeriales* are usually scattered on the thallus and are variously protected by sheaths, scales, flaps, and slime hairs. At maturity, the sporophyte bursts through the calyptra, the capsule splits open into two to four valves, and spores and elaters are released. Some species also produce gemmae. Simple thalloid liverworts grow in the same range of habitats as leafy liverworts and are often intermingled with them.

Complex thalloid liverworts, or *chamber liverworts*, are placed in the class *Marchantiopsida*. They have an upper layer of loosely packed green filaments in boxlike "air chambers" and a lower layer of compact food storage cells. Each air chamber has a pore in its "roof." The waxy epidermis of the "roof" repels excess water, while the pores permit the gas exchange necessary for photosynthesis. Although pores cannot be opened and closed (as can stomata of higher plants), the complex pores of some species can shrink under dry conditions. Although water-conducting cells occur in the midribs of some species, chamber liverworts, like all bryophytes, rely primarily on capillary water. Capillary spaces are abundant and occur among ventral scales and within a dense mat of rhizoids, smooth vertical rhizoids and horizontal rhizoids (with "pegged," wavy walls) that conduct water along the liverwort's underside.

Chamber liverworts grow by means of apical initials (protected by scales) in marginal notches. Thalli appear to branch dichotomously, repeatedly forking in two's. However, this growth is pseudodichotomous; in true dichotomies, each apical initial splits into two new initials. As in most bryophytes, colonies "grow ahead and die behind," so that one colony fragments into two (or more) new colonies.

Reproductive structures of chamber liverworts are highly specialized. In *Marchantia*, raindrops splash gemmae out of gemma cups. A constriction in the cup speeds up the water's movement and enhances dispersal. Also in *Marchantia*, thallus branches have been modified into umbrella-like gametangiophores; these elevate antheridia and sporangia and thereby enhance rain dispersal of sperm and wind dispersal of spores. In male plants, rain strikes the "umbrellas," with their sunken antheridia, and splashes out sperm. In female plants, sporophytes (with reduced setae) are borne on the underside of the "umbrellas"; mature capsules burst through the calyptrae, tear open irregularly, and release spores and elaters. Asexual reproduction (via gemmae) is favored by short days, whereas sexual reproduction (via sporophytes) is favored by long days.

Other chamber liverworts are less specialized than *Marchantia*. For example, *Conocephalum* has female umbrellas only and lacks gemma cups. In *Riccia* and *Ricciocarpus*, gametangia and sporangia are sunken into the thalli, and spores are liberated when the thalli decay. In both genera, spore release by disintegration is synchronized with seasonal change and is just as adaptive as the complex "umbrellas" of *Marchantia*. *Riccia fluitans* and *Ricciocarpus natans* form floating mats on ponds, but other *Riccia* species dominate the extensive "cryptogamic crusts" on arid plains in Australia. *Marchantia* is found on recently burned ground in humid areas, whereas *Conocephalum* frequently grows on shaded ledges along streams. Chamber liverworts have been extensively used as experimental subjects. Sex chromosomes in plants were first discovered in the chamber liverwort *Sphaerocarpos*.

Susan Moyle Studlar

See also: Bryophytes; Hornworts; Oil bodies; Mosses.

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LOGGING AND CLEAR-CUTTING

Categories: Economic botany and plant uses; environmental issues; forests and forestry

Logging is the removal of timber from forestlands with the intention of using it for a specific purpose, such as lumber, fuelwood, or the production of pulp or chemicals. Clear-cutting is a harvesting technique in which all timber is removed from a stand at the same time.

Many people believe commercial logging is responsible for the loss of all forestland. However, acres of forestland are cleared for other purposes, particularly in tropical areas. Rain forests in Amazonia, for example, are often bulldozed to create pastureland for cattle. Rather than being harvested for timber, the wood is simply pushed into piles and burned at the site.

The Logging Process

Logging, whether of one tree or one thousand trees, involves four basic steps: selecting the timber to be harvested, felling the trees, trimming away waste material, and removing the desired portion of the tree from the woods. Equipment used in logging ranges from simple hand tools, such as axes and crosscut saws, to multifunction harvesting machines. Mechanized feller bunchers, for example, can fell the tree, trim off the branches, cut the stem into logs, and stack logs to await removal from the forest. The choice of equipment utilized in harvesting a specific stand of timber depends on factors such as the terrain, the type of timber to be logged, and whether the logger intends to harvest only selected trees or to clear-cut the site.

Soil and Atmospheric Effects

Logging and clear-cutting, if improperly done or motivated by short-term economic goals, can pose significant threats to the environment. Logging always involves some disturbance to soil and wildlife. If performed in environmentally sensitive areas, it can destroy irreplaceable habitat and contribute to erosion. Heavy equipment can compact soil, leaving ruts that may persist for many years, while clear-cutting hillsides can lead to erosion, stream siltation, and flooding. In Asia, for example, clear-cutting in the mountains of Nepal and India has caused disastrous floods in Bangladesh.

Even when logging does not inflict long-term damage on the immediate environment, the removal of trees can contribute to the threat of global warming. *Slash* (the unmarketable portions of the tree, such as tops and branches) burned at logging sites emits greenhouse gases into the atmosphere, while the loss of forest means that there are fewer trees to break those gases down into oxygen and organic compounds.

Clear-Cutting

Clear-cutting is the practice of cutting all the trees on a tract of land at the same time. At one time a standard practice in lumbering, it has become one of the most controversial harvesting techniques used in modern logging. A tract that has been clear-cut will have no trees left standing. With its windrows of slash and debris, a clear-cut tract of land may appear to the untrained eye as though a catastrophic event has devastated the landscape. Wildlife studies have indicated that certain species of birds and mammals are threatened when their habitats are clear-cut, as they either lose their nesting areas or are exposed to increased risk from predators. The northern spotted owl, for example, becomes easy prey for great horned owls when it is forced to fly across large open areas.

Clear-cutting steep hillsides can leave the land susceptible to erosion, as the removal of all trees leaves nothing to slow the flow of rainfall. The hillsides can, as a result, lose topsoil at a rapid rate, choking nearby streams with sedimentation and killing aquatic life. The large amounts of slash, or debris, left behind can pose a fire hazard. The alternative, selective harvesting, may offer better results.

PhotoDisc

Clear-cutting removes all the trees on a tract of land, leaving none standing. At one time a standard practice in logging, it has become one of the most controversial harvesting techniques used in modern logging. With its windrows of slash and debris, a clear-cut tract of land may appear as though a catastrophic event has devastated the landscape.

By contrast, however, for some species of trees selective harvesting simply does not work. Clear-cutting occurs in forests where the desired species of trees need large amounts of sunlight to regenerate. Many conifers, such as Douglas fir, are shade-intolerant. Landowners will occasionally decide to change the dominant species on a tract and so will clear-cut existing timber to allow for replanting with new, more commercially desirable trees.

Loggers are more likely to clear-cut if the timber is plantation-grown and of a uniform age and size. Clear-cutting remains an appropriate harvesting method in certain situations, as when plantation stands are harvested in rotation. Modifications in its application can help prevent damage to the environment.

Selective Harvesting

Selective harvesting, in contrast with clear-cutting, leaves trees standing on the tract. This method can be utilized with even-age plantation stands as a way of thinning them. More commonly, it is used in mixed- and uneven-age stands to harvest only trees of a desired species or size. In cutting hardwood for use as lumber, for example, 12 inches (30 centimeters) may be considered the minimum diameter of a harvestable tree. Trees smaller than that will be left in the woods to continue growing.

Selective harvesting can also be ecologically damaging, however. Logging may create stress on the residual standing timber, leading to disease and die-off of the uncut trees, while the operation of mechanized equipment can be as disrupting to nesting and foraging habits of wildlife as clear-cutting the stand would have been.

An individual, noncommercial woodcutter may fell only a few trees per year on small parcels of land. Commercial loggers, in contrast, annually harvest hundreds of thousands of trees and operate on large parcels of land. Nonetheless, significant acres of forestland are annually cleared by people who rely on noncommercial logging for wood for their own needs, such as fuel for cooking or heating their homes. Although some woodcutters may cut more than they need for their own use and then sell the surplus, fuelwood for individual households is usually gathered by members of that household. Other examples of noncommercial logging include farmers cutting trees for use as fencing or building materials on their own property.

From an environmental viewpoint, the biggest difference between commercial and noncommercial logging would seem to be one of scale, but this is not always true. An improperly logged small parcel can have more of an impact on a *watershed* or other *ecosystem* than a professionally harvested large stand. Even if no single household's logging practices pose a problem, collectively the gathering of fuelwood or other timber can be devastating. Many nations have developed programs in which professional foresters provide advice on environmentally sound harvesting practices and timber-stand improvement for small property owners, but the availability of such help varies widely from country to country. With no guidance from professional foresters, trees are logged based on convenience for the woodcutter rather than principles of sustainable forestry or watershed management.

Nancy Farm Männikkö

See also: Deforestation; Forest management; Forests; Greenhouse effect; Old-growth forests; Sustainable forestry; Timber industry; Wood; Wood and charcoal as fuel resources.

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LYCOPHYTES

Categories: *Plantae*; seedless vascular plants; taxonomic groups; water-related life

The lycophytes, which compose the phylum Lycophyta, *are one of four phyla of seedless plants having vascular, or conducting, tissue. The living lycophytes are all small and herbaceous, whereas the extinct lycophytes included large trees, which were important in the formation of coal.*

There are at least twelve genera and twelve hundred species of living lycophytes. These include plants known as club mosses and spike mosses (though none are true mosses) and quillworts. The lycophytes consist of three families, each belonging to a separate order. The family *Selaginellaceae* has a single genus, *Selaginella*. Similarly, the family *Isoetaceae* has a single genus, *Isoetes*. The remaining genera belong to the family *Lycopodiaceae*. The living lycophytes are widely distributed but reach their greatest species diversity in the tropics. The lycophytes are similar to the higher vascular plants—the gymnosperms and angiosperms—in having vascular tissue and true leaves, stems, and roots.

Reproduction

The alternation of generations in lycophytes resembles, in an important way, this life cycle in the higher vascular plants: The sporophyte (the spore-bearing generation), rather than the gametophyte (the gamete-bearing generation), is the larger, more obvious generation. In contrast, in the bryophytes (mosses and their relatives, in the phylum *Bryophyta*), which are an earlier, nonvascular evolutionary line, the gametophyte is the larger, dominant generation.

Unlike the higher plants, however, the lycophytes do not produce seeds. Like all seedless plants, the lycophytes require water for the sperm to swim to the egg. In addition, the stem tip in most lycophytes forks repeatedly, resulting in branches that are of about equal length, whereas in higher plants, there is a single main axis, from which lateral branches arise.

Evolutionary Origins

Some of the features that lycophytes and the higher vascular plants have in common differ in their evolutionary origins. Such characteristics are considered convergent, or analogous, having arisen to meet similar environmental demands. The different origins are attributable to the early divergence of the lycophytes from the main lineage of vascular plants. The lycophytes first appear in the fossil record in the early Devonian period of the Paleozoic era, about 400 million years ago; they probably arose from early members of the *Zosterophyllophyta*, a phylum of seedless vascular plants that became extinct during the Devonian.

Leaves are one of the features that developed independently in lycophytes and higher plants. The leaves of lycophytes are called microphylls and are characteristic of all members of the group, extinct and living. In two of the three living lycophyte families, the microphylls are short. In all lycophytes, the microphylls are narrow and have a single, unbranched vein. In contrast, the leaves of the higher vascular plants typically have a complex system of branching veins and are called megaphylls.

Carboniferous Period

Some extinct lycophytes had, in addition to microphyllous leaves, other features analogous to, but derived independently of, those of higher vascular plants. These included tree forms and structures analogous to seeds. These do not occur in living lycophytes. Especially noteworthy among the extinct lycophytes were the scale trees. For most of the Age of Coal, in the Paleozoic's late Carboniferous period (322 million to 290 million years ago), these trees were among the dominant plants of swamp forests in what is now North America and Europe. They grew 10 to 35 meters tall and included the genera *Lepidodendron* and *Sigillaria*. The remains of these large trees contributed greatly to formation of the world's coal beds.

The trunks of most tree lycophytes branched only near the top. Stabilizing them at their bases were shallow, forking, rootlike structures, which produced spirally arranged rootlets. The stems were supported mostly by a massive bark surrounding a relatively small amount of secondary xylem, or wood. The reproductive structures were borne in cones. Like the living genera *Selaginella* and *Isoetes*, lycophyte trees were heterosporous, forming spores of two different sizes rather than a single size. Some species produced structures analogous to seeds.

The tree lycophytes vanished in the late Carboniferous period, about 296 million years ago, as the climate changed and swamps began to dry. The nearest living relative of the tree lycophytes is the

Classification of Lycophytes

Class *Lycopodiopsida*
- Order *Isoetales*
  - Family *Isoetaceae* (quillworts)
    - Genus *Isoetes*
- Order *Lycopodiales*
  - Family *Lycopodiaceae* (club mosses)
    - Genus *Lycopodium*
    - Genus *Phylloglossum*
- Order *Selaginellales*
  - Family *Selaginellaceae* (spike mosses)
    - Genus *Selaginella*

Source: Data are from U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Image Not Available

herbaceous plant *Isoetes* in the family *Isoetaceae*. Herbaceous members of the two other living lycophyte families, *Lycopodiaceae* and *Selaginellaceae*, also existed in the Carboniferous, and representatives of some of them survive today.

Lycopodiaceae

The family *Lycopodiaceae* includes 10 to 15 genera, with a total of 350 to 400 species, most of them tropical. The family is also represented in the temperate zone and even in the Arctic but not in arid regions. In the United States and Canada, there are seven genera, with twenty-seven species which occur in the East and Northwest but not in the dry Southwest. The most familiar of these are probably the club mosses, which belong to the family's largest genus, *Lycopodium*.

Lycopodiaceae consists mainly of trailing plants. A horizontal, branching, underground stem, or rhizome, produces roots and upright, aerial branches. The small, microphyllous leaves are generally spirally arranged. In some genera, the sporophylls—the leaves that bear the spores—look like ordinary microphylls and are interspersed with them along the aerial stems. In other genera, the sporophylls do not resemble ordinary microphylls and are grouped in cones at the ends of the aerial stems.

The spores in *Lycopodiaceae* all the same size. Each spore gives rise to a free-living gametophyte that bears both male and female reproductive structures. In some species, the gametophyte grows aboveground and produces its own food photosynthetically; in others, it grows belowground, is not photosynthetic, and is associated with a fungus. Young sporophytes may remain attached to the gametophyte for some time before becoming independent.

Selaginellaceae

Selaginella, or spike moss, is the sole genus in the family *Selaginellaceae*. With more than seven hundred species, the *Selaginellaceae* is the largest of the living lycophyte families. As with the *Lycopodiaceae*, most species of *Selaginella* are tropical, but some occur in temperate zones. In the United States and Canada, there are thirty-eight species. Many species of *Selaginella* grow in damp places, but a few occur in deserts, where they become dormant during the driest season. The resurrection plant, *Selaginella lepidophylla*, which grows in Texas, New Mexico, and Mexico, can recover from several months of complete drying.

Selaginella has a branched, prostrate stem, which produces roots and upright branches that grow a few inches tall. In some species, the horizontal and upright stems are sheathed with small leaves in four longitudinal rows. Both microphylls and sporophylls bear a small, scalelike outgrowth, called a *ligule*, at the bases of their upper surfaces.

Selaginella forms cones at the ends of the branches. The spores are of two sizes: large ones, called megaspores, and smaller ones, called microspores. Megaspores germinate to form megagametophytes, which bear egg-producing archegonia. Microspores germinate to form microgametophytes, which bear sperm-producing antheridia.

In contrast to the fully free-living gametophytes of the *Lycopodiaceae*, the gametophytes of *Selaginella* develop mostly within the spore walls. When a microgametophyte is mature, the spore wall ruptures, releasing the sperm. The megaspore wall also ruptures, allowing the megagametophyte to protrude from the wall; archegonia develop in the exposed part. Neither the microgametophyte nor the megagametophyte has chlorophyll; thus, the gametophytes, and the developing embryos in the archegonia, must obtain their nutrition from food stored within the spore.

Isoetaceae

Known as the quillwort family, the *Isoetaceae* is the smallest of the lycophyte families. Its single genus, *Isoetes*, includes about 150 species. Unlike the *Lycopodiaceae* and *Selaginellaceae*, which are predominantly tropical, *Isoetes* occurs mostly in cooler climates. In the United States and Canada, there are twenty-four species. Most Isoetes species grow partially or totally submerged in fresh water.

Unlike the *Lycopodiaceae* and *Selaginellaceae*, *Isoetes* is not a trailing plant. Instead, it has a short, thick, fleshy, bulblike underground stem, or corm. Roots grow on the lower surface of the corm, and microphyllous leaves grow on the upper surface. The corm undergoes secondary growth, which thickens it. The microphylls are not small, as they are in the *Lycopodiaceae* and *Selaginellaceae*, but instead are elongated, slender, and stiff, reaching 15 to 50 centimeters in height. They resemble quills, giving *Isoetes* the look of a young onion or a tuft of grass or rush. They are spoon-shaped at the base, where they surround the corm. As in *Selaginella*, the leaves have ligules.

Isoetes species do not produce cones. Each microphyll is a potential sporophyll. As in *Selaginella*, there are two kinds of spores: microspores and megaspores. The sporophylls that bear microspores are located nearer the center of the plant than are the sporophylls that bear megaspores. Gametophyte development takes place largely within the spore walls, as in *Selaginella*. Some species of *Isoetes* from highlands in the tropics obtain their carbon for photosynthesis from the soil rather than in the usual way, from the atmosphere. These plants have an unusual kind of photosynthesis, called CAM (crassulacean acid metabolism) photosynthesis.

Jane F. Hill

See also: Bryophytes; Coal; C_4 and CAM photosynthesis; Evolution: convergent and divergent; Evolution of plants; Fossil plants; Reproduction in plants; Seedless vascular plants; *Spermatophyta*; *Zosterophyllophyta*.

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MARINE PLANTS

Categories: Algae; microorganisms; pollution; water-related life

Marine plants grow near the surface of salt water and ice, within reach of sunlight necessary for photosynthesis. Algae, the most plentiful type of marine plant, form the foundation of the food chain and crucial to a balanced ecosystem.

Water is essential to life. The earliest plants, primarily algae, formed in bodies of saline water covering prehistoric Earth. During the Silurian period, approximately 441 million to 410 million years ago, some aquatic plants began to grow on land, but many plants remained solely water-based. These marine plants have provided fundamental nourishment in the food chain. No marine animals would have evolved or been able to survive if marine plants had not existed. Marine plants support all higher saltwater life-forms. Marine sediments formed by algae often contain fossils that reveal aspects of marine plants' evolutionary history. The distribution of marine plants was affected by plate tectonics as continents moved and ocean shapes changed.

Oceans cover most of the earth's surface. Almost 99 percent of organisms, representing approximately five million species (most of them unclassified) live in oceans. As a result, oceans are significant to the well-being of life and economies. Marine plants consist of two major types, the *sea grasses* and the algae and *seaweeds*. Sea grasses represent members of some of the more complex plants, while algae and seaweeds display simple forms and are often microscopic.

Marine plants range from tiny single-celled organisms to large, intricate forms. Because all marine plants require sunlight to manufacture food, they mostly develop near water surfaces. Nutrients are also gathered from particles that currents wash up from sea floors. Marine plants can adapt to specific conditions, such as limited light and underwater caves. Some are phosphorescent, generating chemical lights.

Types

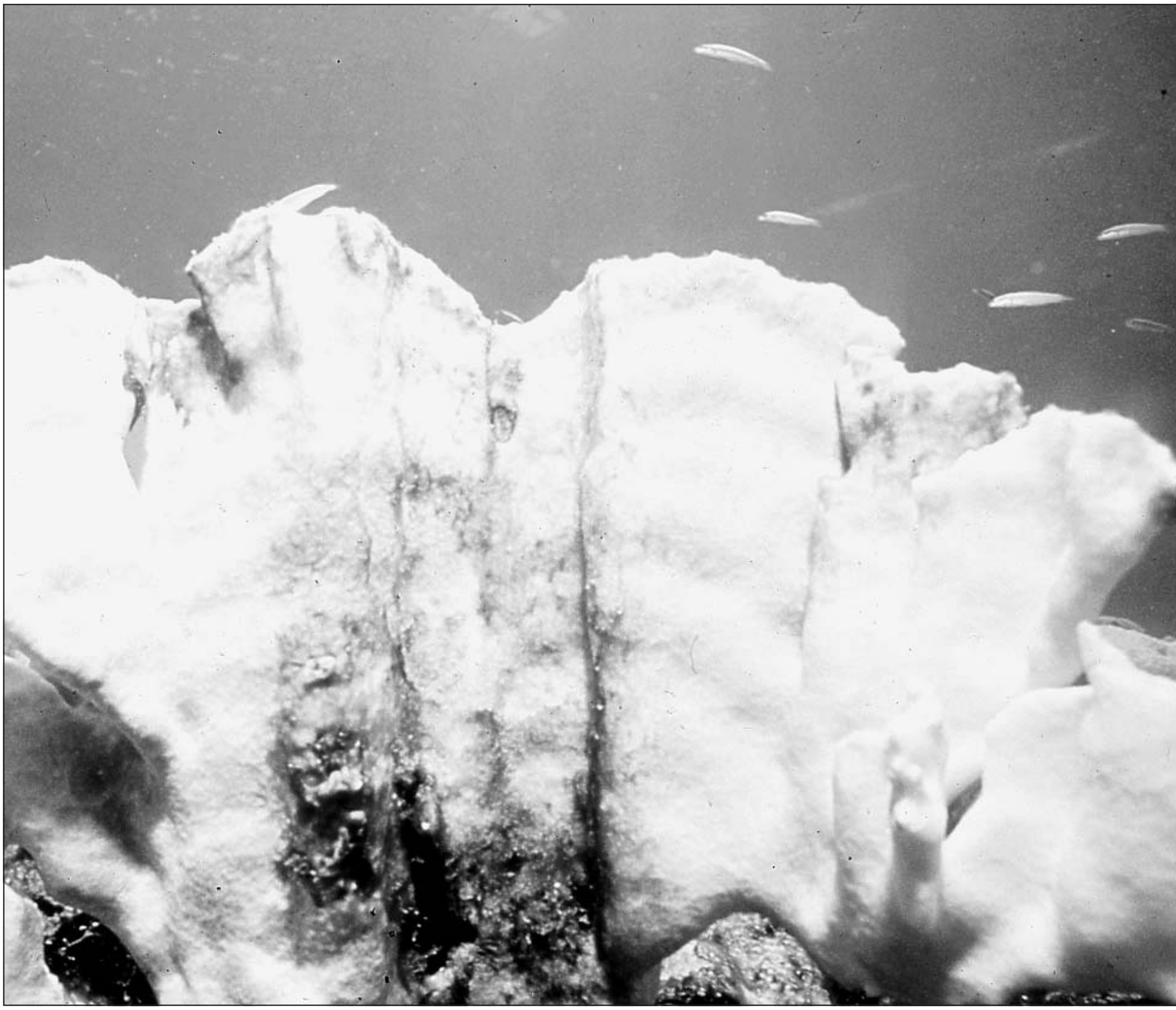
The smallest marine plants are *phytoplankton*, which are single-celled and form the basis of the marine food chain. *Diatoms* (*Bacillariophyta*) are glassy microscopic cells which frequently link together in chains. Few marine plants are angiosperms, although along tropical coasts, flowering marine plants often accumulate. *Green algae* (*Chlorophyta*) is the most common marine plant. Chlorophyll causes these algae to have bright green coloring. When algae leaves calcify, they add layers to ocean sediments. Botanists believe that 200,000 algae species exist, even though only 36,000 have been identified.

Red algae (*Rhodophyta*), tinted by the pigment phycoerythrin, are the largest type of marine plants and the most diverse. Some red algae adhere to corals, thus creating reefs. Both green and red algae species prefer warm water to cold water. In contrast, *brown algae* (*Phaeophyta*), colored with fucoxanthin pigment, are usually found in cold or temperate water, and few species live in the tropics. On reefs, brown algae frequently are the dominant organisms. Blue-green bacteria, or cyanobacteria (formerly called blue-green algae) are primarily microscopic strands which convert nitrogen from the atmosphere into forms that most marine plants can use.

Habitats

Marine plants live in diverse habitats near shores or in salt marshes and open seas worldwide. Giant kelp, a seaweed found in the South Pacific, grows in groups in warm coastal waters. In contrast, sea ice algae live on floating ice sheets. Migrating marine plants drift in a variety of water conditions.

On reefs, marine plants have several roles. Primarily, marine plants, including macroalgae and sea grasses, provide nourishment and shelter for animals. Marine plants assist corals in constructing reefs; then some plants, such as coralline algae, hold the reefs intact.



NOAA/National Undersea Research Program Collection

Coral throughout the Caribbean Sea are expelling algal marine plants as a result of unusually warm water temperatures. The coral appear bleached white because the algae remove the coral's energy and color source.

Algae live inside marine animals. Coral tissues host several million algae per square inch, and these marine plants provide 90 percent of nutrients needed by the coral. The symbiotic relationship is based on a cycle of coral enzymes which cause algae to release carbohydrates and algae to receive nitrogen from coral waste. Algae are shaded from intense sunlight by coral pigments. Algae also live in panels inside giant clams and in sponges and flatworms. In kelp bed forests, marine plants serve as food and habitats for such diverse animals as seals, eels, and octopi. Marine plants also benefit from animals; for example, some can secure nitrogen from seabird guano.

Marine plants are vulnerable to pollution. Seagrass beds and reefs have been damaged by toxins or destroyed by industrial development projects. Dredging and harvesting coral injures marine plants. Fertilizers, pesticides, oils, radioactive material, sewage, and hazardous wastes are drained into oceans. Often tropical commercial fishers use explosives to stun fish, inadvertently destroying marine plant habitats. Sea grasses have died in Maryland's polluted Chesapeake Bay.

Some scientists speculate that the growing ozone hole might place Antarctic marine plants at risk. Changing tides affect marine plant distribution because they alter water levels. Overfishing and acid spills intensify toxic sites. Toxins sicken fish, which develop cancerous tumors, and people who consume this diseased fish are often poisoned. Fungi and bacteria transported in freighters' ballast water from other regions can harm marine plants; for example, slime molds kill turtle grass. Algae frequently develop fungi because excessive nitrogen causes them to produce amino acids and deplete carbon supplies. Marine plants can be relocated by shipping vessels and can overtake native plants in distant areas.

An overabundance of algae can smother coral reefs if the supply of nitrogen is not balanced. If coral become too warm and expel algae, the coral appears bleached white because the algae remove the coral's energy and color source. When too much nitrogen floods an area, sometimes an algal bloom or toxic red tide occurs and can have devastating results. As algae multiply because of excessive nutrients, creating *algal blooms*, they usurp oxygen from other marine plants and organisms, which starve. In 1996 many Florida manatees were killed by a red algal tide. The next year, the U.S. National Aeronautical and Space Administration's Sea-Viewing Wide Field-of-View Sensor satellite began to detect concentrations of marine plants by using light wavelengths.

Uses

The oceans represent 95 percent of the earth's biosphere and affect planetary climatic conditions. Marine plants are estimated to generate approximately 70 percent of oxygen on earth and help regulate oxygen in the atmosphere. The status of marine organisms' health indicates environmental problems that humans and land organisms might encounter.

Humans have historically appropriated marine plants for medicinal uses. Because many marine plants have biotoxins, they are valuable for the development of pharmaceuticals. Using submersible technologies, oceanographers gather samples and cooperate with pharmaceutical manufacturers to seek new chemical compounds to combat disease. Because of the diversity and novelty of marine plants, scientists hope to offer new treatments for diseases resistant to existing nonmarine-plant-derived drugs. Future marine sanctuaries are envisioned to protect such potentially potent natural resources.

Marine plants have also been used as a source of nutrients. Algae with docosahexaenoic acid (DHA), a chemical usually found in human milk and vital to infants' brain development, are commercially processed. Approximately 40 percent of baby formula is made from these algae. The algae *Dunaliella bardawil* contains the orange pigment beta-carotene, which the human body converts into vitamin A. Commercial production of this algae manufactures carotene. Red algae are the chief ingredient of some seaweed drinks and are also useful as thickeners for cooking.

Other commercialization of marine plants includes harvesting seaweed for a variety of products, including foods and fertilizer. Researchers aspire to transfer proteins identified in *Dunaliella bardawil*, which resist extreme saltiness and sun exposure, to land plants that are cultivated in places with high salinity and sunlight conditions.

In an attempt to reduce crop losses, scientists study the physiological relationship of algae and water for optimum cell growth and photosynthesis to understand how such terrestrial plants as corn can manage moisture better, thereby withstanding droughts. Researchers conduct molecular examinations of marine and land plants to comprehend how water supply influences growth rate and metabolism. The cells of the alga *Chara corallina* are large enough that scientists can easily observe how dehydration affects them over a short time period.

Marine plants have a direct relationship to Earth's climate. Iron deficiencies can be detrimental when marine plants become anemic. Oceanic iron and plant absorption of carbon dioxide is connected to ice age cycles and global warming. Paleoceanographers investigated sediment samples to study the impact of a 150,000-year-period of global warming that occurred fifty-five million years ago. They hypothesize that marine plants increased in number to remove atmospheric carbon dioxide and reduce temperatures but warn that modern emissions would be too great for similar resolution.

Elizabeth D. Schafer

See also: Algae; Animal-plant interactions; Aquatic plants; Bioluminescence; Brown algae; Chrysophytes; Diatoms; Evolution of plants; Food chain; Green algae; Greenhouse effect; Medicinal plants; Nitrogen cycle; Ozone layer and ozone hole debate; Phytoplankton; Red algae.

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MEDICINAL PLANTS

Categories: Economic botany and plant uses; medicine and health

Because plants are so biochemically diverse, they produce thousands of substances commonly referred to as secondary metabolites. Many of these secondary metabolites have medicinal properties that have proven to be beneficial to humankind.

The use of plants for medicinal purposes predates recorded history. Primitive people's use of trial and error in their constant search for edible plants led them to discover plants containing substances that cause appetite suppression, stimulation, hallucinations, or other effects. Written records show that drugs such as opium have been in use for more than five thousand years.

From antiquity until fairly recent times, most physicians were also botanists or at least herbalists. Because modern commercial medicines are marketed in neat packages, most people do not realize that many of these drugs were first extracted from plants. Chemists have learned how to synthesize many natural products that were initially identified in a plant. However, in many cases a plant is still the only economically feasible source of the drug.

Antibacterial and Anti-inflammatory Agents

The first effective antibacterial substance was carbolic acid, but the first truly plant-derived antibacterial drug was *penicillin*, which was extracted from a very primitive plant, the fungus *Penicillium*, in 1928. The success of penicillin led to the discovery of other fungal and bacterial compounds that have antibacterial activity. The most notable of these are cephalosporin and griseofulvin.

Inflammation can be caused by mechanical or chemical damage, radiation, or foreign organisms. For centuries poultices of leaves from coriander

(*Coriandrum sativum*), thornapple (*Datura stramonium*), wintergreen (*Gaultheria procumbens*), witch hazel (*Hamamelis virginiana*), and willow (*Salix niger*) were used to treat localized inflammation. In the seventeenth and eighteenth centuries, cinchona bark was used as a source of quinine, which could be taken internally. In 1876 salicylic acid was obtained from the salicin produced by willow (*Salix*) leaves. Today, salicylic acid, also known as aspirin, and its derivatives, such as ibuprofen, are the most widely used anti-inflammatory drugs in the world.

Drugs Affecting the Reproductive System

A home remedy for preventing pregnancy was a tea made from the leaves of the Mexican plant zoapatle (*Montana tomentosa*). The drug zoapatanol and its derivatives were extracted from this plant to produce the first effective birth control substance. It has not been used in human trials, however, because of potential harmful side effects. Other plant compounds that affect the reproductive system include diosgenin, extracted from *Dioscorea* species and used as a precursor for the progesterone used in birth control pills; gossypol from cotton (*Gossypium* species), which has been shown to be an effective birth control agent for males; ergometrine, extracted from the ergot fungus (*Claviceps*) and used to control postpartum bleeding; and yohimbine, from the African tree *Corynanthe yohimbe*, which apparently has some effect as an aphrodisiac.

Circulatory, Analgesic, and Cancer-Fighting Drugs

Through the ages, dogbane (*Apocynum cannabinum*) and milkweed (*Asclepias*) have been prized for their effects on the circulatory system. These

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plants contain compounds called cardiac glycosides. Foxglove (*Digitalis*) has produced the most useful cardiac glycosides, digitalis and digoxin.

Opiate alkaloids such as opium, extracted from a poppy (*Papaver sonniferum*), and its derivatives, such as morphine as well as cocaine, from *Erythroxylum coca* and *Erythroxylum truxillense*, have long been known for their *analgesic* (pain-relieving) properties through their extremely dangerous and addictive effects on the central nervous system.

The primary plant-derived anticancer agents are vincristine and vinblastine, extracted from *Catheranthus roseus*, maytansinoids from *Maytentus serrata*, ellipticine and related compounds from *Ochrosia elliptica*, and paclitaxel (commonly known as taxol) from the yew tree *Taxus baccata*.

Fighting Asthma, Gastrointestinal Disorders, Parasites

The major anti-asthma drugs come from ephedrine, extracted from the ma huang plant (*Ephedra sinaica*), and its structural derivatives. Plant-derived drugs that affect the gastrointestinal tract include castor oil, senna, and aloes as laxatives, opiate alkaloids as antidiarrheals, and ipecac from *Cephaelis acuminata* as an emetic. The most useful plant-derived antiparasitic agent is quinine, derived from the bark of the chincona plant (*Chincona succirubra*). Quinine has been used to control malaria, a disease that has plagued humankind for centuries.

The Future

More plant-derived medicines await discovery, many from tropical rain-forest vegetation. Biotechnology has provided methods by which plants can be genetically modified to produce novel pharmaceuticals. Progress toward the production of specific proteins in transgenic plants provides opportunities to produce large quantities of complex pharmaceuticals and other valuable products in traditional farm environments rather than in laboratories. These novel strategies open up routes for production of a broad array of natural or nature-based products, ranging from foodstuffs with enhanced nutritive value to biopharmaceuticals.

D. R. Gossett

See also: Biotechnology; Culturally significant plants; Herbs; Metabolites: primary vs. secondary; Paclitaxel; Plants with potential.

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MEDITERRANEAN SCRUB

Category: Biomes

Mediterranean scrub vegetation is dominated by fire-adapted shrubs. The biome fringes the Mediterranean Sea, for which it is named, but is also found along western coasts of continents in areas with warm, dry summers and moist, cool winters.

Regions with mediterranean vegetation are coastal regions between 30 and 45 degrees north latitude or between 30 and 45 degrees south latitude. The air circulating around high-pressure zones over adjacent oceans guides storms away from the coast in the warm season but changes position in concert with the tilt of the earth on its axis and brings storms onto the coast in the cool season. As a result, the warm season is dry, and the cool season is moist. Fire is an important component of mediterranean environments, especially after the warm, dry summer.

North America's representative of mediterranean scrub is the *chaparral* of the Pacific Coast of Southern California and northern Baja California, Mexico. In chaparral and some other mediterranean regions, winds blowing from continental high-pressure regions toward the coast help push storm tracks offshore during the warm season. In California these winds are called Santa Ana winds and are best known for driving chaparral fires. Lightning started such fires before human settlement, but they are often started by careless people today. With the lower temperatures of autumn and winter the continental pressure wanes, and the Santa Ana winds decrease. At the same time, the oceanic high-pressure region shifts, and winter storms track onto the coast, bringing the cool season rains.

Character and Components

Mediterranean scrub is found in small, scattered areas around the world. The plant species that occur in this biome on one continent are unrelated to

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those that occur in the same biome on other continents. As a result, mediterranean scrub presents a classical example of convergent evolution, the environmentally driven development of similar characteristics in unrelated species. Under the influence of mediterranean climate, entire communities of unrelated species become similar to one another. Many mediterranean areas also contain a large number of endemic plant species, species that grow nowhere else.

Mediterranean scrub is dominated by shrubs well adapted to fire. Some species have specialized underground structures that are undamaged by the fire and send up new growth shortly after the fire passes. Other species have specialized, long-lived seeds that require intense heat to stimulate germination. Still other species combine the two strategies. In communities that burn regularly, such species have a great advantage over their competitors.

Mediterranean shrubs are not just adapted to recover after a fire; they are actually adapted to carry the fire once it is started. These species synthesize and store highly flammable chemicals in their leaves and stems. The flammable vegetation ensures that most fires will burn large areas.

The most widespread shrub in North American chaparral is chamise (*Adenostoma fasciculatum*), which sprouts from underground structures and produces large numbers of seedlings after a fire. Various species of manzanita (*Arctostaphylos*) and wild lilac (*Ceanothus*) are also widespread throughout chaparral. Some species in each genus both sprout and produce large numbers of seedlings after fires. Other species in each genus depend entirely on heat-stimulated seeds to reestablish their presence in a burned area.

Mediterranean vegetation also occurs on western coasts in southern Australia, where it is called *mallee*; the Cape region of South Africa (*fynbos*); the central coast of Chile (*matorral*); and around the Mediterranean Sea (*maquis*). In all these areas, the vegetation has the same adaptive characteristics and appearance, but the species are not related to those of other areas. Although there are differences among the regions besides the species that occur in each, the similar physical and vegetational characteristics lend a continuity that is widely recognized as the mediterranean scrub biome.

Concerns

As people moved into Mediterranean scrub regions, two major and related concerns surfaced. First, the fires, which are such an important part of scrub ecology, were destructive and dangerous, leading to *fire suppression*. Second, fire suppression may actually increase fire damage and may threaten the mediterranean scrub biome's very existence when combined with other human activities. A comparison of the fire history in the chaparral of California and that of Baja California lends credibility to the idea that fire suppression increases fire damage. Fire suppression has long been practiced in Southern California. In contrast, much less fire suppression has gone on in Baja. Fewer, larger, and more destructive fires burn in Southern California chaparral than in Baja chaparral. The simplest explanation is that fire suppression allows fuel to build up, so that when a fire starts it is essentially unstoppable, as often occurs in California chaparral. With less fire suppression and less fuel accumulation, Baja fires burn more frequently but are smaller and less destructive. The small fires remove the fuel periodically, thus decreasing the danger of large, destructive fires.

There are other differences between California and Baja chaparral that may account for the differences in the fire regimes, but the foregoing hypothesis is interesting from the perspective of human impact on chaparral as well as that of fire's impact on humans. Population growth and its attendant activities threaten the very existence of the chaparral. Humans destroy chaparral to build home sites, suppress fires, and plant grass in burned areas to stabilize the soil and to mitigate future fires. The grasses compete with chaparral plants and retard chaparral recovery. The impact of these and other activities on the native chaparral ecosystem is not well understood but is almost certainly negative. Other mediterranean scrub areas suffer similar fates. Although mediterranean scrub is still well represented in comparison to some biomes, its response to human impact should be carefully studied and monitored, both to protect human investment in mediterranean ecosystems and to preserve the intriguing mediterranean scrub and its many unique plant species.

Carl W. Hoagstrom

See also: African flora; Australian flora; Biomes: types; Central American flora; Community-ecosystem interactions; European flora; Evolution: convergent and divergent; Forest fires; North American flora; South American flora.

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MEMBRANE STRUCTURE

Categories: Anatomy; cellular biology; physiology

All cells, whether prokaryotic or eukaryotic, are surrounded by a membrane called the plasma membrane, an essential barrier between the external environment and the cytoplasm inside the cell. In addition, eukaryotic cells contain other membranes that are part of a variety of organelles, such as nuclei, plastids, mitochondria, vacuoles, Golgi bodies, and the endomembrane system.

Compartmentalization by membranes allows the function of competing processes, such as respiration and photosynthesis, in separate areas of the same cell. In addition, membranes control which molecules enter or leave the cell and the various organelles. Finally, proteins associated with membranes are responsible for extracellular interactions and the energy transactions involved in photosynthesis and respiration.

Fluid Mosaic Model

In the 1960's it was believed that all cellular membranes were structured as two outer layers of protein surrounding a lipid layer. In 1972 Jonathan Singer and Garth Nicolson proposed the now-accepted *fluid mosaic model*. The lipid component of the membrane forms the basic structure, while the proteins act as enzymes, receptors, and transporters. The lipid molecules, most of which are phospholipids, each have a hydrophilic ("water-loving") end and a hydrophobic ("water-fearing") end and associate together such that they form a lipid bilayer. The hydrophobic ends of the lipids from one layer point toward the hydrophobic ends of the other layer and, by associating only with each other, avoid all contact with water. The hydrophilic ends then form the two water-exposed surfaces.

The major lipids in plant cell membranes are phospholipids (lipids with a phosphorus atom bonded to the hydrophilic end) and sterols. In addition, sugar-containing lipids (glycolipids) and sulfur-containing lipids (sulfolipids) are found to different degrees, depending on the particular membrane. By having different hydrophilic ends, the two surfaces can have a different chemical composition and, therefore, different *membrane properties*.

Proteins are associated with membranes in one of two ways. Those that are loosely bound to the surface are called peripheral proteins, while those tightly bound to the interior through hydrophobic interactions are referred to as integral proteins. Integral proteins may also have large hydrophilic portions extending from the surface on either or both sides of the membrane. Some of the membrane-associated proteins are able to diffuse sideways within the plane of the membrane, giving the membrane a certain fluidity. Membrane proteins with sugar groups attached to the hydrophilic ends are termed glycoproteins and are very common on the membrane surface facing the outside of the cell.

Membrane Properties

The lipid and protein makeup of membranes provides them with several important properties. Due to the hydrophobic nature of the membrane interior, water, some gases, and a few small, non-charged molecules are the only compounds that can cross freely. All other molecules need the help of a transport protein. Membranes have a high electrical resistance and therefore are capable of maintaining a difference in voltage (called a *membrane potential*) from one surface to the other. Membrane potentials are used to drive the transport of charged ions and are also involved in sensing of the environment. In addition, membranes have a low surface tension (that is, they are very "wettable") and a net negative surface charge, so they are capable of binding a variety of water-soluble minerals, ions, and proteins (such as the peripheral proteins).

Transport Across Membranes

Large, hydrophilic, or electrically charged solutes cannot pass directly through a cell membrane, yet plants need to be able to move a variety of molecules among the various organelles in the cell. Therefore, the transport of these solute molecules across membranes is made possible by specific integral, membrane-associated proteins called transport proteins, of which there are two basic types: *channel proteins* (usually just called channels) and *carrier proteins* (also called carriers, transporters, or porters).

Several channel proteins together form a pore through the membrane that is filled with water and lined with electrical charges. The size of the pore and the types and number of charges inside it make each individual channel specific for a particular water-soluble ion. Because the charged solutes merely diffuse through the channel in response to a concentration gradient, no metabolic energy is expended during this type of transport, which is therefore called passive transport.

For carrier proteins, the solute to be transported binds to a portion of the carrier protein, which induces a change in its shape, and that causes the solute to be moved to the other side of the membrane, where it is released. The carrier protein assumes its previous shape and is then available to bind and transport another solute molecule. Frequently, energy (in the form of adenosine triphosphate, or ATP) is consumed during the operation of carrier proteins in what is known as active transport.

Robert R. Wise

See also: Active transport; Cell wall; Cytosol; Lipids; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Plasma membranes; Proteins and amino acids; Vesicle-mediated transport.

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METABOLITES: PRIMARY VS. SECONDARY

Categories: Cellular biology; physiology; poisonous, toxic, and invasive plants

Metabolites are compounds synthesized by plants for both essential functions, such as growth and development (primary metabolites), and specific functions, such as pollinator attraction or defense against herbivory (secondary metabolites).

Metabolites are organic compounds synthesized by organisms using enzyme-mediated chemical reactions called *metabolic pathways*. Primary metabolites have functions that are essential to growth and development and are therefore present in all plants. In contrast, secondary metabolites are variously distributed in the plant kingdom, and their functions are specific to the plants in which they are found. Secondary metabolites are often colored, fragrant, or flavorful compounds, and they typically mediate the interaction of plants with other organisms. Such interactions include those of plant-pollinator, plant-pathogen, and plant-herbivore.

Primary Metabolites

Primary metabolites comprise many different types of organic compounds, including, but not limited to, carbohydrates, lipids, proteins, and nucleic acids. They are found universally in the plant kingdom because they are the components or products of fundamental metabolic pathways or cycles such as glycolysis, the Krebs cycle, and the Calvin cycle. Because of the importance of these and other primary pathways in enabling a plant to synthesize, assimilate, and degrade organic compounds, primary metabolites are essential.

Examples of primary metabolites include energy-rich fuel molecules, such as sucrose and starch, structural components such as cellulose, informational molecules such as DNA (deoxyribonucleic acid) and RNA (ribonucleic acid), and pigments, such as chlorophyll. In addition to having fundamental roles in plant growth and development, some primary metabolites are precursors (starting materials) for the synthesis of secondary metabolites.

Secondary Metabolites

Secondary metabolites largely fall into three classes of compounds: alkaloids, terpenoids, and phenolics. However, these classes of compounds

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also include primary metabolites, so whether a compound is a primary or secondary metabolite is a distinction based not only on its chemical structure but also on its function and distribution within the plant kingdom.

Many thousands of secondary metabolites have been isolated from plants, and many of them have powerful physiological effects in humans and are used as medicines. It is only since the late twentieth century that secondary metabolites have been clearly recognized as having important functions in plants. Research has focused on the role of secondary metabolites in plant defense. This is discussed below with reference to alkaloids, though it is relevant to many types of secondary metabolites.

Alkaloids

Alkaloids are a large group of nitrogen-containing compounds, examples of which are known to occur in approximately 20 percent of all flowering plants. Closely related plant species often contain alkaloids of related chemical structure. The primary metabolites from which they are derived include amino acids such as tryptophan, tyrosine, and lysine. Alkaloid biosynthetic pathways can be long, and many alkaloids have correspondingly complex chemical structures. Alkaloids accumulate in plant organs such as leaves or fruits and are ingested by animals that consume those plant parts. Many alkaloids are extremely toxic, especially to mammals, and act as potent nerve poisons, enzyme inhibitors, or membrane transport inhibitors. In addition to being toxic, many alkaloids are also bitter or otherwise bad-tasting. Therefore, the presence of alkaloids and other toxic secondary metabolites can serve as a deterrent to animals, which learn to avoid eating such plants.

Sometimes domesticated animals that have not previously been exposed to alkaloid-containing plants do not have acquired avoidance mechanisms, and they become poisoned. For example, groundsel contains the alkaloid senecionine, which has resulted in many recorded cases of livestock fatalities due to liver failure. More frequently, over time, natural selection has resulted in animals developing biochemical mechanisms or behavioral traits that lead to avoidance of alkaloid-containing plants.

In other, more unusual cases, animals may evolve a mechanism for sequestering (storing) or breaking down a potentially toxic compound, thus "disarming" the plant. For instance, caterpillars of the cinnabar moth can devour groundsel plants and sequester senecionine without suffering any ill effects. Moreover, the caterpillars thereby acquire their own weapon against predators: the plant-derived alkaloid stored within their bodies. Over time, plants acquire new capabilities to synthesize additional defense compounds to combat animals that have developed "resistance" to the original chemicals. This type of an "arms race" is a form of coevolution and may help to account for the incredible abundance of secondary metabolites in flowering plants.

Medicinal Alkaloids

Many potentially toxic plant-derived alkaloids have medicinal properties, as long as they are administered in carefully regulated doses. *Alkaloids* with important medicinal uses include morphine and codeine from the opium poppy and cocaine from the coca plant. These alkaloids act on the nervous system and are used as painkillers. Atropine, from the deadly nightshade plant, also acts on the nervous system and is used in anesthesia and ophthalmology. Vincristine and vinblastine from the periwinkle plant are inhibitors of cell division and are used to treat cancers of the blood and lymphatic systems. Quinine from the bark of the cinchona tree is toxic to the *Plasmodium* parasite, which causes malaria, and has long been used in tropical and subtropical regions of the world. Other alkaloids are used as stimulants, including caffeine, present in coffee, tea, and cola plants (and the drinks derived from these plants), and nicotine, which is present in tobacco. Nicotine preparations are, paradoxically, also used as an aid in smoking cessation. Nicotine is also a very potent insecticide. For many years ground-up tobacco leaves were used for insect control, but this practice was superseded by the use of special formulations of nicotine. More recently the use of nicotine as an insecticide has been discouraged because of its toxicity to humans.

Terpenoids

Terpenoids are derived from acetyl coenzyme A or from intermediates in glycolysis. They are classified by the number of five-carbon isoprenoid units they contain. Monoterpenes (containing two C_5-units) are exemplified by the aromatic oils (such as menthol) contained in the leaves of members of the mint family. In addition to giving these plants their characteristic taste and fragrance, these aromatic oils have insect-repellent qualities. The pyrethroids, which are monoterpene esters from the flowers of chrysanthemum and related species, are used commercially as insecticides. They fatally affect the nervous systems of insects while being biodegradable and nontoxic to mammals, including humans.

Diterpenes are formed from four C_5-units. Paclitaxel (commonly known by the brand name Taxol), a diterpene found in bark of the Pacific yew tree, is a potent inhibitor of cell division in animals. At the end of the twentieth century, paclitaxel was developed as a powerful new chemotherapeutic treatment for people with solid tumors, such as ovarian cancer patients.

Triterpenoids (formed from six C_5-units) comprise the plant steroids, some of which act as plant hormones. These also can protect plants from insect attack, though their mode of action is quite different from that of the pyrethroids. For example, the phytoecdysones are a group of plant sterols that resemble insect molting hormones. When ingested in excess, phytoecdysones can disrupt the normal molting cycle with often lethal consequences to the insect.

Tetraterpenoids (eight C_5-units) include important pigments such as beta-carotene, which is a precursor of vitamin A, and lycopene, which gives tomatoes their red color. Rather than functioning in plant defense, the colored pigments that accumulate in ripening fruits can serve as attractants to animals, which actually aid the plant in seed dispersal.

The polyterpenes are polymers that may contain several thousand isoprenoid units. Rubber, a polyterpene in the latex of rubber trees that probably aids in wound healing in the plant, is also very important for the manufacture of tires and other products.

Phenolic Compounds

Phenolic compounds are defined by the presence of one or more aromatic rings bearing a hydroxyl functional group. Many are synthesized from the amino acid phenylalanine. Simple phenolic compounds, such as salicylic acid, can be important in defense against fungal pathogens. Salicylic acid concentration increases in the leaves of certain plants in response to fungal attack and enables the plant to mount a complex defense response. Interestingly, aspirin, a derivative of salicylic acid, is routinely used in humans to reduce inflammation, pain, and fever. Other phenolic compounds, called *isoflavones*, are synthesized rapidly in plants of the legume family when they are attacked by bacterial or fungal pathogens, and they have strong antimicrobial activity.

Lignin, a complex phenolic macromolecule, is laid down in plant secondary cell walls and is the main component of wood. It is a very important structural molecule in all woody plants, allowing them to achieve height, girth, and longevity. Lignin is also valuable for plant defense: Plant parts containing cells with lignified walls are much less palatable to insects and other animals than are nonwoody plants and are much less easily digested by fungal enzymes than plant parts that contain only cells with primary cellulose walls.

Other phenolics function as attractants. Anthocyanins and anthocyanidins are phenolic pigments that impart pink and purple colors to flowers and fruits. This pigmentation attracts insects and other animals that move between individual plants and accomplish pollination and fruit dispersal. Often the plant pigment and the pollinator's visual systems are well matched: Plants with red flowers attract birds and mammals because these animals possess the correct photoreceptors to see red pigments.

Valerie M. Sponsel

See also: Angiosperm evolution; Animal-plant interactions; Biochemical coevolution in angiosperms; Calvin cycle; Coevolution; Estrogens from plants; Glycolysis and fermentation; Hormones; Krebs cycle; Medicinal plants; Paclitaxel; Pheromones; Pigments in plants; Pollination; Resistance to plant diseases; Rubber.

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MAGILL'S ENCYCLOPEDIA OF SCIENCE

PLANT LIFE

Volume 3

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Microbial Nutrition and Metabolism–Sustainable Agriculture

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PUBLISHER'S NOTE

Magill's Encyclopedia of Science: Plant Life is designed to meet the needs of college and high school students as well as nonspecialists seeking general information about botany and related sciences. The definition of "plant life" is quite broad, covering the range from molecular to macro topics: the basics of cell structure and function, genetic and photosynthetic processes, evolution, systematics and classification, ecology and environmental issues, and those forms of life—archaea, bacteria, algae, and fungi—that, in addition to plants, are traditionally studied in introductory botany courses. A number of practical and issue-oriented topics are covered as well, from agricultural, economic, medicinal, and cultural uses of plants to biomes, plant-related environmental issues, and the flora of major regions of the world. (Readers should note that, although cultural and medicinal uses of plants are occasionally addressed, this encyclopedia is intended for broad information and educational purposes. Those interested in the use of plants to achieve nutritive or medicinal benefits should consult a physician.)

Altogether, the four volumes of *Plant Life* survey 379 topics, alphabetically arranged from *Acid precipitation* to *Zygomycetes*. For this publication, 196 essays have been newly acquired, and 183 essays are previously published essays whose contents were reviewed and deemed important to include as core topics. The latter group originally appeared in the following Salem publications: *Magill's Survey of Science: Life Science* (1991), *Magill's Survey of Science: Life Science, Supplement* (1998), *Natural Resources* (1998), *Encyclopedia of Genetics* (1999), *Encyclopedia of Environmental Issues* (2000), *World Geography* (2001), and *Earth Science* (2001). All of these previously published essays have been thoroughly scrutinized and updated by the set's editors. In addition to updating the text, the editors have added new bibliographies at the ends of all articles.

New appendices, providing essential research tools for students, have been acquired as well:

- a "Biographical List of Botanists" with brief descriptions of the contributions of 134 famous naturalists, botanists, and other plant scientists
- a Plant Classification table
- a Plant Names appendix, alphabetized by common name with scientific equivalents
- another Plant Names appendix, alphabetized by scientific name with common equivalents
- a "Time Line" of advancements in plant science (a discursive textual history is also provided in the encyclopedia-proper)
- a Glossary of 1,160 terms
- a Bibliography, organized by category of research
- a list of authoritative Web sites with their sponsors, URLs, and descriptions

Every essay is signed by the botanist, biologist, or other expert who wrote it; where essays have been revised or updated, the name of the updater appears as well. In the tradition of Magill reference, each essay is offered in a standard format that allows readers to predict the location of core information and to skim for topics of interest: The title of each article lists the topic as it is most likely to be looked up by students; the "Category" line indicates pertinent scientific subdiscipline(s) or area(s) of research; and a capsule "Definition" of the topic follows. Numerous subheads guide the reader

through the text; moreover, key concepts are italicized throughout. These features are designed to help students navigate the text and identify passages of interest in context. At the end of each essay is an annotated list of "Sources for Further Study": print resources, accessible through most libraries, for additional information. (Web sites are reserved for their own appendix at the end of volume 4.) A "See also" section closes every essay and refers readers to related essays in the set, thereby linking topics that, together, form a larger picture. For example, since all components of the plant cell are covered in detail in separate entries (from the *Cell wall* through *Vacuoles*), the "See also" sections for these dozen or so essays list all other essays covering parts of the cell as well as any other topics of interest.

Approximately 150 charts, sidebars, maps, tables, diagrams, graphs, and labeled line drawings offer the essential visual content so important to students of the sciences, illustrating such core concepts as the parts of a plant cell, the replication of DNA, the phases of mitosis and meiosis, the world's most important crops by region, the parts of a flower, major types of inflorescence, or different classifications of fruits and their characteristics. In addition, nearly 200 black-and-white photographs appear throughout the text and are captioned to offer examples of the important phyla of plants, parts of plants, biomes of plants, and processes of plants: from bromeliads to horsetails to wheat; from Arctic tundra to rain forests; from anthers to stems to roots; from carnivorous plants to tropisms.

Reference aids are carefully designed to allow easy access to the information in a variety of modes: The front matter to each of the four volumes includes the volume's contents, followed by a full "Alphabetical List of Contents" (of all the volumes). All four volumes include a "List of Illustrations, Charts, and Tables," alphabetized by key term, to allow readers to locate pages with (for example) a picture of the apparatus used in the *Miller-Urey Experiment*, a chart demonstrating the genetic offspring of *Mendel's Pea Plants*, a map showing the world's major zones of *Desertification*, a cross-section of *Flower Parts*, or a sampling of the many types of *Leaf Margins*. At the end of volume 4 is a "Categorized Index" of the essays, organized by scientific subdiscipline; a "Biographical Index," which provides both a list of famous personages and access to discussions in which they figure prominently; and a comprehensive "Subject Index" including not only the personages but also the core concepts, topics, and terms discussed throughout these volumes.

Reference works such as *Magill's Encyclopedia of Science: Plant Life* would not be possible without the help of experts in botany, ecology, environmental, cellular, biological, and other life sciences; the names of these individuals, along with their academic affiliations, appear in the front matter to volume 1. We are particularly grateful to the project's editor, Bryan Ness, Ph.D., Professor of Biology at Pacific Union College in Angwin, California. Dr. Ness was tireless in helping to ensure thorough, accurate, and up-to-date coverage of the content, which reflects the most current scientific knowledge. He guided the use of commonly accepted terminology when describing plant life processes, helping to make *Magill's Encyclopedia of Science: Plant Life* easy for readers to use for reference to complement the standard biology texts.

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MICROBIAL NUTRITION AND METABOLISM

Categories: Algae; bacteria; fungi; microorganisms; nutrients and nutrition; *Protista*

The diverse metabolic activities of microorganisms make them a critical component of all the earth's ecosystems and a source of many useful products for human industry.

Microorganisms—bacteria, fungi, algae, and protists—are found in every environment on the earth that supports life. Microorganisms have been found in hot springs where temperatures exceed 80 degrees Celsius as well as in rocks of Antarctic deserts. To ensure survival in a variety of habitats, microorganisms have developed a fascinating variety of strategies for survival. The study of microbial ecology involves consideration of the mechanisms employed by microorganisms to obtain nutrients and energy from their environment.

Nutritional Modes

To maintain life processes and grow, all cellular organisms require both a source of carbon (the principal element in all organic molecules) and a source of energy to perform the work necessary to transform carbon into all the molecular components of cytoplasm. Among plants and animals, two main nutritional modes have evolved to meet these requirements. All plants are *photoautotrophs*, fixing carbon from inorganic carbon and obtaining energy from light. All animals are *chemoheterotrophs*, meeting their carbon needs by taking preformed organic molecules from the environment and extracting energy from chemical transformation of the same organic molecules.

Both of these nutritional modes, photoautotrophy and chemoheterotrophy, are found among microorganisms; for example, all algae are photoautotrophs, while all fungi are chemoheterotrophs. In addition, certain specialized bacteria exhibit a mode of nutrition, chemoautotrophy, found in no higher organisms. Like photoautotrophs, chemoautotrophs are able to use carbon dioxide for all of their carbon requirements; however, they do not use light as an energy source. Instead, chemoautotrophic bacteria capture energy from inorganic chemical reactions, such as the *oxidation* of ammonia. Chemoautotrophic bacteria are highly specialized and can be found in unusual environments. The most spectacular display of chemoautotrophic energy metabolism is exhibited at the hydrothermal vents found in certain locations on the ocean floor. There, where sunlight cannot penetrate, chemoautotrophic bacteria serve as the producers for a rich and diverse ecosystem.

An appreciation of the metabolic diversity displayed by microorganisms enhances understanding of the ways in which matter and energy are transformed in the biosphere. Consideration of microbial contributions to the flow of carbon, nitrogen, and other elements is critical to defining the balance of ecosystems and the effects of changes in environmental chemistry and species composition. Microorganisms are, by definition, unseen, and many people become aware of them only in their negative manifestations as agents of disease and spoilage. In fact, however, the diverse metabolic activities of microorganisms make them a critical component of all the earth's ecosystems and a source of many useful products for human industry.

Cellulose Digestion

Even among chemoheterotrophs, microorganisms possess metabolic capabilities unknown in higher organisms. These include the ability of some bacteria and fungi to digest *cellulose*, a linear polymer of glucose that is the principal molecular constituent of paper. Sixty percent of the dry mass of green plants is in the form of cellulose, although no animal that eats the plants is directly able to obtain carbon or energy from cellulose. Microorganisms that digest cellulose do so by secreting *exoenzymes*, proteins that cause cellulose to be broken into simpler molecular units that are absorbed by the microorganism. Cellulose-digesting microorganisms are found in most terrestrial ecosystems and in the digestive tracts of animals, such as cattle and termites, that depend on cellulose-rich plant material as a nutrient source. By breaking down cellulose and other complex organic polymers, microorganisms make a significant contribution to the cycling of carbon in ecosystems.

Nitrogen Fixation

Digestion of complex organic polymers is only one of the ways in which microorganisms contribute to the cycling of elements in the environments they inhabit. Microorganisms also perform chemical transformations involving nitrogen, which is found in all cellular proteins and nucleic acids. Plants incorporate nitrogen from the soil in the form of nitrate or ammonium ions, and animals obtain nitrogen from the same organic compounds they use as carbon and energy sources.

When dead plant and animal tissue is decomposed by chemoheterotrophic microorganisms, the nitrogen is released as ammonia. A group of chemoautotrophic bacteria, the nitrifying bacteria, obtain their metabolic energy from the conversion of ammonia to nitrate; in this way, the *nitrifiers* convert the nitrogen released during decomposition to a form readily used by plants, thus contributing to soil fertility. A second group of bacteria converts nitrate to atmospheric nitrogen gas, which cannot be used by plants; these bacteria are called *denitrifiers* because (in contrast to the nitrifiers) their metabolic activities cause a net loss of nitrogen from the soil.

Nitrogen lost from the environment by denitrification is replaced by ammonia released during decomposition and by the metabolic activity of *nitrogen-fixing bacteria*, so called because they "fix" nitrogen gas from the atmosphere in the form of ammonia. Nitrogen fixation requires a great quantity of energy, and nitrogen-fixing bacteria are often

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found in symbiotic association with plants, especially legumes. The bacteria provide nitrogen in a usable form to the plant, while the plant provides carbon and energy in the form of organic compounds to the chemoheterotrophic nitrogen-fixing bacteria. The presence of nitrogen-fixing bacteria is often indicated by the formation of characteristic nodules on the roots of plants involved in the associations. Free-living nitrogen fixers are also known, and these may play a significant role in the nitrogen balance of aquatic ecosystems.

Respiration and Fermentation

Chemoheterotrophic microorganisms are found both in *aerobic* environments, where oxygen is available, and in *anaerobic* environments, where oxygen is lacking. The availability of molecular oxygen may determine the type of energy metabolism employed by a microorganism. Where oxygen is available, many microorganisms obtain energy by *respiration*. In respiration, electrons removed from organic nutrient sources are transferred through a complex sequence of reactions to molecular oxygen, forming water and carbon dioxide. In the process, energy is made available to the organisms. In the absence of oxygen, some microorganisms are able to carry out a form of anaerobic respiration using nitrate or sulfate in place of oxygen. Denitrification is an example of anaerobic respiration.

Other anaerobic microorganisms employ *fermentation*. In fermentation, electrons removed from organic nutrient sources are transferred to organic molecules, forming fermentation products, such as alcohols and organic acids, which may be used as nutrient sources by other chemoheterotrophs. A number of bacteria, the *facultative anaerobes*, are capable of performing either aerobic respiration or fermentation, depending on the availability of oxygen. These bacteria are able to achieve optimum growth in environments, such as soils, where the availability of oxygen may vary over time.

Effects and Uses

The contributions of microorganisms to the chemical transformations which characterize an ecosystem are many. Along with higher plants, photoautotrophic and chemoautotrophic microorganisms capture inorganic carbon dioxide and, using energy from sunlight or chemical reactions, synthesize organic molecules, which are used by animals and by chemoheterotrophic microorganisms as sources of carbon and energy. Through the processes of respiration and fermentation, chemoheterotrophs return inorganic carbon dioxide to the environment.

Much of this recycling of carbon from organic molecules to carbon dioxide depends on the activities of microbial decomposers, which are able to break down organic polymers, such as cellulose. Nitrogen, released from organic molecules by chemoheterotrophs in the form of ammonia, may be made available to chemoheterotrophs in the form of nitrate by nitrifying bacteria. Nitrate which is lost from an ecosystem through the activities of denitrifiers may be returned by nitrogen-fixing microorganisms.

Although the nature of the microbial world has been known only since about the turn of the twentieth century, the metabolic activities of microorganisms have been exploited throughout human history. The manufacture of alcoholic beverages, cheeses, vinegars, and linen depends on the metabolic activities of microorganisms. Farmers employed practices designed to optimize the availability of nitrogen to plants for centuries before the role of microorganisms in nitrogen cycling was understood. Composting and other decomposition processes, including sewage treatment, are consequences of the metabolic activities of mixed populations of microorganisms.

The number of organic compounds used as nutrients by one or another chemoheterotrophic microorganism is extraordinary. Some soil bacteria have been shown to use more than one hundred different organic molecules as their sources of carbon and energy. By using selective enrichment techniques, it has been possible to isolate microorganisms capable of degrading pesticides, complex petroleum by-products, and other toxic chemicals previously assumed to be resistant to natural decomposition processes. Through application of appropriate engineering technologies, these microorganisms may play a part in solutions to toxic waste disposal issues.

Kenneth A. Pidcock

See also: Algae; Anaerobes and heterotrophs; *Archaea*; Bacteria; Biofertilizers; Biopesticides; Biotechnology; Carbon cycle; Chemotaxis; Fungi; Legumes; Nitrogen cycle; Nitrogen fixation; Nutrients; Phosphorus cycle; Photosynthesis; *Protista*; Respiration.

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MICROBODIES

Categories: Anatomy; cellular biology; transport mechanisms

Microbodies, found in cells, are spherical, membrane-bound organelles that play a part in photorespiration and the conversion of fats into sucrose.

Peroxisomes and *glyoxysomes* are the two major types of microbodies in plant cells. Their *vesicles* ("packages") vary in size from 0.3 to 1.5 micrometers in diameter and are self-replicating. New microbodies are formed by incorporation of required proteins and lipids from the cytoplasm and subsequent splitting when they reach a certain size. Although structurally similar, their roles, and thus their contents, are different.

Functions of Peroxisomes

Peroxisomes are present in leaves, and their oxidative enzymes are involved in the breakdown of hydrogen peroxide and, more important, in photorespiration. Photorespiration occurs when carbon dioxide levels in the leaves drop and oxygen levels increase, a typical phenomenon on hot, sunny days when a plant is experiencing some level of water stress. Under these conditions, the enzyme (Rubisco) that normally catalyzes the attachment of carbon dioxide to ribulose bisphosphate (RuBP) begins to have a higher affinity for oxygen than for carbon dioxide. When oxygen is used instead of carbon dioxide, RuBP is split into two molecules, phosphoglycolate and 3-phosphoglycerate (PGA). PGA can be used in another part of the Calvin cycle, but phosphoglycolate must be extensively processed to be useful.

Phosphoglycolate is hydrolyzed and converted to glycolate in the chloroplast. Glycolate is then transported out of the chloroplast and into nearby peroxisomes. Peroxisomal oxidase converts glycolate to glyoxylate, and hydrogen peroxide is produced as a by-product. Because hydrogen peroxide is toxic, it is quickly converted by a catalase to water and oxygen. Glyoxylate goes through several more steps which involve reactions in the mitochondria and then back again in the peroxisomes. Eventually, glycerate is formed in the peroxisomes. Glycerate is then transported out of the peroxisomes and into a chloroplast, where it is converted to PGA, which can reenter the Calvin cycle.

Functions of Glyoxysomes

Glyoxysomes are found in the cells of fat-rich seeds. Fats are synthesized and stored as *oil bodies*, sometimes called *spherosomes*. Spherosomes are surrounded by a single layer of lipids instead of a lipid bilayer and are therefore not organelles in the strict sense. Glyoxysomes are responsible for converting fats and fatty acids into sucrose. The fat used by glyoxysomes comes from spherosomes.

Glyoxysomes are considered to be a type of peroxisome. In some plants, small glyoxysomes are found in the cotyledons of developing seeds. During germination and seedling development, they mature into fully functional glyoxysomes. They function until the fats are completely digested into sucrose. The energy from sucrose is required to drive early seedling development before photosynthesis begins. Large fat molecules are difficult to transport into the plant embryo; they must be converted to the more mobile sucrose molecules.

Breakdown of fats is a collaborative effort between enzyme-containing glyoxysomes and fat-containing spherosomes. Direct contact between spherosomes and glyoxysomes must occur. Fats from spherosomes leak out close to the membrane of glyoxysomes. Most of the activity of lipase enzymes does not take place in spherosomes but rather in or near the membrane of glyoxysomes. Lipases in glyoxysomes hydrolyze the ester bonds of fats and release the three fatty acids and one glycerol from each fat molecule. Glycerol is converted, at the cost of adenosine triphosphate (ATP), to glycerol phosphate, which is then oxidized by nicotinamide adenine dinucleotide (NAD^+) to dihydroxyacetone phosphate, most of which is converted to glucose.

Domingo M. Jariel

See also: ATP and other energetic molecules; Calvin cycle; Cytosol; Lipids; Membrane structure; Oil bodies; Peroxisomes; Vacuoles; Vesicle-mediated transport.

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MICROSCOPY

Categories: Cellular biology; methods and techniques

In biology and botany, light microscopy is used for the observation of large numbers of cells or for the location of single cells. Scanning electron microscopy is used in the examination of the surface profiles of cells. Transmission electron microscopy is used to probe the interiors of cells to elucidate their structures. The scanning tunneling microscope can be used to examine still smaller structures. Each of the techniques described has been used extensively in the biological sciences.

Light Microscopes

The first microscopes used a beam of light to form an image and were probably invented in the Netherlands, where the devices were used in the manufacture of spectacles and cloth. Dutch microscopist Antoni van Leeuwenhoek (1632-1723) improved upon the cloth merchants' microscopes and used his version to study small objects from nature, such as single-celled organisms and red blood cells. English scientist Robert Hooke (1635-1703), using his own simple microscope, discovered "cells" in a slice of cork.

The human eye by itself is able to resolve images of about 100 micrometers (0.1 millimeter). This means that two objects (such as lines or dots) less than 100 micrometers apart will appear to blur into one object. The highest resolution available in light microscopes will improve upon the human eye five hundred times, allowing it to distinguish objects that are 0.2 micrometer (200 nanometers) apart. Resolution by a light microscope is limited because the shortest wavelength of visible light itself is about 0.4 micrometer (400 nanometers). This limits the effective magnification of a light microscope to about 2,000 times. At this magnification most bacteria are readily visible, as are a variety of organelles within plant cells, such as vacuoles, nuclei (including chromosomes during cell division), chloroplasts, and mitochondria. Smaller structures, such as ribosomes and microtubules (as well as other components of the cytoskeleton), are not visible using a light microscope.

Electron Microscopes

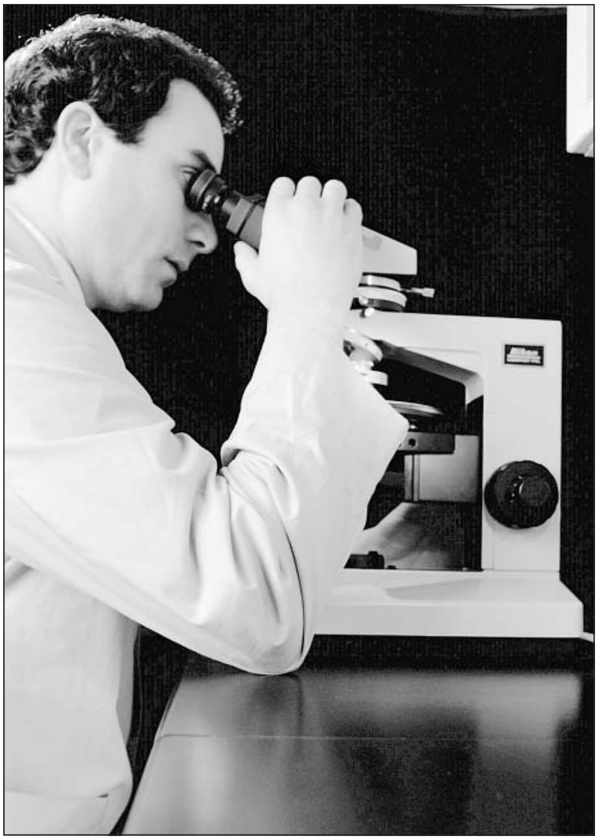
The *electron microscope* was invented in 1931 by Ernst Ruska, who won the Nobel Prize in Physics for this effort in 1986. Since the time of its invention, several different types of electron microscope have been developed. Electron microscopy uses a beam of electrons instead of a beam of light to form an image. Light is a form of *electromagnetic radiation*, a process that transfers energy as a wave without transferring matter. An electromagnetic wave can be visualized in terms of a wave traveling on the surface of a pool of water: The undulating pattern of peaks and troughs constitutes the wave. In the case of electromagnetic radiation, the undulations that constitute the wave occur in electric and magnetic fields that are perpendicular to each other.

Waves and Wavelengths

It is usual to consider light as a wave, or a ray, and to consider electrons as particles. According to quantum physics, however, waves and particles are two aspects of the same phenomenon. Light can be considered as a stream of particles, and a stream of electrons can be considered as a wave. This behavior is usually referred to as wave-particle duality.

One property of a wave is its *wavelength*. The wavelength of a wave is the distance between adjacent peaks (or adjacent troughs) in the waveform. Wavelength is important because when a wave interacts with matter, any structures that are smaller than one-quarter of the wavelength are "invisible" to the wave. In approximate terms, the smallest object that a wave can be used to image is equal in size to the wavelength of the wave used to form the image. The wavelength of visible light is between approximately 400 nanometers and 700 nanometers (a nanometer is one one-billionth of a meter).

A stream of electrons has a smaller wavelength than a beam of light, and electrons can therefore be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The human eye by itself is able to resolve images of about 100 micrometers. This means that two objects (such as dots) less than 100 micrometers apart will appear to blur into one object. The highest resolution available in a light microscope (shown here) will improve upon the human eye five hundred times, allowing it to distinguish objects that are 0.2 micrometer (200 nanometers) apart. The resolving power of a scanning tunneling microscope is sufficient to determine the positions of individual atoms in the surface layer of a material.

used to form images of small objects—such as cells. If distinct images of separate objects are formed, the images are said to be resolved. Because the wavelength of an electron is much smaller than the wavelength of light, the electron microscope can resolve images of objects that are a million times smaller than the objects seen in traditional optical microscopes. The resolving power of a scanning tunneling microscope (STM) is sufficient to render it capable of determining the positions of individual atoms in the surface layer of a material.

There are several different types of electron microscope. The basic types include the transmission electron microscope, the scanning electron microscope, and the scanning tunneling microscope. The specimen in an electron microscope is usually observed in a vacuum in order to prevent scattering of the electrons by air molecules; the need for a vacuum presents the greatest difficulty in the application of electron microscopy to biological systems.

Transmission Electron Microscopes

The simplest electron microscope is the *transmission electron microscope* (TEM). Electrons are produced by an electron gun and are accelerated by a potential difference (voltage). The electrons from the electron gun pass through a condenser lens and are then used to illuminate the specimen. The electrons which pass through the specimen are then allowed to pass through an electron lens objective. The objective magnifies the image, and then a second electron lens, which plays the role of the eyepiece in the standard microscope, is used to focus the image for observation. The "lenses" used in electron microscopes are not lenses in the usual sense; instead, they are electric and magnetic fields, and they are accordingly referred to as electrostatic or magnetic lenses.

The image can then be formed on a photographic plate or observed on a fluorescent screen, or the electrons can be collected by a charge-sensitive device to produce an image on a cathode-ray tube. Higher magnification can be achieved by using more lenses.

The sample thickness will affect the resolving ability of the TEM. Usually, at least in the case of biological samples, the sample should be no more than ten times thicker than the structures that are to be analyzed. The resolving power of the TEM is such that it can observe structures that are slightly larger than atoms, but since the development of other systems, it has become less used, even though its resolution often exceeds that of the scanning electron microscope. Typical resolutions are in the subnanometer range, with magnifications of up to 500,000 times.

The interpretation of the electron micrographs produced by a TEM is sometimes difficult. The major source of difficulty is that the image is produced by transmitted radiation. The eye is accustomed to interpreting images that are produced by reflection. In the absence of a sample, a TEM beam would saturate a film plate used to record an image. The sample prevents some of the electrons from reaching the film plate; the image produced by a TEM is somewhat similar to a negative produced in a normal camera. Much of the difficulty can be removed by photographing the micrograph and converting it to a positive image—there are, however, some residual interpretation difficulties caused by shadows.

High-Voltage and Scanning Electron Microscopes

The *high-voltage electron microscope* (HVEM) is a variant of the TEM. The conventional TEM works best on particles less than 0.5 nanometer thick; electrons of higher speed can be produced by increasing the voltage used to accelerate them, and thicker samples can then be analyzed. The wavelength of the electrons decreases as their speed (hence, their kinetic energy) increases. These short-wavelength electrons are less likely to collide with atoms as they pass through the specimen, and they are therefore able to render a sharper image of a thicker sample.

The *scanning electron micrscope* (SEM) works on a different principle. Electrons are again produced and accelerated by an electron gun, but in an SEM the beam is focused by electron lenses and used to scan a sample. The scanning will result in two different electron beams being emitted by the sample, a primary beam of backscattered electrons produced by reflection and a secondary beam of electrons emitted by the atoms of the sample. By scanning the entire sample and collecting the primary and secondary electrons, the operator can produce an image of a sample on a cathode-ray tube.

Scanning Tunneling Electron Microscopes

The *scanning tunneling electron microscope* (STM) works on a completely different principle. It was developed by Gerd Binnig and Heinrich Rohrer at an International Business Machines (IBM) research laboratory in the 1980's. Binnig and Rohrer shared the 1986 Nobel Prize in Physics with Ernst Ruska for their work. The STM uses *quantum tunneling*. Quantum tunneling is the penetration of a barrier by a particle that, when analyzed by classical physics, does not have enough energy to pass through the barrier. Quantum mechanics predicts that there is a finite probability of a particle passing through a barrier, even if it lacks the energy to pass over it. The number of particles passing through the barrier will vary with the barrier thickness and the particle energy.

This principle is used in the STM by allowing electrons to tunnel across a vacuum, from a stylus to a sample. The quantum tunneling of electrons sets up a "tunneling current" that increases as the vacuum gap between the stylus and the sample decreases. The variation in tunneling current can be used to map the surface of the sample as the stylus moves across its surface. The STM is capable of detecting structures 0.1 nanometer in size in the direction parallel to the motion of the scanning stylus. This means that atoms can be easily detected. The performance in the vertical direction is even more impressive: The STM can detect irregularities on the order of 0.01 nanometer. Thus, the STM, with its higher resolving power than the SEM or TEM, has little difficulty in the imaging of atoms.

Preparing Samples

The principal accommodations that must be made in the examination of biological samples using electron microscopy occur in the preparation of the sample. A commonly used method is the construction of replicas, made by the vacuum deposition of thin layers of carbon, metals, or alloys on the surface of the sample. These films provide a replica of the surface, which can be scanned. Another useful technique, which is the standard technique of sample preparation used in optical microscopy, is the sectioning of samples and their impregnation with stains. The stains that are useful in electron microscopy are usually chemical compounds of heavy metals. These are effective stains because they strongly scatter electrons.

Many methods of sample preparation have been developed to enable electron microscopy to be more widely used on biological samples. *Freeze-fracture* and *freeze-etch* are methods of sample preparation that have been widely used. Freeze-fracture involves the freezing and splitting of a water-containing sample. Freeze-etch is a second step, in which ice is allowed to sublime (vaporize without forming a liquid) before the sample is analyzed in an electron microscope. Both techniques are used to examine the internal structure of materials without subjecting them to chemical changes. Freeze-fracture and freeze-etch allow the interior layers of water-containing samples to be investigated without the straining and chemical preparations that are needed to render internal structures visible in a standard light microscope. In particular, these techniques allow the observation of cell walls and cell membranes in a state which is as close as possible to the living state.

Uses

While light microscopy remains important in the identification, location, and observation of cells both singly and in groups, the electron microscope has revolutionized scientists' understanding of the microscopic world in the biological, medical, and physical sciences. Although it is not possible to observe living materials using electron microscopy, freeze-fracture and freeze-etch have allowed the observation of biological materials in an almost natural state. *Correlative microscopy*, an increasingly popular method, involves the examination of a sample using both light microscopy and electron microscopy; this method allows the acquisition of a variety of views of the same structure, and it removes the ambiguities that may result from views produced by a single microscope.

The transmission electron microscope (TEM) was the first electron microscope to be developed, and it is the most common type. The TEM has more in common with light microscopes than it does with any other electron microscope. It also shares the chief disadvantage of the optical microscope—that is, it gives little impression of the vertical scale of the specimen under observation. This means that the structures present in the specimen are imaged, but the subtleties of the surface of the specimen are lost. Furthermore, the TEM imposes severe constraints on the type of specimens which can be analyzed. The sample must be thin enough to permit the beam of electrons to pass through it, and it must be resilient enough to resist being damaged by the imaging electrons.

Most biological materials are too thick to be observed under the TEM, so it is necessary to prepare *ultra-thin sections* of samples prior to their analysis. Both plant and animal samples have been examined using the TEM, and their analysis has led to the discovery of a variety of internal structures. The internal structure of the mitochondria, which had previously been discovered with light microscopy, has been probed. The TEM has also been used to examine the interiors of the nuclei of cells. The examination of the cell nuclei has enabled the investigation of chromosome organization and gene structure. This examination of the microstructure of cells has contributed to the development of molecular biology and genetic engineering.

The TEM has also been used to examine bacteria and viruses. The TEM detected the presence of nucleic acids in bacteria and produced the first images of viruses; most viruses are too small to be resolved in light microscopes. In plants, the TEM has been used in the study of chloroplasts and the walls of cells. The observation of chloroplasts led to the discovery of the internal membranes called *thylakoids*, which absorb light for the process of photosynthesis. The discovery of the thylakoids has enhanced the understanding of photosynthesis.

The scanning electron microscope (SEM) has been widely used in the biological sciences. Physical laws impose no constraints on the size of the sample to be examined—they are, instead, imposed by the available sample chambers. The SEM is usually used in the magnification range of 10 to 100,000 times. When compared with the light microscope, the main advantage of the SEM is that it is able to produce three-dimensional images. These images are possible because the entire sample can be observed in focus at the same time, and the sample can be observed from a variety of angles.

The SEM has allowed images to be formed of algae, bacteria, spores, molds, and fungi. These images have enabled the structure and function of these samples to be determined. The xylem and phloem cells that transport water through the stems of plants have been examined in the SEM, thus allowing the water transportation process to be better understood. The SEM also has applications in exploring the pathology of cells. Many structures formed by living cells are better understood because sample preparation techniques such as freeze-fracture and freeze-etch have allowed the examination of lifelike samples under the SEM.

Stephen R. Addison, updated by Bryan Ness

See also: Cell theory; Fluorescent staining of cytoskeletal elements.

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MITOCHONDRIA

Categories: Anatomy; cellular biology

An organelle of eukaryotic cells, a mitochondrion is bounded by a double membrane. It is the major source of adenosine triphosphate (ATP), which is derived from the breakdown of organic molecules and contains the enzymes used in the Krebs cycle and the electron transport system.

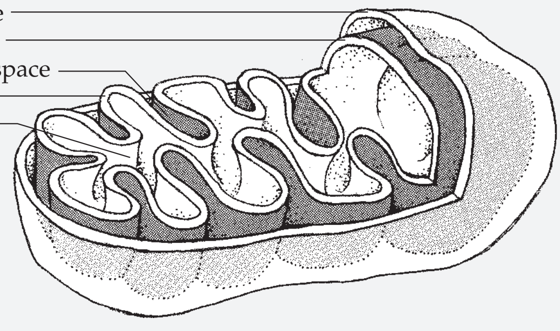
With the exception of a few metabolically inert types, such as the red blood cells of many higher animals, eukaryotic cells of animals, plants, fungi, and protozoa contain mitochondria. Most cells contain several hundred. The efficiency of mitochondria in *adenosine triphosphate* (ATP) production provides the energy source that powers all the varied activities of eukaryotic cells. For these reasons, mitochondria have been aptly termed the "powerhouses" of the cell.

Structure

In most cells, mitochondria appear as spherical, elongated bodies about 0.5 micrometer in diameter and 1 to 2 micrometers in length. Their size is roughly the same as that of bacterial cells. In some cells mitochondria may measure several micrometers in diameter, with lengths up to 10 micrometers. The name "mitochondrion" comes from Greek words meaning "thread" (*mitos*) and "granule" (*chondros*). Mitochondria appear in either elongated, threadlike forms or more spherical, granular shapes. Under the light microscope, mitochondria can be seen to grow, branch, divide, and fuse together.

Mitochondria are surrounded by two separate membranes. The outer membrane is a continuous, unbroken membrane that completely covers the surface of the organelle. It is smooth in appearance. The inner membrane is also continuous and unbroken. It is convoluted, with infoldings called *cristae* that greatly increase its surface area.

Structure of a Mitochondrion



Mitochondria are special cellular organelles where respiration—the release of energy from organic molecules as ATP—occurs. Mitochondria are surrounded by two separate membranes. The outer membrane is a continuous, unbroken membrane that completely covers the surface of the organelle. The inner membrane is also continuous and unbroken but is convoluted, with infoldings called cristae that greatly increase the inner membrane's surface area.

The outer and inner membranes separate the mitochondrial interior into two distinct compartments. The *intermembrane space* is located between the outer and inner membranes. The innermost compartment, enclosed by both membranes, is the *mitochondrial matrix*. Each membrane and compartment carries out specific functions important to the production of ATP.

The outer membrane is more permeable than the inner membrane and allows molecules up to the size of small proteins to pass freely from the surrounding cytoplasm into the intermembrane space. Larger proteins are prevented from escaping into the surrounding cytoplasm, and certain cytoplasmic proteins, such as potentially destructive enzymes, are prevented from entering.

Electron Transport

The innermost compartment, the matrix, contains a battery of enzymes that catalyze the *oxidation* of fuel substances of many types, including simple sugars, fats, amino acids, and other organic acids. The primary goal of oxidation is the removal of high-energy electrons and the use of them to perform chemical work.

High-energy electrons are used in the membrane that immediately surrounds the matrix, the inner membrane. This membrane contains a group of proteins that work as electron-driven protons (hydrogen ions or H^+) pumps. The proteins, called *electron transport carriers*, accept electrons at a higher energy level and release them at a lower level. The energy released by the electrons causes the shape of the carrier proteins to change, which allows them to transport protons across the inner membrane. The various electron transport carriers accept and release electrons at different energy levels, allowing them to act in a series called the *electron transport chain*. The electrons released by one carrier have sufficient energy to power the pumping activity of the next one in line. When operating at peak efficiency, a mitochondrion of average size conducts about 100,000 electrons through the electron transport chain per second. After passing through several carriers, most of the energy of the electrons has been tapped off.

As a consequence of proton pumping, protons become depleted in the matrix and become more concentrated in the intermembrane space. This creates an *electrochemical gradient* between the intermembrane space and the matrix. It is called an electrochemical gradient because there is a concentration gradient across the inner membrane and because protons have an electrical charge, so there is also an *electrical potential* (a charge difference) across the membrane. Electrochemical gradients represent a form of stored energy capable of doing work and in this case is used to drive the synthesis of ATP.

At the very end of the electron transport chain, the electrons have so little energy that the last carrier molecule donates these low-energy electrons to oxygen that is already in the matrix. The oxygen eukaryotes need to survive thus has its primary biological role as the final acceptor of spent electrons released by the electron transport chain. When an oxygen molecule receives four electrons, it then picks up two protons from the matrix, and water (H_2O) is produced. The protons used in this process cause an additional reduction in proton concentration in the matrix, increasing the electrochemical gradient across the inner membrane.

ATP Synthesis

A protein complex embedded in the inner membrane uses the proton gradient to make ATP. This complex, called *ATP synthase*, is a molecular "machine" that acts as a hydrogen-driven ATP synthesizer. It takes ADP (adenosine diphosphate) from the matrix and combines it with inorganic phosphate (P_i) to make ATP.

The proteins of the inner mitochondrial membrane thus work in two coordinated groups. One, the electron transport chain, uses the energy of electrons removed in oxidative reactions to pump protons hydrogens from the matrix to the intermembrane space. The second group, the ATP synthases, uses the proton gradient created by the electron transport chain as an energy source to make ATP from ADP and P_i. ADP comes from the matrix itself and from other regions of the cell in which ATP is used to facilitate cellular activities such as growth and movement. Much of the ATP produced in this way is then transported out of the mitochondria for use in other parts of the cell.

mRNA and DNA

When examined with an electron microscope, a number of structures are visible in mitochondrial matrix, including granules of various sizes, fibrils, and crystals. Among the granules are *ribosomes*. These structures, like their counterparts in the cytoplasm, are capable of protein assembly, using directions encoded in *messenger ribonucleic acid* (mRNA) molecules as a guide. The mitochondrial ribosomes are more closely related in structure and function to prokaryotic ribosomes than to ribosomes in the cytoplasm.

Also in the mitochondrial matrix are molecules of *deoxyribonucleic acid* (DNA). *Mitochondrial DNA* (mtDNA) stores the information required for synthesis of some of the proteins needed for mitochondrial functions. Unlike nuclear DNA, which is linear, mtDNA is circular, like bacterial DNA. The presence of bacterialike DNA and ribosomes inside mitochondria has given rise to the *endosymbiotic theory*, which proposes that mitochondria may have evolved from bacteria that invaded the cytoplasm of other prokaryotic cells and established a symbiotic relationship. Over long periods of time, these bacteria are believed to have lost their ability to live independently and gradually became transformed into mitochondria. The evolutionary advantage to the host provided by the bacterial invaders may have been greater efficiency in ATP production.

Stephen L. Wolfe, updated by Bryan Ness

See also: ATP and other energetic molecules; Chloroplast DNA; Chloroplasts and other plastids; Cytoplasm; DNA in plants; DNA replication; Extranuclear inheritance; Krebs cycle; Membrane structure; Mitochondrial DNA; Oxidative phosphorylation; RNA.

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MITOCHONDRIAL DNA

Categories: Cellular biology; genetics

Plant cells have three sets of DNA to code for proteins: one set in the chromosomes of the nucleus, another in the chloroplasts, and a third genome in mitochondria. The mitochondrial genomes of higher plants are larger than those of animals and form a complex series of linear and circular molecules of different sizes.

Mitochondria play an essential role in the generation of energy in eukaryotic cells. Mitochondria are the organelles that are the main "chemical factories" of the cell where cellular aerobic respiration—using the Krebs (citric acid) cycle and respiratory electron transport to produce NADH (nicotinamide adenine dinucleotide) and ATP (adenosine triphosphate)—occurs. In the light microscope, mitochondria look like short rods or thin filaments about 0.5 to 2 microns long. A mitochondrion is made up of a smooth outer membrane and an inner membrane that is folded into tubular shapes called cristae. Many aerobic respiration reactions are catalyzed by enzymes that are bound to mitochondrial membranes. Other reactions occur in the space between the inner and outer mitochondrial membranes. Cells may contain several hundred mitochondria. Cells that are dividing and cells that are metabolically active need larger amounts of ATP and usually have large numbers of mitochondria.

Size and Structure

All eukaryotic cells except some primitive protozoans contain mitochondria. All mitochondria contain their own DNA (genomes). There are typically between twenty and one hundred copies of the mitochondrial genome per mitochondrion. The mitochondria of multicellular animals contain genomes of 14 to 20 kilobases (kb), present as single circles. The mitochondrial DNA of some organisms, such as some protozoa, algae, and fungi, is organized in linear molecules with ends of chromosomes (telomeres) much like nuclear chromosomes.

In contrast, the mitochondrial DNA of higher plants is larger and more complex—from 200 to 2,500 kb—and is present in many different molecules. The size and organization of the mitochondrial genome vary widely from one plant species to another. Electron micrographs of mitochondrial DNA show linear and circular DNAs of a variety of sizes and complex, branched molecules that are larger than the size of the genome.

Cloning the mitochondrial DNA and comparing the sequences of the clones show that the entire complexity of a plant mitochondrial genome can be represented as a "master circle." Also, it has been learned that sequences are repeated on the master chromosome. The repeated sequences differ for different plant species. A series of recombination events between these identical repeated sequences results in a series of rearrangements of mitochondrial DNA and forms the complex, multiple molecules of varying sizes that are the physical structure of the plant mitochondrial genome.

Adding to the complexity of mitochondrial DNAs in higher plants is the fact that some plants, such as corn, contain extrachromosomal mitochondrial nucleic acids. Plasmid-like DNAs (circular double-stranded molecules) and double-stranded and single-stranded RNAs have been found in some corn strains.

Genes Encoded by Mitochondrial DNA

In addition to containing their own genomes, mitochondria contain enzymes for DNA replication and transcription, and ribosomes and transfer RNAs for protein synthesis. (Transfer RNA, or tRNA, carries the building blocks of proteins, called amino acids, to the ribosome, where they are assembled according to the instructions found in messenger RNA.) The ribosomes of mitochondria are different from those of chloroplasts and the cytoplasm, using a slightly different genetic code (a sequence of three bases that codes for a particular amino acid). Mitochondrial genomes code for all of the ribosomal RNAs found in mitochondria and for most of the tRNAs. Mitochondria make only a small number of proteins that are needed for electron transport and ATP production. The other proteins needed in mitochondria are coded by nuclear DNA, translated in the cytoplasm of the cell, then transported into the mitochondria. Plant mitochondria do not encode a full set of tRNAs, and some are imported from the cytoplasm.

Even though the mitochondrial genome of higher plants is much larger than that of animals, the plant mitochondrial genome codes for only a few more genes. The mitochondrial genome of *Arabidopsis* has been sequenced and contains thirty-two protein-coding genes, twenty-two tRNA genes, and three ribosomal RNA genes.

Exchange of DNA

Mitochondrial DNA from plants also differs from that of animals in that mitochondrial DNAs contain segments of DNA that originally were in nuclear and chloroplast DNAs. There appear to have been exchanges of DNAs between all three of the higher plant genomes. There is evidence that mitochondrial genes have been transferred to the nucleus and some mitochondrial tRNAs appear to be of chloroplast origin. Changes in nuclear genes have been shown to lead to changes in the copy number of the different mitochondrial DNA configurations.

RNA Editing

Mitochondria and chloroplasts contain the biochemical machinery to alter the sequence of the final messenger RNA (mRNA) product in a process called *RNA editing*. The most common editing is changing a cytosine to a uracil (two of the bases found on the "rungs" of DNA molecules and which are responsible for determining the nucleotide sequences that form the genetic code).

Inheritance of Mitochondrial DNA

Given the complex branched network of plant mitochondrial DNA, it is difficult to see how the inheritance of a complete genome is ensured. It is still not clearly understood how this complex network of DNAs is passed to daughter cells in a way that assures that all of the genetic information is maintained.

Susan J. Karcher

See also: Chloroplast DNA; Chloroplasts and other plastids; Chromosomes; Cytoplasm; DNA in plants; DNA replication; Extranuclear Inheritance; Gene regulation; Genetic code; Genetics: post-Mendelian; Mitochondria; Nucleus; Oxidative phosphorylation; RNA.

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MITOSIS AND MEIOSIS

Categories: Cellular biology; reproduction

Mitosis is the process of cell division in multicellular eukaryotic organisms. Meiosis is the process of cell division that produces haploid gametes in sexually reproducing eukaryotic organisms.

Organisms must be able to grow and reproduce. Prokaryotes, such as bacteria, duplicate deoxyribonucleic acid (DNA) and divide by splitting in two, a process called *binary fission*. Cells of eukaryotes, including those of animals, plants, fungi, and protists, divide by one of two methods: mitosis or meiosis. Mitosis produces two cells, called *daughter cells*, with the same number of chromosomes as the parent cell, and is used to produce new somatic (body) cells in multicellular eukaryotes or new individuals in single-celled eukaryotes. In sexually reproducing organisms, cells that produce gametes (eggs or sperm) divide by meiosis, producing four cells, each with half the number of chromosomes possessed by the parent cell.

Chromosome Replication

All eukaryotic organisms are composed of cells containing *chromosomes* in the nucleus. Chromosomes are made of DNA and proteins. Most cells have two complete sets of chromosomes, which occur in pairs. The two chromosomes that make up a pair are homologous, and contain all the same *loci* (genes controlling the production of a specific type of product). These chromosome pairs are usually referred to as *homologous pairs*. An individual chromosome from a homologous pair is sometimes called a *homolog*. For example, typical lily cells contain twelve pairs of homologous chromosomes, for a total of twenty-four chromosomes. Cells that have two homologous chromosomes of each type are called *diploid*. Some cells, such as eggs and sperm, contain half the normal number of chromosomes (only one of each homolog) and are called *haploid*. Lily egg and sperm cells each contain twelve chromosomes.

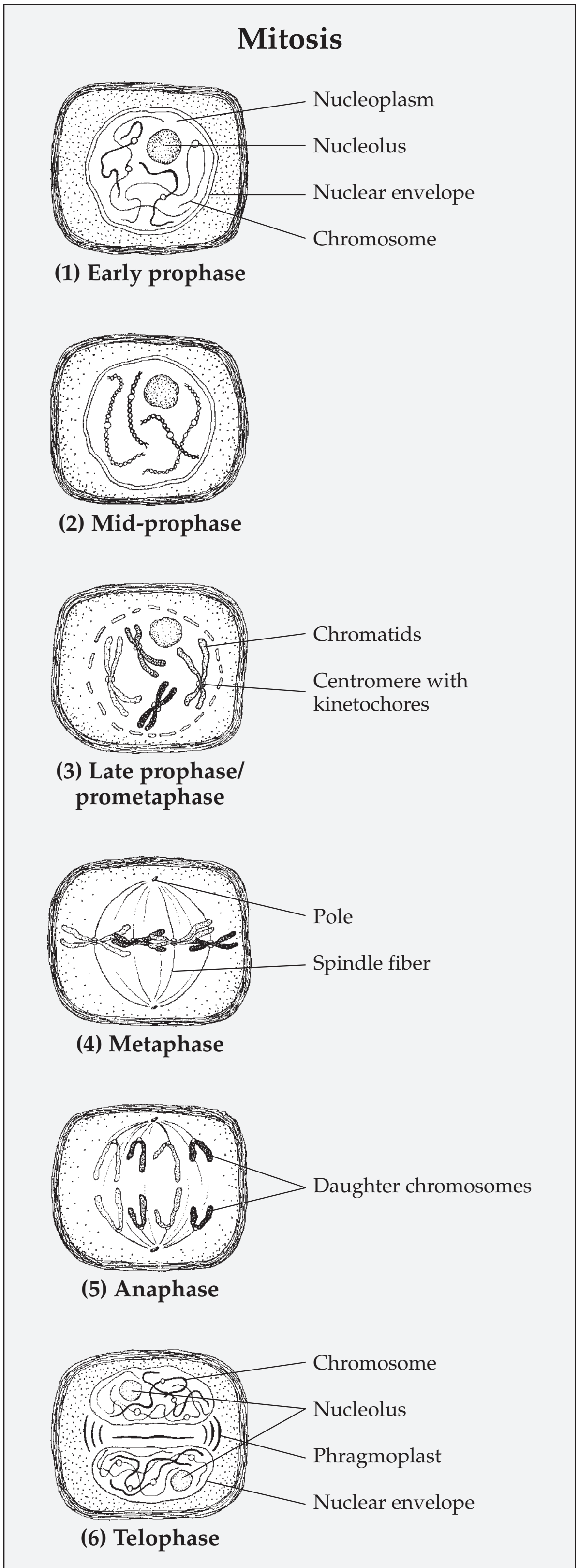
DNA must replicate before mitosis or meiosis can occur. If daughter cells are to receive a full set of genetic information, a duplicate copy of DNA must be available. Before DNA replication occurs, each chromosome consists of a single long strand of DNA called a *chromatid*. After DNA replication, each chromosome consists of two chromatids, called sister chromatids. The original chromatid acts as a template for making the second chromatid; the two are therefore identical. Sister chromatids are attached at a special region of the chromosome called the *centromere*. When mitosis or meiosis starts, each chromosome in the cell consists of two sister chromatids.

Mitosis and meiosis produce daughter cells with different characteristics. When a diploid cell undergoes mitosis, two identical diploid daughter cells are produced. When a diploid cell undergoes meiosis, four unique haploid daughter cells are produced. It is important for gametes to be haploid, so that when an egg and sperm fuse, the diploid condition of the mature organism is restored.

Cellular Life Cycles

Mitosis and meiosis occur in the nuclear region of the cell, where all the cell's chromosomes are found. *Nuclear control mechanisms* begin cell division at the appropriate time. Some cells rarely divide by mitosis in adult organisms, while other cells divide constantly, replacing old cells with new. Meiosis occurs in the nuclei of cells that produce gametes. These specialized cells occur in reproductive organs, such as flower parts in higher plants.

Cells, like organisms, are governed by life cycles. The life cycle of a cell is called the *cell cycle*. Cells spend most of their time in *interphase*. Interphase is divided into three stages: *first gap* (G_1), *synthesis* (S), and *second gap* (G_2). During G_1, the cell performs its normal functions and often grows in size. During the S stage, DNA replicates in preparation for cell division. During the G_2 stage, the cell makes materials needed to produce the mitotic apparatus and for division of the cytoplasmic components of the cell.



Kimberly L. Dawson Kurnizki

At the end of interphase, the cell is ready to divide. Although each chromosome now consists of two sister chromatids, this is not apparent when viewed through a microscope. This is because all the chromosomes are in a highly relaxed state and simply appear as a diffuse material called *chromatin*.

Mitosis

Mitosis consists of five stages: *prophase*, *prometaphase*, *metaphase*, *anaphase*, and *telophase*. Although certain events identify each stage, mitosis is a continuous process, and each stage gradually passes into the next. Identification of the precise state is therefore difficult at times.

During prophase, the chromatin becomes more tightly coiled and condenses into chromosomes that are clearly visible under a microscope, the *nucleolus* disappears, and the *spindle apparatus* begins to form in the cytoplasm. In prometaphase, the nuclear envelope breaks down, and the spindle apparatus is now able to invade the nuclear region. Some of the spindle fibers attach themselves to a region near the centromere of each chromosome called the *kinetochore*. The spindle apparatus is the most obvious structure of the mitotic apparatus. The nuclear region of the cell has opposite poles, like the North and South Poles of the earth. Spindle fibers reach from pole to pole, penetrating the entire nuclear region.

During metaphase, the cell's chromosomes align in a region called the *metaphase plate*, with the sister chromatids oriented toward opposite poles. The metaphase plate traverses the cell, much like the equator passes through the center of the earth. Sister chromatids separate during anaphase. The sister chromatids of each chromosome split apart, and the spindle fibers pull each sister chromatid (now a separate chromosome) from each pair toward opposite poles, much as a rope-tow pulls a skier up a mountain. Telophase begins as sister chromatids reach opposite poles. Once the chromatids have reached opposite poles, the spindle apparatus falls apart, and the nuclear membrane re-forms. Mitosis is complete.

Meiosis

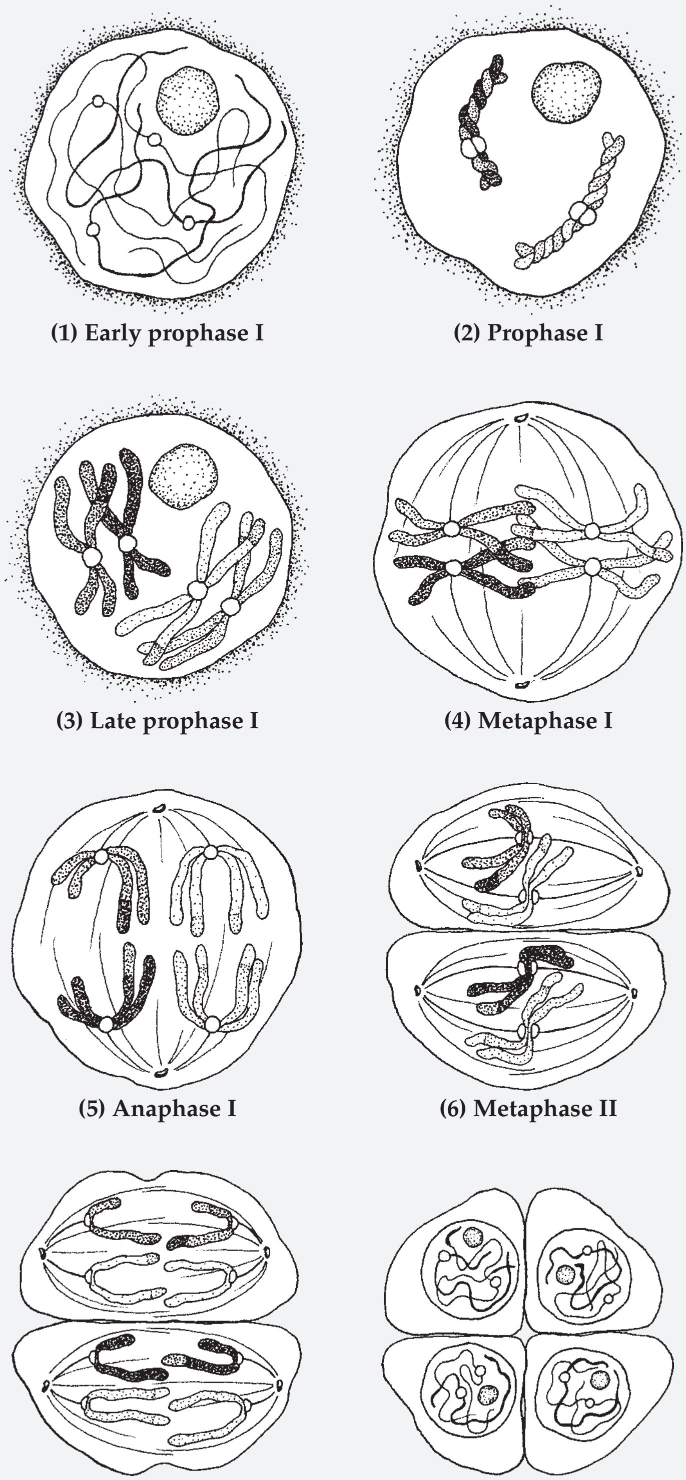
Meiosis is a more complex process than mitosis and is divided into two major stages: *meiosis I* and *meiosis II*. As in mitosis, interphase precedes meiosis. Meiosis I consists of prophase I, metaphase I, anaphase I, and telophase I. Meiosis II consists of prophase II, metaphase II, anaphase II, and telophase II. In some cells, an interphase II occurs between meiosis I and meiosis II, but no DNA replication occurs.

During prophase I, the chromosomes condense, the nuclear envelop falls apart, and the spindle apparatus begins to form. Homologous chromosomes come together to form *tetrads* (a tetrad consists of four chromatids, two sister chromatids for each chromosome). The arms of the sister chromatids of one homolog touch the arms of sister chromatids of the other homolog, the contact points being called *chiasmata*. Each chiasma represents a place where the arms have the same loci, so-called homologous regions. During this intimate contact, the chromosomes undergo *crossover*, in which the chromosomes break at the chiasmata and swap homologous pieces. This process results in *recombination* (the shuffling of linked *alleles*, the different forms of genes, into new combinations), which results in increased variability in the offspring and the appearance of character combinations not present in either parent.

Tetrads align on the metaphase plate during metaphase I, and one spindle fiber attaches to the kinetochore of each chromosome. In anaphase I, instead of the sister chromatids separating, they remain attached at their centromeres, and the homologous chromosomes separate, each homolog from a tetrad moving toward opposite poles. Telophase I begins as the homologs reach opposite poles, and similar to telophase of mitosis, the spindle apparatus falls apart, and a nuclear envelope re-forms around each of the two haploid nuclei. Because the number of chromosomes in each of the telophase I nucleus is half the number in the parent nucleus, meiosis I is sometimes called the reduction division.

Meiosis II is essentially the same as mitosis, dividing the two haploid nuclei formed in meiosis I. Prophase II, metaphase II, anaphase II, and telo-

Meiosis: Selected Phases



(1) Early prophase I | (2) Prophase I | (3) Late prophase I | (4) Metaphase I | (5) Anaphase I | (6) Metaphase II | (7) Anaphase II | (8) Late telophase II

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phase II are essentially identical to the stages of mitosis. Meiosis II begins with two haploid cells and ends with four haploid daughter cells.

Nuclear Division and Cytokinesis

Mitosis and meiosis result in the division of the nucleus. Nuclear division is nearly always coordinated with division of the cytoplasm. Cleaving of the cytoplasm to form new cells is called *cytokinesis*. Cytokinesis begins toward the middle or end of nuclear division and involves not just the division of the cytoplasm but also the organelles. In plants, after nuclear division ends, a new cell wall must be formed between the daughter nuclei. The new cell wall begins when vesicles filled with cell wall material congregate where the metaphase plate was located, producing a structure called the *cell plate*. When the cell plate is fully formed, cytokinesis is complete. Following cytokinesis, the cell returns to interphase. Mitotic daughter cells enlarge, reproduce organelles, and resume regular activities. Following meiosis, gametes may be modified or transported in the reproductive system.

Alternation of Generations

Meiotic daughter cells continue development only if they fuse during fertilization. Mitosis and meiosis alternate during the life cycles of sexually reproducing organisms. The life-cycle stage following mitosis is diploid, and the stage following meiosis is haploid. This process is called *alternation of generations*. In plants, the diploid state is referred to as the *sporophyte generation*, and the haploid stage as the *gametophyte generation*. In nonvascular plants, the gametophyte generation dominates the life cycle. In other words, the plants normally seen on the forest floor are made of haploid cells. The sporophytes, which have diploid cells, are small and attached to the body of the gametophyte. In vascular plants, sporophytes are the large, multicellular individuals (such as trees and ferns), whereas gametophytes are very small and either are embedded in the sporophyte or are free-living, as are ferns. The genetic variation introduced by sexual reproduction has a significant impact on the ability of species to survive and adapt to the environment. Alternation of generations allows sexual reproduction to occur, without changing the chromosome number characterizing the species.

Joyce A. Corban and Randy Moore

See also: Cell cycle; Chromosomes; DNA replication; Gene regulation; Genetic equilibrium: linkage; Genetics: Mendelian; Genetics: mutations; Genetics: post-Mendelian; RNA.

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MITOSPORIC FUNGI

Categories: Fungi; microorganisms; taxonomic groups

Mitosporic fungi—also known as Deuteromycota, Deuteromycotina, *fungi imperfecti, and deuteromycetes—are fungi that are unable to produce sexual spores and are therefore placed in a separate phylum.*

The term "mitosporic" is a combination of the words "mitosis" and "sporic." Mitosis is the process of asexual cell division, which results in the daughter cells having the same genetic makeup as the mother cell. "Sporic" is used to denote the creation of spores. Therefore, the fungi in *Deuteromycota* do not produce sexual spores. The groupings in this phylum are artificial.

Conidium

The asexual spore produced by mitosporic fungi is the *conidium*. Conidia are produced from cells called condiogenic cells without the combination of nuclei; therefore the conidia are a product of mitosis. The conidial phase is a repetitive one. Thousands of conidia can be produced under adequate environmental conditions. These conidia will then continue the repetitive cycle.

Parasexuality

The genetic content of most fungi is dikaryotic. Each fungal cell has two individual and genetically distinct haploid nuclei. This state is originally formed by the combination of haploid mycelia. During *parasexuality*, the formation of diploid nuclei occurs, and then these revert back to the haploid state. Parasexuality permits the exchange of genetic information between the two haploid nuclei. The resultant haploid nuclei may be genetically modified. This is of great importance with plant pathogens, as parasexuality may help reduce genetic resistance of the host. Parasexuality is not considered to be a meiotic state, as no resultant sexual structure (such as an ascus or basidium) is formed.

Teleomorphs vs. Anamorphs

The *teleomorph* is the form of a fungus that occurs when sexual reproduction has occurred. These forms are found in the *Ascomycota* and the *Basidiomycota*. The *anamorph* is the form of a fungus that occurs when no sexual recombination has occurred. Anamorphs are important, as they are often a repetitive phase of the fungus and are able to produce spores without the additional requirement of sexual recombination.

When a specific teleomorph has been identified by scientists, the anamorphic phase is referred to as a subset of the teleomorph. For example, the anamorph fungus that produces blight of rice is known as *Pyricularia oryzae*. The teleomorph of this fungus is know as *Magnaporthe grisea*. The proper name for the anamorph is then the *Pyricularia anamorph* (or state) of *Magnaporthe grisea*.

Classification

Classification of the fungi in this group is based on the presence of conidia, kind of conidia (shape, color, size), and whether or not the conidia are produced in fungal structures called *conidiomata*. Conidiomata may have the generalized shape of a flask made of fungal tissue (a pycnidium); a pin cushion (sporodochium); or a mass of conidiophores located under either the epidermis or cuticle of a plant host (aecervulus).

There are three classes in this grouping. The *hyphomycetes* contain the fungi that produce conidia and conidiophores on hyphae or groups of hyphae. The *agonomycetes* do not produce conidia. The *coelomycetes* contain the fungi that produce conidia in distinct conidiomata.

Classification is dependent on the fungus meeting the following requirements. First, there must be the absence or presumed absence of the teleomorph. Second, there may be the absence or presumed absence of any meiotic or mitotic reproductive structure (as in agonomycetes). Finally, there may be the production of conidia from mitosis. There must not be any sexual structures.

Challenges

One of the challenges of the classification of mitosporic fungi is that these are form-genera of fungi that include both fungi that do not have teleomorphic states and fungi that do. For example, the teleomorph genus *Cochliobolus* has anamorphs in both the anamorphic form-genera *Bipolaris* and *Curvularia*. At the same time, there are several form-species in both anamorphic genera *Bipolaris* and *Curvularia* that have no teleomorph stage.

The reason the teleomorph can be found in some species and not in others is not known. Some isolates of anamorph species are distinct mating types and can be crossed with the other distinct mating type. When distinct mating types occur, it is possible that over time the mating types could be separated or that one mating type could be destroyed. Over time, without having the pressure to sexually reproduce, it is possible that the ability to sexually reproduce may have declined. Also, it is possible that the proper environmental conditions for sexual reproduction may not be known. Whether these fungi are best covered in the form-phylum mitosporic fungi or the form-phylum *Deuteromycota* is a question that will continue to be discussed. Because only fungi that form sexual stages are recognized as legitimate species, the distinct species and genera of the anamorphic fungi will have to be covered in this artificial phylum.

J. J. Muchovej

See also: Ascomycetes; Basidiomycetes; Basidiosporic fungi; Deuteromycetes; Fungi.

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MODEL ORGANISMS

Category: Methods and techniques

Practitioners in various areas of experimental biology recognize particular organisms as standard objects of study within their specialties. These model organisms are species that are used to exemplify a given category of organisms. For example, the laboratory rat is a common model used to study mammals, and Arabidopsis thaliana *is commonly used as a model to study plants.*

The characteristics of well-chosen model organisms, such as their genetic makeup or their development, make them suited to be the subjects of biological research. They are often developed specifically for laboratory study of pure-breeding strains that can be relied upon to provide a consistent medium for experimentation or examination. Biologists planning an experiment might specify a particular breed of rat, for example, whose traits are well defined and that are familiar to their peers. When a given model organism has become the standard in a particular field, it can become a kind of common currency that facilitates exchange among scientists.

Under these circumstances, a great deal of knowledge about individual model organisms may be accumulated rapidly. The crucial assumption, based on the theory of evolution, that underlies the use of specific organisms as models is that species sharing a common ancestor will have fundamental similarities of physiology and biochemistry. Among ubiquitous model organisms are the bacterium *Escherichia coli*, the yeast *Saccharomyces cerevisiae*, the roundworm *Caenorhabditis elegans*, the fruit fly *Drosophila melanogaster*, and the plant *Arabidopsis thaliana*.

Common Features

Above all else, model organisms must be practical to observe and use in experiments. They must be easy to breed or propagate and resilient enough to withstand manipulation. For knowledge gained in the study of model organisms to be applicable on a larger scale, the organisms must be representative of the taxonomic group in question. Clearly, the applicability of studies performed on a particular model organism varies, depending on the nature of the inquiry. For example, the yeast *S. cerevisiae* is broadly representative of the fungi as a whole, but its study may also provide insights into specific molecular processes common to all eukaryotes, including humans. Model organisms are often chosen because they are among the simplest examples of the group being studied. They may have a particularly small genome, a short life cycle, or even a small size that makes them convenient organisms with which to work. They may also lend themselves very well to the study of specific features. For example, fruit flies are commonly used in the study of genetics because they have a small genome from which it is easy to induce and detect mutations.

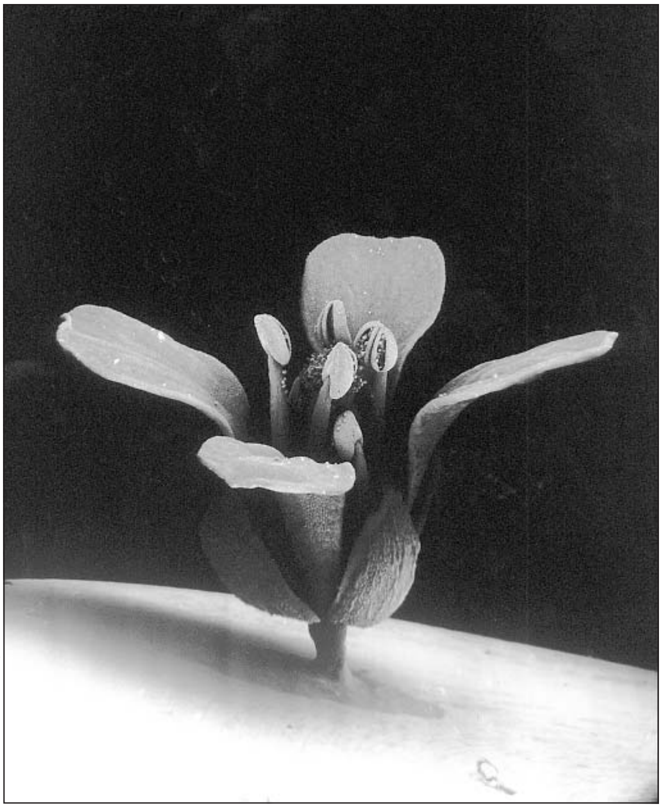
Well-chosen model organisms, those that possess some or all of the aforementioned characteristics, have been valuable tools for scientific research. Given these characteristics, it is easy to identify two types of scientific inquiry that are well served by the use of model organisms. There are studies in which a category of organisms is investigated by studying one of its simplest members and those in which a particular feature or biological process is illuminated by examining an organism in which it is especially accessible. Thus, the mouse is frequently used as a model for all mammals, and the green alga *Chlamydomonas* is used to study photosynthesis.

If a specific organism becomes the consensus model for a given category, the situation lends itself well to a speedy advancement of knowledge. The fact that many clusters of researchers choose to focus on the same model promotes collaboration and the more rapid accumulation of a body of knowledge about the organism, enhancing the likelihood of broader insights or theoretical advances. Having a research subject organism in common facilitates communication among researchers and leads to the formation of standard terminology. The widespread study of a single organism promotes the development and propagation of effective techniques for its use and allows for the introduction of standard experimental practices. Many observers have argued that the very success of science as a collaborative activity relies on scientists having some consensus about the tools and objects of their research and the terminology with which they describe it.

Although there are many advantages of a model organism becoming widespread in a particular field, there are some limitations to what can be achieved by the study of model organisms. There must always be a question of the applicability to other species of knowledge gained from the study of a model organism. A poor choice of an organism for a model can hinder the production of scientific knowledge just as much as research on a valid model can be beneficial. There is also the risk that focusing a discipline on one or a few models may inhibit understanding of diversity. As the botanist Dina Mandoli has pointed out, "flowering plants have an estimated 300,000 species . . . no one plant, not even *Arabidopsis thaliana*, can encompass this enormous diversity at the whole plant, physiologic, chemical, genetic, or molecular level." It is important, therefore, that research be carried out on enough model organisms to produce adequate breadth of knowledge. To that end, there are dozens of model plants in use representing a cross-section of the kingdom, of which *Arabidopsis* has been the most widely and successfully employed.

Arabidopsis

Arabidopsis is a genus of the mustard family that is closely related to food plants such as canola, cabbage, cauliflower, broccoli, radish, and turnip. Furthermore, although *Arabidopsis* is not used in agriculture, it is assumed that its study can lead to better knowledge of crop plants such as corn and soybeans because of evolutionary similarities among the genomes of all angiosperms. In the 1980's *Arabidopsis thaliana* (thale cress) became the



Elliot Meyerowitz/Courtesy of the National Science Foundation

Among plants, the most ubiquitous model organism is the plant Arabidopsis thaliana, *thale cress.*

primary model organism used in botany. Many characteristics lend it to such use, including its small size—plants are a few inches tall when mature—and its short life cycle of less than six weeks. The short life cycle allows researchers to see the effects of experimentation across successive generations in a relatively short span of time. *A. thaliana* also has a small genome and the least amount of DNA (deoxyribonucleic acid) per haploid cell of any known flowering plant. The haploid complement of *A. thaliana* is 117 million base pairs, compared to 1.6 billion in tobacco. As a result, it is comparatively easy to trace effects of experimentation to specific genes. It is valuable in the laboratory because of its prolific seed production and the availability of numerous mutations. It may be efficiently transformed with the bacterium *Agrobacterium tumefaciens*, which is used as a vector for the introduction of foreign DNA to the plant genome.

Arabidopsis was publicly recognized for its potential as a model organism in the 1960's. In 1985 it was first promoted as a model for molecular genetic research, and the first molecular map of one of the five *Arabidopsis* chromosomes was published in 1988. In 1990 the *Arabidopsis* Genome Project was begun (in part because of support by the codiscoverer of DNA James Watson). Thanks to a multinational effort, by the year 2000 the *Arabidopsis* gene sequence was fully decoded. The sequencing project was itself acclaimed as a model, because the researchers strove to be systematic and comprehensive in their investigation of the genome. It is now known that the *Arabidopsis* has slightly more than twenty-five thousand genes, making it comparable in its genetic complexity to a fruit fly.

Prior to the widespread use of *Arabidopsis*, many prominent scientists claimed that progress in botanical research was hindered by the study of too many organisms at once. Since *Arabidopsis* became a principal subject of research, botanical knowledge has advanced markedly. Researchers concentrating on *Arabidopsis* have helped to unify the studies of classical and molecular genetics, plant development, plant physiology, and plant pathology. These advances have led to a more fundamental understanding of many processes of plant growth and development at a molecular level.

Some specific areas in which *Arabidopsis* research has produced important advances are light perception, floral induction, flower development, and response to pathogenic and environmental stresses. For example, the functions of individual phytochromes, which are photoreceptors involved in many aspects of plant growth and development, were elucidated in *Arabidopsis*. Likewise, the first hormone receptor isolated in plants, that for ethylene, was discovered as a result of using *Arabidopsis* mutants. The next goal for the community of *Arabidopsis* scientists is to assign functions to all of the plant's genes by the year 2010.

Chlorella and Chlamydomonas

Chlorella pyrenoidosa and *Chlamydomonas reinhardtii* are unicellular green algae that have been used extensively as model organisms. They have many features in common with other model organisms, including short and simple life cycles and easily isolated mutants. Although not strictly members of the plant kingdom, they have been important tools for botanically related research because they are photosynthetic eukaryotic organisms. They therefore offer less complex subjects through which to study many processes that are central to plant life. There are no unicellular members of the plant kingdom, so study of many important botanical processes may be more easily undertaken on *Chlorella* or *Chlamydomonas* than on any plant.

In the mid-twentieth century Melvin Calvin used *Chlorella* in his Nobel Prize-winning research, which elucidated the cycle involved in photosynthetic carbon fixation which now bears his name, the Calvin cycle. This is a perfect example of model organisms' value in research. It is often easier to work out a mechanism in a simple organism and see whether it operates the same way in complex organisms (the understanding of which may be the ultimate purpose of the research) than to attempt the investigation on a complex organism in the first place. Once the Calvin cycle had been explained in *Chlorella*, it was shown to be ubiquitous in the chloroplasts of higher plants.

Chlamydomonas is the green alga most commonly used as a model organism in contemporary research. A *Chlamydomonas* genome project is under way with efforts taking place in the United States and Japan. Among the topics of research in which *Chlamydomonas* is the model organism of choice, one of the most compelling is that of chloroplast biogenesis and inheritance. *Chlamydomonas* is often referred to as the "green yeast," and like the yeast *S. cerevisiae*, it is an important eukaryotic model system. For studying certain aspects of cell biology to which yeast is not applicable, *Chlamydomonas* is chosen in preference. Such areas include cell motility caused by flagella, phototaxis (phototaxy), photosynthesis, and the study of centrioles, basal bodies, and chloroplasts.

Other Prominent Model Organisms

For areas other than those just mentioned, yeast is the most commonly used simple eukaryotic model organism. In 1996 *S. cerevisiae* became the first eukaryote to have its genome fully sequenced; its size is approximately one-tenth of that of *Arabidopsis*, or twelve million base pairs. Around the same time, the genome project was completed for the preeminent prokaryotic model organism, *E. coli*. This bacterium has become crucial not only as a focus of experiment but also as a biotechnological workhorse. Genes can be cloned by their insertion into *E. coli*, and gene products can therefore be mass-produced in large-scale fermentations of the bacteria.

Alistair Sponsel

See also: Calvin cycle; Cell cycle; Chromatin; Chromosomes; Eukaryotic cells; Green algae; History of plant science; Mitochondrial DNA; Plant biotechnology; Thigmomorphogenesis; Yeasts.

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MOLECULAR SYSTEMATICS

Categories: Cellular biology; classification and systematics; disciplines; evolution

Molecular systematics is the discipline of classifying organisms based on variations in protein and DNA in order to make fine taxonomic categorizations not solely dependent on morphology.

T*axonomy*, sometimes called *systematics*, is the study of categorizing organisms into logically related groupings. Historically, the way to perform taxonomy was to examine physical characteristics of organisms and classify species according to the most commonly held traits. Unfortunately, this method of systematizing plants and animals assumed that because they have common physical traits, they have common ancestry. A gross form of this miscategorization might take place, for example, if one suggested that since both mushrooms and ivy can grow on the sides of trees, they are closely related. The two species certainly have common physical traits but only vaguely resemble each other.

It is such a realization that motivated systematists to begin using molecular differences to compare species and populations. Molecular systematics uses variations in *protein* and *deoxyribonucleic acid* (DNA) molecules to determine how similar, or dissimilar, sets of organisms are. These molecular differences provide a much more accurate taxonomic picture.

Systematics and Evolution

The real power of molecular systematics is that it allows the examination of how species have changed over evolutionary time, as well as of the relationships between species that have no common physical characteristics. Molecular changes can be used to explore *phylogenetics* (how populations are related evolutionarily and genetically). It has been suggested that the amount of change that takes place in DNA over time can act as a *molecular clock*, gauging how much evolutionary time has passed. The clock is set by first examining geological and historical records to determine how long two species have been physically separated. By examination of the number of molecular changes that have occurred between those species over that known time, a time frame of change can be established. Genes are thought to evolve and mutate at a constant, predictable rate, giving rise to this evolutionary clock hypothesis.

There are three major domains of life: prokaryotes (modern bacteria), *Archaebacteria* (descendants of ancient bacteria), and eukaryotes (cellular organisms with nuclei and organelles). All these organisms share a common ancestry of hundreds of millions of years. All species over time are connected to one another through a web of interlacing DNA as they reproduce, separate to become new species, and reproduce again. All organisms carry their ancestors' genetic information with them as a bundle in each cell, and the more closely related organisms are to one another, the more similar the contents of that bundle will stay over time. Humans share common genes, unchanged over millennia, with all other organisms—from the bacterium *Escherichia coli* to barley to gophers. The more important the job of a gene, the less it changes over time; this concept is called *conservation*. Conservation is the force that keeps a biological or genetic link between every species on earth.

Protein-Level Analysis

Proteins were the earliest biomolecules used to study phylogenetics. Initially, protein differences could be studied only at the grossest levels. It was found that populations of organisms could be distinguished based on possessing different alleles (genetic sites) that made proteins possessing the same function but with different chemical structures. These enzymes were called *isozymes*. Isozymes can be separated and compared for size by employing a technique called gel electrophoresis. Gel electrophoresis uses a slab of gelatin-like medium and an electric field to separate molecules on the basis of size and electric charge. The genetic similarity of two different species can be determined based on common molecular weight of the isozymes.

Proteins are composed of strings of the twenty amino acids common to all life on earth. It is possible to ascertain the amino acid sequence of a protein. If the amino acid sequence of the same protein is ascertained among several different species, that sequence should be more similar between closely related species than more distantly related species. These differences allow taxonomists to gauge similarity of populations.

Antibodies are biomolecules that are able to recognize and bind very specifically to other molecules. Biologists employ antibodies that specifically recognize molecules at the surface of cells to test relationships between species. Antibodies that recognize cell-surface molecules on one species should recognize those same molecules in closely related species, but not from distantly related species, allowing a researcher to gauge similarity between species.

DNA-Level Analysis

The most common method used to establish taxonomic relationships is to compare DNA sequences between species. DNA is the double-stranded, polymeric molecule that encodes the proteins that direct the inner workings of all cells. The DNA molecule is structure like a ladder, with rungs formed by pairings of of four molecules, the bases guanine (G), adenine (A), thymine (T), and and cytosine (C). These bases, arranged in unique order, are read by special enzymes and encode messages that are translated into proteins. Sequences encoding for the same protein can change between species. In taxonomy, DNA sequences are obtained from several populations of organisms. Analysis of these sequences allows one to obtain a picture of how different populations have changed over time. This *DNA sequencing* may be used to compare many different types of DNA: regions that encode for genes, do not encode for genes, reside in chloroplast DNA, or reside in mitochondrial DNA.

Another common method of DNA phylogenetic analysis is called *restriction mapping*. In this method, DNA from different species is subjected to enzymatic treatment from proteins called *endonucleases*. These endonucleases have the ability to cleave DNA into fragments. Where the enzymes cleave the DNA is determined by the DNA sequence itself. The size and pattern of the fragments created by this treatment should be more similar in related species than in unrelated species.

A fairly new method of DNA analysis examines repetitive DNAs, called *microsatellite sequences*, that are found in all eukaryotic organisms. Microsatellite sequences are short arrangements of bases, such as GATC, repeated over and over. The number of repeats at a particular genetic location is usually more similar in related species than in unrelated ones. The differences in these repeated sequences are called "simple sequence polymorphisms" and are detected by a special enzymatic reaction called the *polymerase chain reaction*. Once detected, the fragments are separated and compared for size by means of gel electrophoresis.

James J. Campanella

See also: Cladistics; DNA in plants; Electrophoresis; Evolution of plants; Genetics: mutations; Nucleic acids; Proteins and amino acids; Systematics and taxonomy; Systematics: overview.

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MONOCOTS VS. DICOTS

Categories: Angiosperms; *Plantae*; reproduction and life cycles

Within the angiosperms (flowering plants), two classes have been traditionally recognized by botanists: monocots and dicots. The terms connote differences between these groups' seed embryos. The recently introduced class, eudicots, literally meaning "true dicots," is increasingly used in place of the term "dicots."

Of the large number of plant species which currently inhabit the earth, most (about one-quarter million) are *angiosperms*, plants that reproduce by means of flowers. The famous naturalist Charles Darwin called angiosperms "an abominable mystery." Even today, much remains to be learned about the ancestry of angiosperms and when and where angiosperms first appeared. It is now believed that the first extant angiosperm is a single species of the genus *Amborella*. This plant, found on an island in the South Pacific, is a shrub with cream-colored flowers.

All angiosperms are assigned to the phylum *Anthophyta*. Within this phylum, considerable diversity occurs. However, two large lineages have traditionally been recognized: class *Monocotyledones* (monocots) and class *Dicotyledones* (dicots).

The monocots include grasses, cattails, irises, lilies, orchids, and palm trees. The dicots include the vast majority of seed plants: herbs, vines, shrubs, and most trees (cone-bearing trees are not angiosperms).

The terms "monocot" and "dicot" reflect the number of *cotyledons*, one or two, respectively, possessed by seeds of the plants. A cotyledon is the central portion of a seed embryo to which the epicotyl (immature shoot) and radicle (immature root) are attached. However, one need not examine the seed of a particular flowering plant in order to assign it to the correct class. Fortunately, each angiosperm possesses a "syndrome" of features, any one of which may be used for the purpose of classification.

Vegetative Parts

Monocots have leaves with parallel veins: The large, easily visible veins are parallel and extend the length of the (usually) linear leaves. In contrast, leaves of dicots are net-veined: The veins branch repeatedly as they extend into the various portions of the leaf. Vascular bundles (clusters of conducting cells) within stems of monocots are scattered, in contrast to those of dicots, which are arranged into a cylinder. These are best seen in a cross-section of the root. Furthermore, stems of monocots rarely produce wood, whereas those of many dicots (trees

Characteristics of Monocots vs. Dicots

Feature	*Monocots*	*Dicots*
Embryos	One cotyledon	Two cotyledons
Pollen	One pore	Three pores
Flowers	Parts in threes	Parts in fours or fives
Leaf veins	Parallel	Netted or reticulated
Vascular bundles	Scattered, complex	Ordered in rings
Woody growth	In 10% of species	In 50% of species
Root system	Adventitious	Primary+adventitious
Species	~65,000	~165,000
Examples	Bromeliads Grasses Irises Lilies Orchids Palms	Asters Cacti Herbs Shrubs Roses Trees

and shrubs) increase their diameter yearly, as wood accumulates within them.

Reproductive Parts

Flowers of monocots typically have their parts arranged in threes and are said to be "3-merous." An example would be a lily flower, which has these parts (designated from the outside toward the center of the flower): three sepals, three petals, six stamens, and one pistil. Flowers of dicots have parts arranged in fours or fives. Also, pollen grains produced by flowers of monocots each have one pore in the outer covering, as compared to three pores in the case of dicot pollen grains. Thus, it is apparent that nearly any part of a flowering plant can be used to place it into the correct subgroup of angiosperms. However, it is the flowers and leaves that are most easily considered (not requiring microscopic examination).

Image Not Available

New Interpretations

Like all areas of science, botany is subject to modification and reinterpretations as a result of the accumulation of new information. One group of plants traditionally considered to be dicots, the magnoliids, have long been problematic. They have some features of dicots, but their floral parts are free (unattached to one another) and arranged spirally. Also, they produce pollen grains, each of which has only a single pore. These features are characteristic of monocots. These traits have thus caused those who study angiosperms to place them into a new, third category, the class *magnoliids*. This most primitive group of angiosperms is thought to be ancestral to both of the other classes. The southern magnolia, *Magnolia grandiflora*, with its huge, white flowers, is a good example of this class. The name *eudicots* is applied to the still-large group that includes the remainder of the dicots.

Thomas E. Hemmerly

See also: Angiosperm evolution; Eudicots; Evolution of plants; Flower structure; Flower types; Leaf anatomy; *Monocotyledones*; Paleobotany; Reproduction in plants; Seeds; Stems; Wood.

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MONOCOTYLEDONES

Categories: Angiosperms; *Plantae*; taxonomic groups

The Monocotyledones*, or monocots, are a large and very distinctive class of angiosperms or flowering plants, phylum* Anthophyta*, consisting of some 133 families, 3,000 genera, and 65,000 species.* Monocotyledones *form one of the two major subdivisions of angiosperms, the other being the* Eudicotyledones *(eudicots), with about 165,000 species.*

Typical monocots have a single *cotyledon* (seedling leaf), stems with scattered vascular bundles, root systems composed entirely of adventitious roots (arising directly from stem tissues), leaves with parallel venation and sheathing bases, and flower parts in threes. Monocots lack the ability to produce secondary growth (wood). In most monocots, stems remain at or below ground level and take the form of rhizomes (horizontal stems), bulbs (short, vertical stems covered with modified, fleshy leaves), corms (short, wide stems), or tubers (wood), which produce new adventitious roots continually or seasonally.

The growing tips (*apical meristems*) or buds of these plants remain below ground, except when they rise to produce flowers, and thus are protected against seasonal cold, drought, fire, and grazing animals. The growing tips are also surrounded and protected by the sheathing bases of the leaves. Monocot leaves are typically long and strap-shaped with numerous parallel veins that connect individually to the stem. Leaves grow primarily from their bases, increasing in length and pushing the earlier formed tips upward but not increasing much in width.

Most monocot flower parts occur in threes, such as three sepals, three petals, six stamens, and three carpels. Some members of the largely aquatic subclass *Alismatidae* have other patterns and show the primitive condition of *apocarpy* (carpels remain free from one another). In most other monocots, carpels are completely fused together into a three-chambered pistil. (Exceptions occur also in some palms). Monocots thus appear to have evolved from primitive anthophytes and have had a long, separate history.

Monocot Families Common in North America

Common Name	*Scientific Name*
Arum family	*Araceae*
Cattail family	*Typhaceae*
Daffodil family	*Amaryllidaceae*
Grass family	*Poaceae*
Iris family	*Iridaceae*
Lily family	*Liliaceae*
Orchid family	*Orchidaceae*
Sedge family	*Cyperaceae*

Note: For a full list of angiosperm families, see the tables that accompany the essay "Angiosperms," in volume 1.
Source: U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Ecology and Variation

Because of their predominantly underground stem structures and basally regenerating leaves, monocots predominate in open habitats with strong seasonal contrasts or unpredictable droughts, such as grasslands. Grasses and similar monocots are particularly well adapted to survive drought, fire, and overgrazing, the three primary threats in grasslands. Bulbs, corms, and tubers are other forms of monocot stems that allow for underground survival, both in grasslands and in other regions that experience long winters or dry seasons.

The numerous monocots that inhabit marshes and aquatic habitats often have elongate petioles that grow from the base to lift their expanded leaf blades above the water level (such as *Sagittaria* and *Aponogeton*). The spectacular Egyptian papyrus plants have highly specialized upright stems that consist of a single *internode* (stem segment between nodes that elongates from the base), lifting a tuft of leaves and reproductive branches above fluctuating water levels. Other submerged aquatic monocots may remain rooted, producing conventional strap-shaped leaves (such as sea grasses) or may drift rootless, with short, whorled leaves produced along the stem.

Many monocots have adapted to live as *epiphytes* (plants that live on top of other plants), particularly on the upper branches of tropical rain-forest trees, a habitat that is often quite dry. The *orchid*, *bromeliad*, and *aroid* (*Philodendron, Anthurium*) families in particular have evolved largely in this habitat. Epiphytic orchids have succulent leaves or roots that store water for use during the dry periods between rains. A bromeliad grows as a rosette of tightly overlapping leaves radiating from the central growing point, forming a water-holding cup, or tank, in the center. Aroids can be found climbing up tree trunks or perched on upper branches and are unusual both for their flower structure and their leaves. Flowers are tiny and crowded on the clublike spadix, which in turn is enveloped by a large, often colored, leaflike structure called a *spathe*, while the leaves are broad, often dissected or divided into separate leaflets, and net-veined—quite unlike the typical monocot leaf.

Lack of the ability to form conventional tree trunks has led to some other novel growth forms in monocots. One of these is the *pseudostem* (false stem). In banana plants, and to a less obvious extent in gingers, heliconias, and other giant tropical herbs, an apparent stem forms from the elongate, tubular, concentric leaf sheaths, and gets taller as each new leaf grows up through the center.

Monocot Trees

Some monocots have become *arborescent* (treelike) by growing upward and developing thick, fibrous trunks without conventional secondary growth. In most arborescent monocots (palms, screw pines), the thickening growth of the stems occurs at the growing tip, in what is known as the *primary thickening meristem*. In these specialized meristems, the dividing cells expand laterally more than vertically. Stems reach their full thickness in this initial growth at the tip of the plant and expand very little after that.

In members of the *Dracena* family, however, a new way of thickening stems has evolved. Extensions from the apical meristem remain active along the sides of the stem and produce new parenchyma tissue and whole vascular bundles (not layers of wood). This allows the plants continually to increase the thickness of the stem and the amount of vascular tissue.

Branching is limited or absent in arborescent monocots, and leaves therefore tend to be large. Screw pines and dracenas have very long, narrow leaves, while palm leaves are broad and dissected into folded linear leaflets in either a *pinnate* (featherlike) or a *palmate* (fanlike) arrangement. Palm leaves are the largest in the world, reaching more than 60 feet (18 meters) in length in some species, and are highly fibrous. Development of these compound leaves is complex, involving multiple meristematic areas.

Frederick B. Essig

See also: Angiosperms; Eudicots; Monocots vs. dicots.

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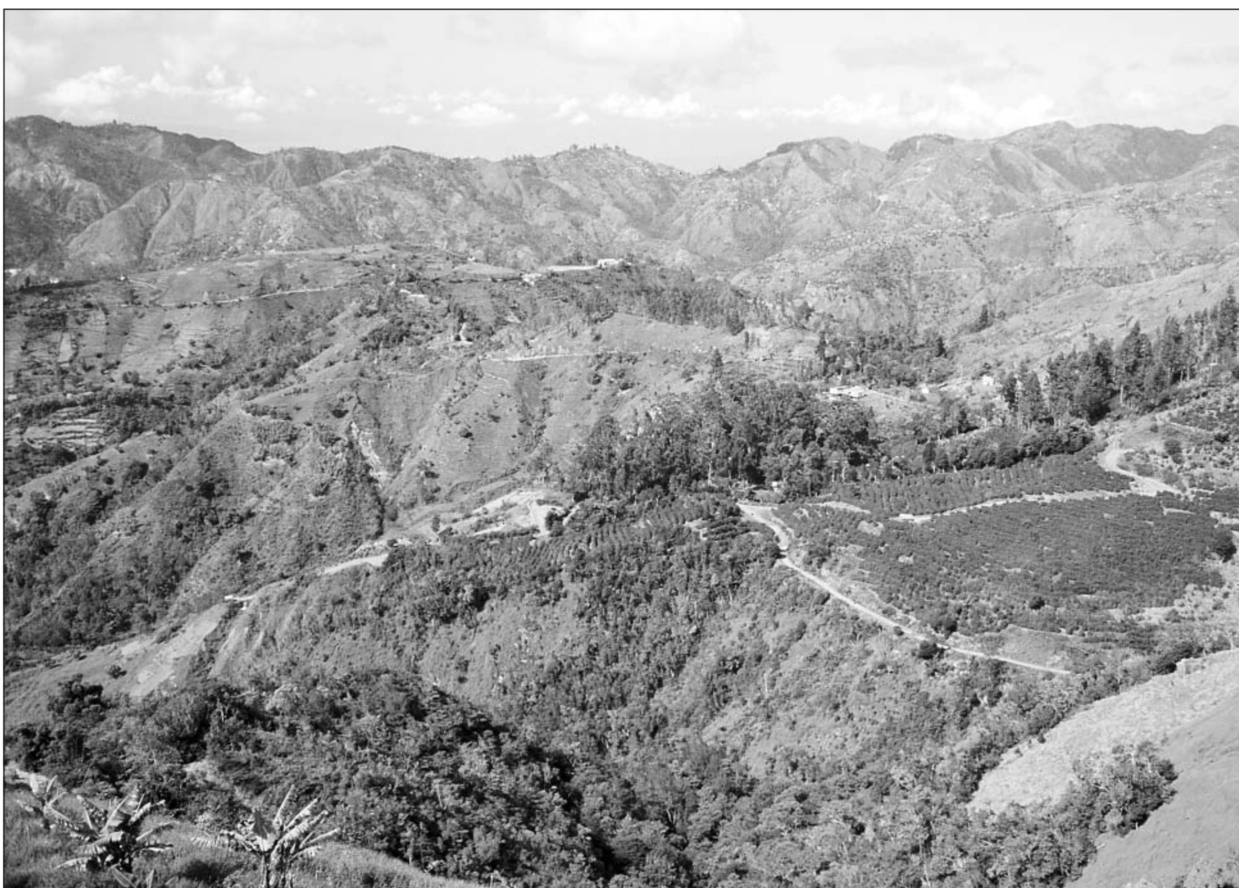
MONOCULTURE

Categories: Agriculture; economic botany and plant uses; environmental issues

Monoculture is the agricultural practice of repetitively planting a single plant species rather than growing a variety of types of plants.

There has been considerable debate regarding the advantages and disadvantages of monoculture agriculture. This type of plant production is a system in which a single plant species, typically one producing grain (such as corn, wheat, or rice), forage (such as alfalfa or clover), or fiber (such as cotton), is grown in the same field on a repetitive basis, to the exclusion of all other species. In its most extreme version, a single variety of a plant species is grown, and all plants are virtually identical to one another. Monoculture can be contrasted with other agricultural production practices, such as multiple



PhotoDisc

In the most extreme version of monoculture agriculture, a single variety of a plant species is grown, and all plants are virtually identical to one another. Monoculture can also apply to perennial produce systems, such as coffee plantations like this one.

cropping (in which sequential monoculture crops are grown in the same year) or intercropping (in which two or more different crops are grown at the same time and place). Monoculture can also apply to perennial produce systems, such as fruiting trees, citrus crops, tea, coffee, and rubber trees.

Advantages

Monocultures are unnatural ecological occurrences. They are maintained through the use of resources such as labor, energy, and capital (fertilizers, chemicals, and so on). Left to itself, a monoculture crop will quickly revert to being a mixed plant community. However, monoculture agriculture has several advantages that caused its widespread adoption from the moment agriculture began. Monocultures allow agriculturalists to focus their energy on producing a single crop best adapted to a particular environment or to a particular market. For example, a premium is paid for white corn, used in making snack foods.

Monoculture is an appropriate agricultural strategy to optimize crop yield per unit of land when either temperature or water conditions limit the growing season. Monoculture agriculture lends itself to mechanization, an important consideration when labor is expensive relative to energy costs. Consequently, monoculture agriculture in the United States has developed in concert with the resources required to support it—markets, credit, chemicals, seed, and machinery—and with the social conditions that have caused the United States to change from a rural to a largely urban and suburban population.

Disadvantages

The disadvantages of monoculture are numerous. There are apparent limits to the increase in crop yields brought about by new hybrid seeds, *fertilizers*, and *pesticides*. Yield increases in monoculture agriculture have diminished since the 1980's. There is an economy of scale at which farm size becomes too small to permit effective mechanization or for which insufficient markets exist for reliance on a single crop. Focus on production of a single crop may lead to unbalanced diets and nutritional deficiencies in agricultural communities where no external supplies of produce are available.

More important, monoculture crops are biologically unstable, and considerable effort must be made to keep other plants and pests out. When every plant under cultivation is the same, these systems are inherently susceptible to natural events (storms, drought, and wind damage) and to *biological invasions* by insects and plant pathogens. The classic example of overreliance on monoculture was the Irish Potato Famine (1845-1850). The famine was instigated by natural climatic conditions that allowed the plant pathogen *Phytophthora infestans* (potato late blight) to destroy successive potato crops in a population too impoverished to afford other food staples that were available.

Mark S. Coyne

See also: Agriculture: modern problems; Green Revolution; High-yield crops; Hybridization; Multiple-use approach; Nutrition in agriculture; Pesticides; Slash-and-burn agriculture; Sustainable agriculture.

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MOSSES

Categories: Nonvascular plants; paleobotany; *Plantae*; taxonomic groups

Members of the ten thousand species of the class Bryopsida *or* Musci *in the order* Bryophyta, *mosses are usually tiny, fragile, nonflowering, spore-bearing plants. They are related to hornworts and liverworts.*

Mosses evolved from green algae before the existence of reptiles and flying insects. Fossils from the Devonian period, about 410 million to 353 million years ago, contain mosses. The first known mosses lived 286 million to 245 million years ago, during the Permian period. By the Tertiary period, approximately 66.4 million to 1.6 million years ago, at least one hundred moss species existed. Fossilized mosses, including *Muscites*, *Palaeohypnum*, and *Protosphagnum*, resemble modern moss species structurally, indicating that mosses have not evolved quickly.

Found globally, mosses prefer damp, shady, sparsely vegetated environments and often grow

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Classification of Mosses

Class *Andreaeopsida* (granite mosses)
- Families:
  - *Andreaeaceae*
  - *Andreaeobryaceae*

Class *Sphagnopsida* (peat mosses)
- Families:
  - *Sphagnaceae*

Class *Bryopsida* (true mosses)
- Families:
  - *Archidiaceae*
  - *Aulacomniaceae*
  - *Bartramiaceae*
  - *Bryaceae*
  - *Catoscopiaceae*
  - *Hypopterygiaceae*
  - *Meesiaceae*
  - *Mniaceae*
  - *Pseudoditrichaceae*
  - *Racopilaceae*
  - *Rhizogoniaceae*
  - *Timmiaceae*
  - *Buxbaumiaceae*
  - *Bruchiaceae*
  - *Bryoxiphiaceae*
  - *Dicranaceae*
  - *Ditrichaceae*
  - *Leucobryaceae*

Class *Bryopsida* (continued)
  - *Fissidentaceae*
  - *Disceliaceae*
  - *Ephemeraceae*
  - *Funariaceae*
  - *Gigaspermaceae*
  - *Oedipodiaceae*
  - *Splachnaceae*
  - *Splachnobryaceae*
  - *Grimmiaceae*
  - *Ptychomitriaceae*
  - *Scouleriaceae*
  - *Callicostaceae*
  - *Daltoniaceae*
  - *Hookeriaceae*
  - *Amblystegiaceae*
  - *Brachytheciaceae*
  - *Entodontaceae*
  - *Fabroniaceae*
  - *Helodiaceae*
  - *Hylocomiaceae*
  - *Hypnaceae*
  - *Leskeaceae*
  - *Myriniaceae*
  - *Plagiotheciaceae*
  - *Pleuroziopsidaceae*
  - *Pterigynandraceae*

Class *Bryopsida* (continued)
  - *Rhytidiaceae*
  - *Sematophyllaceae*
  - *Stereophyllaceae*
  - *Thamnobryaceae*
  - *Theliaceae*
  - *Thuidiaceae*
  - *Fontinalaceae*
  - *Anomodontaceae*
  - *Climaciaceae*
  - *Cryphaeaceae*
  - *Hedwigiaceae*
  - *Leptodontaceae*
  - *Leucodontaceae*
  - *Meteoriaceae*
  - *Neckeraceae*
  - *Pterobryaceae*
  - *Erpodiaceae*
  - *Orthotrichaceae*
  - *Rhachitheciaceae*
  - *Polytrichaceae*
  - *Calymperaceae*
  - *Encalyptaceae*
  - *Pottiaceae*
  - *Schistostegaceae*
  - *Seligeriaceae*
  - *Tetraphidaceae*

Source: U.S. Department of Agriculture, National Plant Data Center, *The PLANTS Database*, Version 3.1, http://plants.usda.gov. National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

on land adjacent to bodies of fresh water and in woods, sometimes appearing carpetlike. Some mosses prefer rotting wood, while others thrive in soil saturated with water or bare soil. Although hardy, mosses are sensitive to pollutants. Mosses need external sources of moisture to transport nutrients. They can adapt to environments, exhibiting variations. Although many mosses live in temperate zones, they also have been found living in tundra. Mosses can grow on rocks, mountains, and brick and cement structures. They are frequently found on tombstones and other memorials.

Mosses are categorized into three groups, the true mosses (*Bryopsida* or *Musci*), the peat mosses (*Sphagnopsida*), and the granite mosses (*Andreaopsida*). The greatest number of moss species are in the subclass *Bryidae*. Some subclasses contain only a few species.

Most mosses are short. Cape pygmy moss (*Ephemerum capensi*), the size of a pencil dot, is the tiniest moss that can be seen without a microscope. The largest mosses are 1 meter (40 inches) long. Water mosses in the order *Bryales* live in streams and ponds, sometimes adhering to tree roots or rocks. Brook moss grows shoots ranging from 30 to 100 centimeters (12 to 40 inches) long. Common mosses include hair-cap, sheet, top, slit, granite, broom, and wind-blown mosses. Luminous mosses, whose curved cells concentrate light on chloroplasts for photosynthesis, grow in dark spaces.

Mosses consist of green stems and leaves that are usually one cell thick and sometimes have midribs. Leaf cell shape and pattern are used to identify mosses, and differences can be detected microscopically. Instead of roots, each moss stem has *rhizoids* which secure the plant to the ground. Lacking a vascular system to conduct fluid, mosses need a watery environment to distribute male gametes.

Life Cycle

Mosses have two reproductive forms, referred to as the alternation of generations. During the gametophytic, or sexual, generation, a gametophyte creates a plant body known as the thallus. Two specialized organs are involved in sexual reproduction. The antheridium is a sac that produces male gametes, each with two flagella, and the archegonium is the bottle-shaped female sexual organ. Short cell filaments, called the paraphyses, are associated with the antheridium. Usually both sexual organs are located on moss leaves.

Sperm fertilizes the egg to create a maroon-colored stalk called a seta, which has a sporangium, or spore capsule, in the sporophytic generation. The sporangium consists of an urn, peristome, annulus, operculum, and calyptra. Capsule components vary by species. This sporangium relies on the gametophyte to deliver necessary nourishment and moisture. When the sporophyte dries, spores are scattered like dust and germinate to become threadlike *protonema*, an immature moss form, which form new gametophytes.

During wet conditions, the capsule can withhold spores by closing from one to two rows of peristome teeth. Because spores are sensitive to moisture, temperature, and soil chemistry and have limited supplies of energy for protonema to grow, odds are that only one spore per million forms a mature moss plant. Mosses also reproduce asexually by growing from fragments of stems and leaves that germinate into new plants.

Uses

Ecologically, mosses serve several purposes. They help secure soil by forming patches of dense mats of ground cover and absorb water to prevent erosion. Mosses also provide nutrients that enrich soils for future plant growth. Mosses are popular terrarium plants. They are often illegally harvested from public lands, including national forests.

The word "moss" in plant names does not always indicate a moss species. The club moss is, in fact, an evergreen herb from the family *Lycopodiaceae*, and its relatives, the spike mosses, are primitive vascular plants in the family *Selaginellaceae*. Often, people in the Northern Hemisphere use moss to tell direction because it grows on the north-facing sides of trees and structures, where sunlight does not shine directly. Green algae that grow on trees' northern sides are referred to as moss but usually are not. Other types of algae, such as pond moss, are incorrectly described as mosses. Spanish moss is one of the best-known plants called a moss, but it actually is a lichen and air plant belonging to the pineapple family, *Bromeliaceae*.

Some moss species in the genus *Sphagnum,* of the order *Sphagnales*, partially decompose into carbonized tissues in acidic, watery areas such as bogs to become peat, which is significant economically as a fuel and as a commercial gardening product. Empty moss cell spaces absorb water, and bogs become drier. Peat mosses float in mats, prevent fungi and bacteria from multiplying, and create an environment that can preserve carcasses. Prior to the development of modern medical techniques, sphagnum moss was used to dress surgical sites because of its antiseptic qualities.

Elizabeth D. Schafer

See also: Algae; Bioluminescence; *Bromeliaceae*; Bryophytes; Hornworts; Liverworts; Lycophytes; Peat.

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MULTIPLE-USE APPROACH

Categories: Agriculture; economic botany and plant uses; environmental issues; forests and forestry

The multiple-use approach is a concept of resource use in which land supports several concurrent managed uses rather than single uses over time and space.

The multiple-use approach is a management practice that is teamed with the concept of sustained yield. Multiple use began as a working policy, generally associated with forestry, and was enacted as law in 1960. As a concept of land-use management, it has most often been applied to the use of forestlands. Historically, multiple use has been linked with another concept, that of *sustained yield*.

Historical Background

The history of the intertwined multiple-use and sustained-yield approaches to land management in the United States dates from the late 1800's. Prior to that time, forestlands were used for timber production, rangeland for grazing, and parklands for recreation. Little attention was given to the interrelated aspects of land use. By the late 1800's, however, some resource managers began to see land as a resource to be managed in a more complex, integrated fashion which would lead to multiple use. This awakening grew out of the need for conservation and sustained yield, especially in the forest sector of the resource economy.

Sustained Yield

Since the earliest European settlement of North America, forest resources had been seen both as a nearly inexhaustible source of timber and as an impediment to be cleared to make way for agriculture. This policy of removal led to serious concern by the late 1800's about the future of American forests. By 1891 power had been granted to U.S. president Benjamin Harrison to set aside protected forest areas. Both he and President Grover Cleveland took actions to establish forest reserves. To direct the management of these reserves, Gifford Pinchot was appointed chief forester. Pinchot was trained in European methods of forestry and managed resources, as noted by Stewart Udall in *The Quiet Crisis* (1963), "on a sustained yield basis." The sustained-yield basis for forest management was thus established. Essentially, the sustained-yield philosophy restricts the harvesting of trees to no more than the ultimate timber growth during the same period.

Multiple Use

Properly managed, forestlands can meet needs for timber on an ongoing, renewable basis. However, land in forest cover is more than a source of timber. *Watersheds* in such areas can be protected from excessive runoff and sedimentation through appropriate management. Forest areas are also *wildlife habitat* and potential areas of outdoor recreation. The combination of forest management for renewable resource production and complex, interrelated land uses provided the basis for the development of multiple use-sustained yield as a long-term forest management strategy.

Multiple Use Joins Sustained Yield

The merging of these two concepts took shape over a period of many years, beginning in the early twentieth century. The establishment of national forests by Presidents Harrison and Cleveland provided a base for their expansion under President Theodore Roosevelt in the early 1900's. With the active management of Pinchot and the enthusiastic support of Roosevelt, the national forests began to be managed on a long-term, multiple-use, sustained-

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yield basis. The desirability of this approach eventually led to its formalization by law: On June 12, 1960, Congress passed the Multiple Use-Sustained Yield Act. To some, this act was the legal embodiment of practices already in force. However, the act provides a clear statement of congressional policy and relates it to the original act of 1897 that had established the national forests.

The 1960 act specifies that "the national forests are established and shall be administered for outdoor recreation, range, timber, watershed, and wildlife and fish purposes." Section 2 of the act states that the "Secretary of Agriculture is authorized and directed to develop and administer the renewable resources of the national forests for multiple use and sustained yield of the several products and services obtained therefrom." The act gives no specifics, providing a great deal of freedom in choosing ways to meet its provisions. It also refrains from providing guidelines for management. In practice, the achievement of a high level of land management under the act has called for advocating a *conservation* ethic, soliciting citizen participation, providing technical and financial assistance to public and private forest owners, developing international exchanges on these management principles, and extending management knowledge.

Jerry E. Green

See also: Agriculture: modern problems; Forest management; Forests; Grazing and overgrazing; High-yield crops; Monoculture; Rangeland; Sustainable agriculture; Sustainable forestry; Timber industry.

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MUSHROOMS

Categories: Economic botany and plant uses; food; fungi; poisonous, toxic, and invasive plants

Members of the kingdom Fungi *and division* Mycota, *mushrooms are members of the class* Basidiomycetes. *This class includes both the hymenomycetes, which reproduce spores using a layer structure called the hymenium, and the gasteromycetes, which include the stinkhorns and puffballs.*

Fossil evidence suggests that mushrooms existed ninety million years ago. The order *Agaricales* represents approximately four thousand species in sixteen families of commonly found mushrooms. The order *Polyporus* consists of fungi that grow on tree limbs or stumps. Although they prefer moist environments, mushrooms are sometimes found in deserts, beaches, and occasionally snowdrifts.

Characteristics

The mushrooms familiar to most people are *hymenomycetes*. They are either edible or poisonous structures lacking chlorophyll. That is, like other fungi, they do not make their own food through photosynthesis but instead are heterotrophs, which feed off other organisms. They are classified as thousands of species, distributed globally. Most mushrooms consist of a fleshy fruiting body called the *sporophore* and a cylindrical *stalk*.

Most mushrooms with the familiar umbrella-shaped sporophore, called the *cap* or *pileus*, belong to the family *Agaricaceae*. The pileus has narrow sheets called *gills* that contain the spores. The pileus sits atop the stalk, known as the *stipe*. Pilei and stipes vary in size.

Sporophores grow from a mat of thin strands called the *mycelium*, or spawn, which is located below the soil surface. Each mycelium grows new sporophores during the annual fruiting season. Mycelial life spans range from several months to centuries, depending on nutrient and moisture sources and suitable temperature. A honey mushroom mycelium in Michigan once spread across 40 acres over fifteen hundred years.

Mushrooms grow quickly, often maturing within several days. A *membrane* joins the cap's edges to the stem. As mushrooms mature, the membrane breaks, revealing the cap's gills. When the agaric mushroom ripens, its color changes from white to pink, then brown. Some mushrooms' colors change when they are exposed to air or water. Mushrooms are *geotropic*, keeping their caps upright and gills vertical and turning the pileus if placed on their sides after being picked.

Species

Wild mushrooms grow in fields, forests, lawns, and gardens. The waxy caps are among the most colorful mushrooms. In spring, morels emerge, often thriving on burned land. Their gills resemble honeycombs. The genus *Gyromitra* includes the false morels, which can be toxic.

The family *Boletaceae* includes mushrooms that contain layers of spores in tubes on the pileus's undersurface. The *Hydnum* mushrooms appear to have teeth, and the *Clavarias* look like coral. Occasionally, sporophores grow in circular patterns popularly called fairy rings.

The *Coprinus comatus*, or shaggy mane, is another spring mushroom which appears through the fall in open areas, with individuals or groups of this species often reemerging in the same place annually. This mushroom has tall, brown caps that appear shaggy because of soft scales on its surface. Unlike most mushrooms, members of *Coprinus* have caps that do not expand at maturity, which causes the compacted gills to liquefy into a black fluid, resulting in the collective name for the one hundred species of this genus, "inky caps."

The species *Agaricaceae campestris* profusely grows in rural areas, especially during the summer. The orange or yellow funnel-capped *Cantherellus cibarius* thrives in European forests, tastes nutty, and has been a preferred edible mushroom since the days of the Roman Empire. By autumn, large mushrooms representing the genus *Boletus* ripen in wooded areas. Veins on caps of *Boletus* species change color from white to yellow, indicating their readiness for picking.

Several mushroom species live on decaying wood hosts. Rotten timber is the habitat for *Polyporus sulfurreus*, which form as orange-yellow shelves that can be meters wide and weigh many kilograms. Pores beneath the layers create spores.

Poisonous Mushrooms

Between sixty and seventy mushroom species are poisonous. If consumed, poisonous mushroom species can cause intense physical reactions, rang-

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ing from sickness to death. The genus *Amanita* includes the most dangerous mushrooms, including *Amanita muscarine*. Only the *Amanita caesarea* is edible. The fly mushroom, *Amanita muscaria*, is a large, colorful mushroom that is deadly to insects. The white *Amanita phalloides*, known as the death cap or death angel, are the most toxic mushrooms and are widely distributed. Other hazardous mushrooms are *Boletus satana* (Satan's mushroom) and *Clitocybe illudens* (jack-o'-lantern), which glows in the dark and is physically similar to the benign *Clitocybe gigantea*.

Alkaloid mycotoxins in mushrooms attack nerve, muscle, blood, and organ cells. Victims suffer digestive symptoms within eight to twelve hours after ingesting mushrooms, then slip into a coma and die several days later. Patients undergo gastrointestinal tract purging and antidote treatment in an effort to counter poisoning.

Uses

Humans have cultivated mushrooms for thousands of years. Some mushrooms lack flavor or are too bitter or woody to consume. Others, such as *Ithyphallus impudicus*, have a foul odor. The *Pleurotus ostreatus* tastes like oysters. Although mushrooms are not especially nutritious because they are 90 percent water, many have pleasing tastes and textures and are low in fat.

Annually, about ten million North Americans hunt common mushrooms, especially morels. The mushroom industry relies on mushrooms picked and sold at wholesale prices totaling millions of dollars. Brokers ship the mushrooms to distributors or retail markets.

Commercial growers produce a safe source of edible mushrooms. These mushrooms are cultivated in specially designed structures, caves, or cellars in which the darkness, humidity, and temperature are regulated. Beds of soil-covered straw and manure are planted with mycelia. The *Agaricus bisporus*, a hybrid developed by researchers, is the most common commercial species. Exotic wild mushrooms, including portobello and shiitake, are cultivated artificially. Liquid nitrogen is used to store spawns and enhances their endurance and quality. Scientists are genetically designing improved mushroom strains.

Some mushrooms are hallucinogenic, and most governments restrict their use as a narcotic, although mushrooms are smuggled into countries that have bans. Various cultures incorporate mushrooms into spiritual rituals, believing the mushrooms have magical powers. Researchers have determined that some mushrooms, specifically the *Gleophyllum odoratum* and *Clitocybe gibba* species, can be therapeutic if thrombin inhibitors are extracted to manufacture anticoagulant pharmaceuticals.

Elizabeth D. Schafer

See also: Ascomycetes; Basidiosporic fungi; *Basidiomycetes*; Bioluminescence; Culturally significant plants; Fungi; Medicinal plants; Plant biotechnology; Poisonous and noxious plants; Tropisms.

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MYCORRHIZAE

Categories: Ecosystems; fungi

"Mycorrhiza" (from the Greek mukes, *meaning "fungus," and* rhiza, *meaning "root") is a term describing a mutualistic, symbiotic relationship between plant roots or other underground organs and fungi. Mycorrhizae are among the most abundant symbioses in the world.*

Mycorrhizal associations have been described in virtually all economically important plant groups. Investigators in Europe detected fungal associations in most European species of flowering plants, all gymnosperms, ferns, and some bryophytes, especially the liverworts. Similar patterns are predicted in other ecosystems. Continuing studies of ecosystems, from boreal forests to temperate grasslands to tropical rain forests and agroecosystems, also suggest that most plant groups are intimately linked to one or more species of fungus.

It is theorized that most of the plants in stable habitats where competition for resources is common probably have some form of mycorrhizal association. Species from all of the major taxonomic groups of fungi, including the *Ascomycotina*, *Basidiomycotina*, *Deuteromycotina*, and *Zygomycotina*, have been found as partners with plants in mycorrhizae.

Considering the prevalence of mycorrhizae in the world today, botanists theorize that mycorrhizae probably arose early in the development of land plants. Some suggest that mycorrhizae may have been an important factor in the colonization of land.

The fungal partner (or *mycobiont*) in a mycorrhizal relationship benefits by gaining a source of carbon. Often these mycobionts are poor competitors in the soil environment. Some mycobionts have apparently coevolved to the point that they can no longer live independently of a plant host.

The plant partner in the mycorrhizal relationship benefits from improved nutrient absorption. This may occur in different ways; for example, the mycobiont may directly transfer nutrients to the root. Infected roots experience more branching, thus increasing the volume of soil that the plant can penetrate and exploit. Evidence also suggests that mycorrhizal roots may live longer than roots without these associations. Comparison of the growth of plants without mycorrhizae to those with fungal partners suggests that mycorrhizae enhance overall plant growth.

Types of Mycorrhizae

Mycorrhizae may be classified into two broad groups: *endomycorrhizae* and *ectomycorrhizae*. Endomycorrhizae enter the cells of the root cortex. Ectomycorrhizae colonize plant roots but do not invade root cortex cells.

The most common form of endomycorrhizae are the *vesicular-arbuscular mycorrhizae*. The fungi involved are zygomycetes. These mycorrhizae have internal structures called *arbuscules*, which are highly branched, thin-walled tubules inside the root cortex cells near the vascular cylinder. It is estimated that 80 percent of all plant species may have vesicular-arbuscular mycorrhizae. This type of mycorrhiza is especially important in tropical trees.

There are several other subtypes of endomycorrhizae. *Ericoid mycorrhizae*, found in the family *Ericaceae* and closely related families, supply the host plants with nitrogen. These are usually restricted to nutrient-poor, highly acidic conditions, such as heath lands. *Arbutoid mycorrhizae*, found in members of the *Arbutoideae* and related families, share some similarities with ectomycorrhizae in that they form more developed structures called the sheath and Hartig net (described below).

Monotropoid mycorrhizae, found in the plant family *Monotropaceae*, are associated with plants that lack chlorophyll. The host plant is completely dependent on the mycobiont, which also has connections to the roots of a nearby tree. Thus the host, such as *Monotropa*, indirectly parasitizes another plant by using the mycobiont as an intermediate. *Orchidaceous mycorrhizae* are essential for orchid seed germination.

Ectomycorrhizae are common in forest trees and shrubs in the temperate and subarctic zones. Well-developed fungal sheaths characterize these mycorrhizae, along with special structures called Hartig nets. Basidiomycetes are the usual mycobionts and often form mushrooms or truffles. Ectomycorrhizae help protect the host plant from diseases by forming a physical fungal barrier to infection.

Anatomy and Development

Individual filaments of a fungal body are called *hyphae*. The entire fungal body is called a *mycelium*. Root infection may occur from fungal spores that germinate in the soil or from fungal hyphae growing from the body of a nearby mycorrhiza. When infection occurs, hyphae are drawn toward certain chemical secretions from a plant root.

In ectomycorrhizae, root hairs do not develop in roots after infection occurs. Infected roots have a *fungal sheath*, or *mantle*, that ranges from 20 to 40 micrometers thick. Fungal hyphae penetrate the root by entering between epidermal cells. These hyphae push cells of the outer root cortex apart and continue to grow outside of the cells. This association of hyphal cells and root cortex cells is called a *Hartig net*. In ectomycorrhizae, the mycobionts never invade plant cells, nor do they penetrate the endodermis or enter the vascular cylinder. The root tip may be ensheathed by fungi, but the apical meristem is never invaded. Main roots experience fewer anatomical changes than lateral roots after infection. Lateral roots become thickened, may show the development of characteristic pigments, and grow very slowly. Infected roots also show different branching patterns than those of uninfected roots.

Endomycorrhizae are highly variable in structure. Many endomycorrhizae do not have sheaths or Hartig nets. In all endomycorrhizae, hyphae penetrate into root cortex cells, while portions of the mycelium remain in contact with the soil. The hyphae that remain in the soil are important in fungal reproduction and produce large numbers of haploid spores. Fungi do not invade root meristems, vascular cylinders, or chloroplast-containing cells in the plant.

Some of the host cells contain fungal extensions called *vesicles* that are filled with lipids. Vesicles are specialized structures that are often thick-walled and may serve as storage sites or possibly in reproduction. Vesicles are also produced on the hyphae that grow in the soil. Near the vascular cylinder, the hyphae branch dichotomously and form large numbers of thin-walled tubules called *arbuscules* that invade host cells. The arbuscules cause the host membranes to fold inward, creating a plant-fungus interface that has a very large surface area. The arbuscules last for about fourteen days before they break down on their own or are digested by the host cell. Host cells whose fungal arbuscules have broken down may be reinvaded by other hyphae.

Darrell L. Ray

See also: Ascomycetes; *Basidiomycetes*; Coevolution; Deuteromycetes; Fungi; Legumes; Nitrogen fixation; Roots; Zygomycetes.

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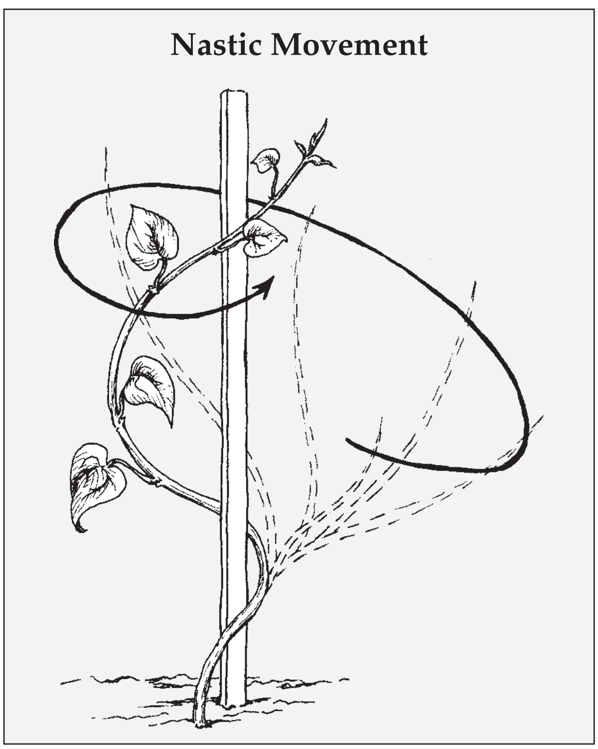
NASTIC MOVEMENTS

Categories: Animal-plant interactions; movement; physiology

Plants, unlike animals, are sedentary organisms, but they are capable of some limited movements. These include nastic movements, which enable plants to adapt rapidly to changes in their environment by changing orientation.

Nastic movements and tropisms, or growth movements, are two important, but different, kinds of movements in plants. In nastic movements, the direction of movement is determined by the anatomy of the plant rather than by the position of the origin of the stimulus. In tropisms, the movement is in a direction either toward or away from the origin of the stimulus. In addition, the orientational changes that occur in nastic movements are temporary; they are reversible and repeatable. The tropisms, in contrast, are generally irreversible.



Kimberly L. Dawson Kurnizki

Nastic movements are controlled by hormones that result in cell growth across stem tips at changing positions. When a twining plant grows, such alterations in growth push the stem tip in different directions. When the stem touches an obstacle such as a stake or other support structure, it will spiral around that structure. Such movement, driven by hormones, is not the same as a tropism, which is a response to external stimuli.

Nastic movements are common in certain plant families, especially among the legumes (family *Fabaceae*, formerly *Leguminosae*). In legumes having leaves that are composed of many leaflets—that is, compound—both the leaflets and the leaves may exhibit the movements. The most widely occurring nastic movements are probably day-and-night movements, known as *nyctinastic movements*. Another important kind is *thigmonastic movements*, triggered by touch or other mechanical stimuli.

Nyctinastic Movements

The leaves of many plants respond to the daily alternation between light and darkness by moving up and down. In these nyctinastic, or sleep, movements, the leaves extend horizontally (open) to intercept sunlight during the day and fold together vertically (close) at night. Leguminous plants exhibiting nyctinastic movements include the sensitive plant (*Mimosa pudica*) and the silk tree (*Albizzia julibrissin*). The movements also occur in some species of oxalis (family *Oxalidaceae*). In the prayer plant, maranta species (family *Marantaceae*), the leaves, which are simple, fold at night into a vertical configuration that suggests praying hands.

Thigmonastic Movements

Mechanical disturbances that may trigger thigmonastic movements include touch, shaking, or electrical or thermal stimulation. The stimulus is transmitted from touch-sensitive cells to responding cells located elsewhere in the plant. Many of the plants that display thigmonastic movements are ones that also exhibit nyctinastic ones, such as some members of the *Fabaceae* and *Oxalidaceae*.

The sensitive plant exhibits pronounced thigmonastic movements. If even a single leaflet is touched, it and the other leaflets of the leaf fold upward in pairs until their surfaces touch. The signal moves down the leaf stalk, or petiole, which droops, and then proceeds to the rest of the shoot. If the plant is allowed to rest, the leaves return to their original orientation in fifteen to twenty minutes. The adaptive significance of thigmonastic movements to most plants is not well understood. Some evidence suggests that the movements may scare off leaf-eating insects.

Many plants require a stronger stimulus than does the sensitive plant in order for a response to be generated. A notable exception is Venus's flytrap (*Dionaea muscipula*, in the family *Droseraceae*). The leaves of this carnivorous plant respond in a rapid, highly specialized way, and the purpose is predatory, not defensive. An insect alighting on a leaf, which has two lobes, stimulates sensitive "trigger" hairs on the leaf epidermis, or surface layer of cells. Within about a half-second, the two lobes of the leaf snap shut. Enzymes digest the insect in one to several days, and the empty trap then reopens.

Physiological Mechanisms

The "motor" that drives most nastic movements is a controlled change in turgor pressure, which is the pressure exerted on a cell wall due to movement of water into the cell. In the sensitive plant and many other thigmonastically responsive plants, these turgor changes occur in certain large, thin-walled cells that function as motor cells, located at the bases of the leaf blades or petioles, and leaflets, if present. The motor cells surround a central strand of vascular, or conducting, tissue, forming a jointlike thickening called a pulvinus.

Movement occurs when there are differential turgor changes in the thin-walled cells on opposite sides of a pulvinus, resulting in differential contraction and expansion of these cells. The turgor changes are triggered when potassium ions (K^+) and other ions move into or out of the cells, and water follows by osmosis (as in the opening and closing of stomata in the leaf epidermis). Cells on one side of the pulvinus function as extensors, and cells on the opposite side function as flexors. Leaves or leaflets open when extensor cells accumulate K+ and then swell with water and flexor cells lose K+ and then shrink from loss of water. Conversely, the leaf or leaflet closes when the extensor cells shrink and the flexor cells swell.

The mechanisms causing these ion fluxes vary. In nyctinastic movements, the fluxes and the pulvinal turgor changes that they trigger are rhythmic and are regulated by interactions between light and the plant's innate biological clock. Phytochrome, a plant pigment involved in many timing processes, including flowering, plays a role in this regulation. In thigmonastic movements, the touching of a leaf or leaflet generates an electrical signal called an action potential. This signal typically moves along the stalk of the leaflet and leaf. It is then translated into a chemical signal that causes the ion fluxes and pulvinal turgor changes.

In Venus's flytrap, touching of the hairs on a leaf surface generates an action potential. There are no pulvini to respond, however. The underlying biochemical mechanisms of trap closure are not well understood. They may involve turgor changes in a layer of photosynthetic cells immediately beneath the leaf's upper epidermis.

Jane F. Hill

See also: Carnivorous plants; Circadian rhythms; Leaf anatomy; Osmosis, simple diffusion, and facilitated diffusion; Photoperiodism; Thigmomorphogenesis; Tropisms; Water and solute movement in plants.

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NITROGEN CYCLE

Categories: Biogeochemical cycles; cellular biology; ecology; nutrients and nutrition

The nitrogen cycle outlines the movement of the element nitrogen from one chemical state to another as it makes its way through a series of complex physical and biological interactions.

Nitrogen (N) is one of the most dynamic elements in the earth's biosphere; it undergoes transformations that constantly convert it between organic, inorganic, gaseous, and mineral forms. Nitrogen is an essential element in all living things, where it is a crucial component of organic molecules such as proteins and nucleic acids. Consequently, nitrogen is in high demand in biological systems.

Unfortunately, most nitrogen is not readily available to plants and animals. Although the biosphere contains 300,000 terrograms (a terrogram is a billion kilograms) of nitrogen, that amount is one hundred times less nitrogen than is in the hydrosphere (23 million terrograms) and ten thousand times less nitrogen than is in the atmosphere (about 4 billion terrograms). Atmospheric nitrogen is almost all in the form of nitrogen gas (N_2), which composes 78 percent of the atmosphere by volume. The greatest reservoir of nitrogen on the earth is the lithosphere (164 billion terrograms). Here the nitrogen is bound up in rocks, minerals, and deep ocean sediments.

Even though living things exist in a "sea" of nitrogen gas, it does them little good. The bond between the nitrogen atoms is so strong that nitrogen gas is relatively inert. For living things to use nitrogen gas, it must first be converted to an organic or inorganic form. The nitrogen cycle is the collection of processes, most of them driven by microbial activity, that converts nitrogen gas into these usable forms and later returns nitrogen gas back to the atmosphere. It is considered a cycle because every nitrogen atom can ultimately be converted by each

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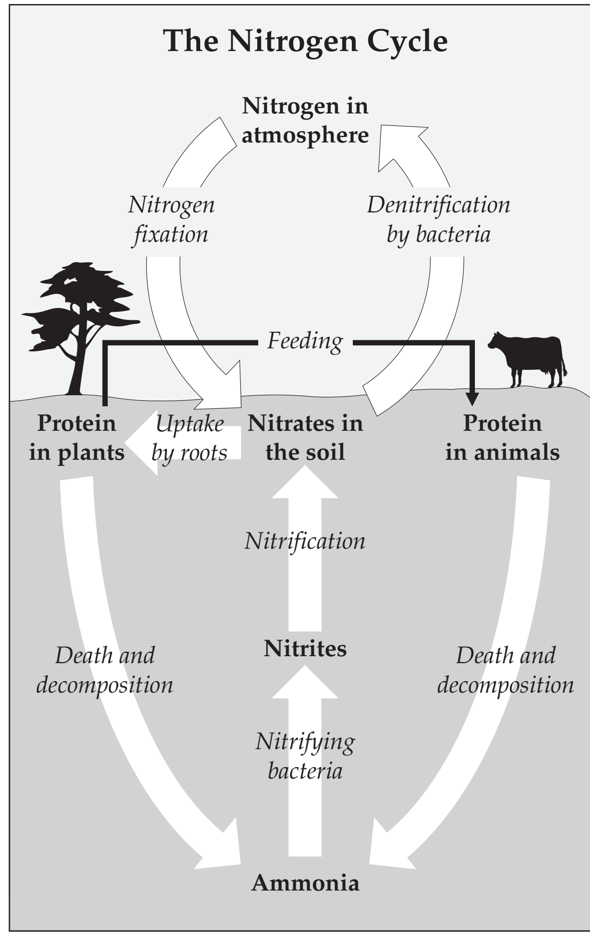
process, though that conversion may take a long time. It is estimated, for example, that the average nitrogen molecule spends 625 years in the biosphere before returning to the atmosphere to complete the cycle.



Nitrogen Fixation

The first step in the nitrogen cycle is *nitrogen fixation*. Nitrogen fixation is the conversion, by bacteria, of nitrogen gas into ammonium (NH_4^+) and then organic nitrogen (proteins, nucleic acids, and other nitrogen-containing compounds). It is estimated that biological nitrogen fixation adds about 160 billion kilograms of nitrogen to the biosphere each year. This represents about half of the nitrogen taken up by plants and animals. The microorganisms that carry out nitrogen fixation are highly specialized. Each one carries a special enzyme complex, called *nitrogenase*, that allows it to carry out fixation at temperatures and pressures capable of permitting life—something industrial nitrogen fixation does not allow.

Nitrogen-fixing microbes, may be either free-living or growing in association with higher organisms such as legumes (in which case the process is called *symbiotic nitrogen fixation*). Symbiotic nitrogen fixation is a very important process and is one reason legumes are so highly valued as a natural resource. Because they are able to form these symbiotic associations with nitrogen-fixing bacteria, legumes can produce seeds and leaves with more nitrogen than other plants. When they die, they return much of that nitrogen to soil, enriching it for future growth.

Mineralization and Nitrification

When plants and animals die they undergo a process called *mineralization* (also called *ammonification*). In this stage of the nitrogen cycle, the organic nitrogen in decomposing tissue is converted back into ammonium. Some of the ammonium is taken up by plants as they grow. This process is called *assimilation* or *uptake*. Some of the ammonium is taken up by microbes in the soil. In this case the nitrogen is not available for plant growth. If this happens, it is said that the nitrogen is immobilized. Some nitrogen is also incorporated into the clay minerals of soil. In this case it is said that the nitrogen is fixed—it is not immediately available for plant and microbial growth, but it may become available at a later date.

Ammonium has another potential fate, and this step in the nitrogen cycle is *nitrification*. In nitrification the ammonium in soil is oxidized by bacteria (and some fungi) to nitrate (NO_3^-) in a two-step process. First, ammonium is oxidized to nitrite. Next, nitrite is rapidly oxidized to nitrate. Nitrification requires oxygen, so it occurs only in well-aerated environments. The nitrate that forms during nitrification can also be taken up by plants and microbes. However, unlike ammonium, which is a cation (positively charged ion) and readily adsorbed by soil, nitrate is an anion (negatively charged ion) and readily leaches or runs off of soil. Hence, nitrate is a serious water contaminant in areas where excessive fertilization or manure application occurs.

Denitrification

Obviously some process is responsible for returning nitrogen to the atmosphere; otherwise organic and inorganic nitrogen forms would accumulate in the environment. The process that completes the nitrogen cycle and replenishes the nitrogen gas is *denitrification*. Denitrification is a bacterial process that occurs in anaerobic (oxygen-limited) environments such as waterlogged soil or sediment. Nitrate and nitrite are reduced by denitrifying bacteria, which can use these nitrogen oxides in place of oxygen for their metabolism. Wetlands are particularly important in this process because at least half of the denitrification that occurs in the biosphere occurs in wetlands.

The major product of denitrification is nitrogen gas, which returns to the atmosphere and approximately balances the amount of nitrogen gas that is biologically fixed each year. In some cases, however, an intermediate gas, nitrous oxide (N_2O), accumulates. Nitrous oxide has serious environmental consequences. Like carbon dioxide, it absorbs infrared radiation, so it contributes to global warming. More important, when nitrous oxide rises to the stratosphere, it contributes to the catalytic destruction of the ozone layer. Besides the potential for fertilizer nitrogen to contribute to nitrate contamination of groundwater, there is the concern that some of it can be denitrified and contribute to ozone destruction.

The nitrogen cycle is a global cycle involving land, sea, and air. It circulates nitrogen through various forms that contribute to life on earth. When the cycle is disturbed—as when an area is deforested and nitrogen uptake into trees is stopped, or when excessive fertilization is used—nitrogen can become an environmental problem.

Mark S. Coyne

See also: Nitrogen fixation; Nutrient cycling; Nutrients.

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NITROGEN FIXATION

Categories: Cellular biology; nutrients and nutrition; physiology

Nitrogen fixation is the process whereby elemental nitrogen from the atmosphere is converted to ammonium, an ionic form of nitrogen available to higher plants.

Nitrogen, the fourth most abundant element in most organisms, can account for as much as 4 percent of a plant's dry weight. The majority of this nitrogen is present as a constituent of protein structure, but it is also a component of numerous other biological compounds, such as the chlorophylls and nucleic acids. Thus, for normal plant growth and development, nitrogen must be maintained at fairly high levels in the soil.

The earth's atmosphere is about 79 percent nitrogen, and the vast majority of atmospheric nitrogen exists in the elemental state. Unfortunately, the elemental form of nitrogen is of no direct value to higher plants; they must acquire their nitrogen in the form of either ammonium or nitrate. These two forms of nitrogen can be supplied to the soil as fertilizer by humans or by nature, as the product of microbial action.

There are three microbial processes that render nitrogen into forms usable by higher plants. These are *ammonification*, *nitrification*, and *nitrogen fixation*. Ammonification is the process whereby various forms of organic nitrogen, such as is present in the proteins in plant and animal residues and animal wastes (manures), are converted to ammonium. Nitrification is the process by which ammonium is converted to nitrate. Both these processes are carried out by populations of free-living soil microorganisms.

In the nitrogen fixation process, atmospheric nitrogen is converted to ammonium. While some of the nitrogen fixers are free-living microbes, bacteria that live symbiotically within the roots of a number of plant species are also responsible for much of this conversion in terrestrial ecosystems.

Nitrogen-Fixing Bacteria

Nitrogen-fixing bacteria have been shown to coexist with a variety of lower plants, including lichens, liverworts, mosses, and ferns. Among the more advanced seed-bearing plants, nitrogen fixers have been found to be associated with some tropical grasses and a number of shrubs and trees, such as the alders. Agriculturally, the legumes are the most important group of plants coexisting with nitrogen-fixing bacteria. Some fifteen hundred species of legumes, including peas, beans, clover, and alfalfa, have been shown to live symbiotically with nitrogen-fixing bacteria called *Rhizobium*. A different species of *Rhizobium* infects each different species of legume.

The bacteria penetrate the root by entering the filamentous projections of epidermal cells called *root hairs*. The epidermal cells respond to the inva-

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sion by enclosing the bacterium in a threadlike structure referred to as an *infection thread*. The infection thread begins to grow and branch, and, as it does so, the Rhizobia reproduce numerous times inside the thread. After penetrating several layers of cells, the infection thread eventually reaches the *root cortex*, where it ruptures and releases the encased bacteria.

The release of the bacteria induces the secretion of plant hormones that stimulate specialized root cortical cells to divide several times. As these cells divide, the Rhizobia are encapsulated, and a nodule is formed. Within the *cytosol* of the nodule cells, the bacteria become nonmotile, increase in size, and accumulate in groups of four to eight *bacteroids*. These bacteroids are responsible for the biochemical conversion of elemental nitrogen to ammonium.

Chemistry of Nitrogen Fixation

Chemically, the fixation of nitrogen requires that six electrons and eight hydrogen ions be transferred to the atmospheric nitrogen molecule. This reaction is an energy-requiring process; therefore, *adenosine triphosphate* (ATP), the cell's form of stored energy, must be available for the reaction to take place. The electrons, hydrogen ions, and ATP are supplied by the cellular respiration process that takes place in the root cells.

The electrons and hydrogen ions are transferred to the atmospheric nitrogen atom by an enzyme called *nitrogenase*. This enzyme consists of two subunits. One subunit takes the electrons and hydrogen ions from the respiratory products and transfers them to the other subunit. The ATP binds with part II of the nitrogenase, and the hydrolysis of the ATP releases the energy stored in the molecule.

This energy drives the reaction and makes it even easier to pass the electrons and hydrogen ions on to the second subunit. In the last step, the nitrogenase transfers the electrons and hydrogen ions to the nitrogen atom. This final transfer results in the production of ammonium. The ammonium moves out of the bacteroids into the cytosol, where it is converted to an organic form of nitrogen that can be transported throughout the plant.

Rates of Fixation

Not all species fix nitrogen at the same rate. A number of factors can account for these differences. Some plants form nodules much more abundantly than others. Because of their more extensive nodule formation, these plants will fix more nitrogen than those that produce fewer nodules.

The nitrogenase of all rhizobial species has a tendency to transfer electrons to hydrogen ions rather than to nitrogen. As a result, hydrogen gas, which escapes into the atmosphere, is produced. This represents a loss of electrons that could have been used to produce ammonium. Some Rhizobia species, however, have a second enzyme, called hydrogenase, which uses the hydrogen gas to produce water. ATP is produced as a byproduct of this process. Consequently, these rhizobial species are more efficient because less energy is wasted.

In addition, the fixation rate and the amount of nitrogen fixed will vary with age or the stage of plant development. In most cases, fixation rates are highest when the fruits and seeds are being produced. The seeds of many plants, and especially legumes, are high in protein. Hence, nitrogen fixation and transport out of the nodules must be higher at the time the seeds are developing. In fact, more than 85 percent of the total nitrogen fixation in legumes occurs at such times.

Plant-Bacteria Mutualism

The nitrogen-fixing bacteria exist in a symbiotic relationship with their plant hosts. The bacteria supply the plant with much-needed nitrogen, while the plant supplies the bacteria with carbohydrates and other nutrients. Some of the energy, derived from the plant-supplied carbohydrates, is used in nitrogen fixation, but there is ample left over to supply the bacteria with all the energy necessary for their survival.

Providing Nitrogen

Plant production throughout the world is limited more by the shortage of nitrogen than by any other nutrient. The root zone that encompasses the upper 15-centimeter layer of soil contains from 100 to 6,000 kilograms of total nitrogen per hectare. This includes all forms of nitrogen, many of which are not available to plants. The total nitrogen content is determined by a number of factors, such as the minerals making up the soil, the kinds of vegetation, and the extent to which these factors are affected over time by climate, topography, and the presence of people.

Ammonium and nitrate are the only forms readily available to plants. These two molecules, in addition to those such as organic nitrogen compounds that can easily be converted to the available forms, are the only ones of ecological or agricultural importance. Unfortunately, these forms of nitrogen are continually being removed from the soil. Crop removal, *leaching* (the removal of minerals as water percolates through the soil), *denitrification* (the process by which anaerobic microbes convert nitrates to gaseous nitrogen-containing compounds that escape the soil), and erosion account for a total loss of approximately 125 kilograms per hectare annually. While some of the lost nitrogen can be replaced by available forms falling to the earth in rain, that amount is much too low to be of value in plant growth. Microbial fixation and the application of fertilizers are the only sources that supply sufficient nitrogen for plant growth.

Research Applications

The nonsymbiotic nitrogen fixers are of extreme ecological importance, especially in nonagricultural soils. Forest, desert, and prairie ecosystems are dependent on nitrogen fixation by free-living species to replace the annual nitrogen loss. Without it, growth of a number of plant species would suffer, and food chains in these ecosystems would soon be disrupted. A number of studies have investigated the advantages of incorporating free-living nitrogen fixers into nonlegume crop production, but clear benefits are uncertain.

On the other hand, knowledge of symbiotic nitrogen fixation have resulted in definite improvements in the production of legume crops. When *Rhizobium* is included with seeds as they are planted, increased yields have been observed in nearly every case. There is considerable interest in enhancing the efficiency of the nitrogen-fixing process by increasing nodulation in the roots of some species or by incorporating the hydrogenase system into species that do not have it. An increase in biological nitrogen fixation could enhance the nitrogen content of the soil and decrease the dependency on commercial nitrogen fertilizers.

The application of nitrogen fertilizers to nonleguminous crops was once one of the best investments a farmer could make. Commercial fertilizers, however, have become very expensive because of increased energy costs. In addition, a number of environmental problems have developed from the accumulation of nitrates from fertilizers in rivers, ponds, and lakes. Consequently, there is a renewed interest in symbiotic nitrogen fixation. For years, before the extensive use of nitrogen fertilizers, farmers planted legume crops alternately with other crops. The legume crops were plowed under to supply nitrogen to the soil. There has been a resurgence in this technique. In fact, there is considerable interest in growing plants containing symbiotic nitrogen fixers in the same fields with plants lacking symbiotic nitrogen fixers, to improve the natural nitrogen balance in certain environments. There are a number of studies directed at incorporating nitrogen fixation into nonlegume crop plants; this research is difficult, however, because the genetics of the process is so complex.

D. R. Gossett

See also: ATP and other energetic molecules; Eutrophication; Fertilizers; Lichens; Mycorrhizae; Nitrogen cycle; Nutrients.

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NONRANDOM MATING

Categories: Genetics; reproduction and life cycles

Nonrandom mating occurs in plants when there is inbreeding or assortative mating. The consequence of nonrandom mating is that population genotype frequencies do not exist in Hardy-Weinberg equilibrium. Although nonrandom mating does not directly drive evolutionary change—meaning allele frequencies are not altered—it can have a profound effect on genotype frequencies and hence can indirectly affect evolution.

There are three main ways for nonrandom mating to occur. First, *positive assortative mating* results when individuals and their mates share one or more phenotypic characteristics with themselves. *Negative assortative mating* occurs when individuals and their mates are dissimilar phenotypically.

Inbreeding is a third form of nonrandom mating that occurs when individuals mate with relatives more often than would be expected by chance. For both inbreeding and assortative mating, genes combine in such a way that offspring genotypes differ from those that are predicted by the most basic population genetic model, described by the *Hardy-Weinberg theorem*. One assumption of the Hardy-Weinberg theorem, which predicts unchanging equilibrium values for genotype and allele frequencies, is that individuals mate at random. Unlike other violations of this model (such as natural selection, genetic drift, mutation), nonrandom mating affects genotype but not allele frequencies.

Inbreeding

Inbreeding is very common in many plant species for two main reasons. First, seed dispersal tends to follow a leptokurtic distribution, such that most seed falls near the parent plant. This results in near neighbors that are closely related and increases the probability that short-distance pollen movement will result in mating among relatives. In small populations with a limited number of potential mates, such matings between relatives are also common. Second, most flowering plants are hermaphroditic or monoecious. Thus, individual plants produce both male and female gametes and are capable of self-fertilization, the most extreme form of inbreeding.

The degree to which inbreeding occurs in a population depends upon the probability that an individual will mate with a relative or with itself. A plant's mating system is characterized by the degree to which *self-fertilization* occurs and can range from complete outcrossing to complete self-fertilization, or selfing. While certain plant families tend to be characterized by a particular mating system (such as the inability to self-fertilize in the passionflower family, *Passifloraceae*), others exhibit great diversity in the levels of inbreeding among species (the grasses, *Poaceae*, and the legumes, *Fabaceae*).

For species with a mixed mating system, and which therefore engage in both selfing and outcrossing, the degree to which individual offspring are inbred is highly variable. Flowers with multiple ovules within an ovary can produce fruits with both selfed and outcrossed seeds. Some plants, such as violets (*Viola*) and jewelweed (*Impatiens*), produce morphologically distinct flowers for selfing and outcrossing.

Consequences of Inbreeding

Inbreeding has a larger evolutionary impact than assortative mating because it can affect all genes in the population. It can have negative consequences for plant survival and reproduction (fitness) because it tends to increase homozygosity and decrease heterozygosity. In response to these negative effects, collectively known as *inbreeding depression*, plants have evolved numerous adaptations to reduce levels of inbreeding. Although evidence for inbreeding depression in plants has been found, many species of plants are almost completely self-fertilizing and do not appear to suffer fitness consequences.

Under certain conditions, inbreeding may be advantageous. For example, rare plants or plants with rare pollinators may have few opportunities for outcrossing, and thus, self-fertilization provides a level of reproductive assurance. Many weedy plant species that tend to colonize disturbed sites are, in fact, capable of self-fertilization. Common crop weeds such as velvetleaf (*Abutilon theophrasti*) and shepherd's purse (*Capsella bursa-pastoris*) predominantly self-fertilize. In these species, inbreeding may provide benefits that outweigh any associated costs. It has also been suggested that inbreeding species are better able to adapt to local environmental conditions because fewer maladapted genes from other populations would enter through outcrossing.

Reducing Inbreeding Depression

Inbreeding depression (which occurs when alleles that decrease fitness drift to fixation, causing a decrease in average fitness within a population) is reduced when plants are genetically or morphologically unable to self-fertilize. Genetic self-incompatibility, which is thought to occur in more than forty different plant families (for example, *Brassicaceae*, *Solanaceae*, and *Asclepiadaceae*) prevents mating between individuals that share certain genes that are involved in the interaction between pollen grains and the stigma or style. Morphological adaptations that reduce self-fertilization include those that separate anther and stigma maturation in time (protandry and protogyny) or space (heterostyly).

The individual hermaphroditic flowers of protandrous plants, such as phlox, shed their pollen prior to the time when the stigma on the same flower is receptive. Protogyny, which is less common than protandry, occurs when stigma receptivity occurs first (as in *Plantago lanceolata*). Dioecious plant species, such as date palms (*Phoenix*) and marijuana (*Cannabis sativa*), avoid selfing by having unisexual male and female flowers on separate individuals. In some hermaphroditic species, selfing is avoided when flower morphology favors crosses between certain flower phenotypes, as in the case of heterostyly.

Assortative Mating

Assortative mating generally affects only those traits important for reproduction. Many primrose (*Primula*) species are distylous, having two types of flowers. Flowers with the pin morphology have a tall style and relatively short stamens, while flowers with thrum morphology have a short style and long stamens. Insect-mediated pollen transfer results in matings between pin and thrum but not between two pin or two thrum plants. The result is nonrandom negative assortative mating. Unlike inbreeding, negative assortative mating tends to increase the level of heterozygosity in a population, at least for those traits that are involved in mate choice (such as relative style length).

Positive assortative mating, like inbreeding, results in increased homozygosity and decreased heterozygosity. Positive assortative mating for flowering time, for example, is common in many plant populations because individuals that flower early in the season will tend to mate with other early-flowering individuals.

Cindy Bennington

See also: Angiosperm life cycle; Flower types; Genetics: mutations; Genetics: post-Mendelian; Hardy-Weinberg theorem; Hybridization; Pollination; Population genetics; Reproduction in plants; Species and speciation.

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NORTH AMERICAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

North American crops include grains, legumes, fruits, vegetables, and plants for clothing and other nonfood uses. A discussion of modern agriculture in North America cannot be complete without some attention to agribusiness, the system of businesses associated with agricultural production in an industrialized society.

In North America, agriculture generally has become mechanized and heavily dependent upon an integrated system of supporting *agribusinesses*, although traditional practices continue in Mexico. In the United States and Canada, most farmers and ranchers depend heavily upon technology, although groups such as the Amish have rejected automation and continue to use animal power for traction. Most farmers practice *monoculture*, relying upon a single crop for their primary income, and have expanded to very large acreages in order to take advantage of economies of scale. Such farms are referred to in terms of the primary crop, for example, a dairy farm, a cattle ranch, or a wheat farm. Some small farms are run by part-time farmers who also have other occupations.

Selected Agricultural Products of North America

Within the United States, there were 2,192,000 farms, cultivating a total of 954,000,000 acres, in the 1990's. These farms produced net returns of $44.1 billion. Although farmers represented less than 2 percent of the U.S. population, they successfully fed the country at a high standard of living, produced grain and other products for export, and still maintained a surplus carryover of as much as 2 percent of the total grown.

Regional Crops and Cultivation

Modern farming techniques in the United States and Canada require specialization in a single *cash crop*. Such specialized farms tend to cluster by region, where the climate and soil quality are appropriate to a given crop. The supporting agribusinesses—such as suppliers of implements, chemical *fertilizers* and *pesticides*, and grain elevators—tend to specialize in products and activities that support the primary crops of their given area.

Wheat, the most important cereal grain in Western diets, grows in the broad, open lands of the Great Plains, in Kansas, Nebraska, North and South Dakota, and the Canadian provinces of Alberta and Saskatchewan.

In the southern part of this region, the primary crop is winter wheat, which is planted in the fall, is dormant during the winter, completes its growth in spring, and is harvested in midsummer. In many of these areas, a farmer then can plant a crop of soybeans, a practice known as *double-cropping*. The soybeans often can be harvested in time to plant the following year's wheat crop in the fall. Farther to the north, where the weather is too harsh for wheat to survive the winter, farmers plant spring wheat, which completes its entire growth during the spring and summer and is harvested in the fall. Wheat is used to make bread, pasta, and many breakfast cereals and is an ingredient in numerous other products.

Corn, which originally was domesticated by American Indians, is the best producer per acre. It requires a longer growing season than wheat, so areas where it can be grown economically are limited. The Midwestern states—Iowa, Illinois, Indiana, Ohio—are the principal areas for cultivation of corn and frequently are referred to as the Corn Belt states. Much corn is used as livestock feed, although a considerable amount is processed into human foods as well, often in the form of cornstarch and corn-syrup sweeteners.

Rice requires flooded fields for successful cultivation, so it can be grown only in areas such as Louisiana, where large amounts of water are readily available. Because labor costs are the primary limiter in U.S. agriculture, American rice growers use highly mechanized, single-field growing techniques rather than the labor-intensive transplantation technique used in Asian countries. Laser levels and computerized controls tied into the Global Positioning System enable farmers to prepare smooth fields with a slight slope for efficient flooding and drainage. Because the ground is usually wet during tilling and harvesting, the machinery typically used in growing rice is fitted with tracks instead of wheels to reduce soil compaction.

Rye, oats, and barley are other major grain crops, although none form the backbone of an area's economy to the extent that wheat, corn, and rice do. Oats, once a staple feed grain for horses, now is used mainly for breakfast cereals, while most barley is malted for brewing beer. Rye typically is used in the production of specialty breads.

Legumes, such as soybeans and alfalfa, form the next major group of crops produced in North America. In addition to being an important source of protein in human and livestock diets, legumes are important in maintaining soil fertility. Nodules on their roots contain bacteria that help to transform nitrogen in the soil into compounds that plants can use. Because of this, soybeans have also become a regular *rotation crop* with corn in much of the U.S. Midwest.

Both corn and soybeans can be grown with the same machinery and sold to the same markets, although harvesting corn requires a specialized cornheader that pulls down the stalks and breaks loose the cob on which the corn kernels grow, rather than the generalized grain platform used with soybeans and small grains. Soybeans for human consumption generally are heavily processed and become filler in other foods, although there is a market for tofu (bean curd) and other soybean products.

Other crops include edible oil seeds, such as sunflower seeds and safflower seeds, which are generally grown as rotation crops with corn or wheat. Sugarcane is grown in Louisiana and other areas on the coast of the Gulf of Mexico that have the necessary subtropical climate. Many varieties of fruits and vegetables are grown in California's irrigated valleys; Florida grows much of the United States' juice oranges. Other citrus crops are grown in Alabama, Mississippi, and Texas, where these warmthloving trees will not be damaged by frost. Fruits such as apples and pears, which require a cold period to break dormancy and set fruit, are grown in northern states such as Michigan and Washington and the eastern provinces of Canada.

Fibrous Plants

In addition to food plants, the production of fibers for textiles is an important part of American agriculture, although such artificial fibers as nylon and polyester have taken a share of the market. Cotton and flax also are important sources of natural fibers. Cotton requires a long growing season and relatively high rainfall levels; therefore, it generally is grown in an area in the southern United States often referred to as the Cotton Belt. Flax has a shorter growing season and is often planted in rotation with such small grains as wheat and oats. Flax stems are used to produce linen, and edible oils and meal are obtained from its seeds.

Trees have become a cultivated species, although their long growth cycle has limited the ability of humans to create particular varieties. During the twentieth century, concerns about the environmental damage done by the *clear-cutting* of virgin forests for lumber and paper encouraged many companies to reseed the cut areas with tree species that could be harvested thirty or forty years later. Another form of tree farming, although on a much smaller scale, is the production of small evergreens for Christmas trees.

The Business of Farming

Because of the intense specialization of modern mechanized agriculture, farming has become a business interlocked with a number of supporting businesses. Farm management—the control of capital outlay, production costs, and income—has become as vital to a farmer's economic survival as skill in growing the crops themselves. Such organizations as Farm Business/Farm Management help farmers develop the skills needed to farm more productively and economically.

Image Not Available

Farmers also have had to become actively involved in the marketing of their crops to ensure an adequate income. In many areas of the United States and Canada, farmers have banded together in cooperatives to gain economic leverage in buying supplies and selling their products. Some of these cooperatives have taken on some of the preliminary and intermediate steps in transforming the raw farm products into consumer goods, thus increasing the prices farmers receive from buyers.

Modern farmers also are concerned with the management of the resources that support agriculture. In earlier generations, it often was assumed that natural resources were unlimited and could be used and abused without consequence. The result of this ignorance was ecological destruction such as the Dust Bowl of the 1930's, in which the *topsoil* over large areas of U.S. Plains States dried up and blew away in the wind, rendering the land unfarmable. To prevent more disasters and the economic dislocation they produced, various soil conservation measures were introduced through government programs that gave farmers financial incentives to change their practices. The use of contour plowing and terracing on steeply sloping hillsides helped to slow the movement of water that could carry away soil, thus preventing the formation of gulleys. Reduced tillage techniques allowed more plant residue to remain on the surface of the soil, protecting it from the ravages of both wind and water.

Leigh Husband Kimmel

See also: African agriculture; Agriculture: modern problems; Asian agriculture; Australian agriculture; Central American agriculture; Corn; Erosion and erosion control; European agriculture; Grazing and overgrazing; Green Revolution; High-yield crops; Legumes; Monoculture; North American flora; Rice; South American agriculture; Wheat.

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NORTH AMERICAN FLORA

Category: World regions

The world's major biomes are all represented in the diverse vegetation of North America, from Arctic tundra in the north to deserts in the Southeast and the grasslands, wetlands, and various forest biomes between.

Forest is the native vegetation of almost half of mainland Canada and the United States. Before European settlement, forestlands dominated the eastern, and much of the northern, part of the continent. Grasses covered a large part of the continental interior. Desert vegetation is native in the Southwest, *tundra* in the far north. Over much of the continent, however, human activity has virtually eliminated native vegetation.

Coniferous Forests of the West

Along the Pacific coast from Alaska to Northern California, evergreen *coniferous forest* grows luxuriantly, watered by moisture-laden winds blowing from the ocean. This lowland forest includes some of the largest and longest-lived trees in the world. North of California, characteristic trees include Sitka spruce, western hemlock, and western red cedar. Douglas fir, one of the major timber species in

North America, is also common. The northwest coastal coniferous forest is sometimes called temperate rain forest because, in its lushness, it resembles the tropical rain forests. Many of the trees of the coastal forest have been cut for timber.

In California, the dominant coastal conifer species is the coast redwood. The tallest tree in the world, coast redwood reaches 330 feet (100 meters) and can live two thousand years. Coniferous forest also grows along the Cascade Mountains and the Sierra Nevada. Trees of the Cascades include mountain hemlock and subalpine fir at high elevations and western hemlock, western red cedar, and firs somewhat lower. Sierra Nevada forests include pines, mountain hemlock, and red fir at high elevations; and red and white firs, pines, and Douglas fir somewhat lower. Ponderosa pine is dominant at low mountain elevations in both of these Pacific ranges.

The giant sequoia, long thought to be the largest living organism on earth, grows in scattered groves in the Sierra Nevada. (The largest organism actually may be a very old tree root-rot fungus that covers 1,500 acres in Washington State.) Although shorter than the coast redwood, the giant sequoia is larger in trunk diameter and bulk. It can reach 260 feet (80 meters) tall and 30 feet (10 meters) in circumference.

Coniferous forest also dominates the Rocky Mountains and some mountainous areas of Mexico. In the Rockies, Englemann spruce and subalpine fir grow at high elevations, and Douglas fir, lodgepole pine, and white fir somewhat lower. Ponderosa pine grows throughout the Rockies at low elevations and is a dominant tree in western North America.

Boreal Coniferous Forest

Just south of the Arctic tundra in North America is a broad belt of *boreal*, *coniferous*, *evergreen forest*. It is often called *taiga*, the Russian name for similar coniferous forests growing in northern Eurasia. However, in large areas of northeastern Siberia, the dominant tree is larch, which is deciduous, whereas the North American taiga is mostly evergreen. Taiga is the most extensive coniferous forest in North America, covering nearly 30 percent of the land area north of Mexico. It grows across Alaska and Canada and southward into the northern Great Lakes states and New England. White spruce and balsam fir dominate much of the Canadian taiga.

Eastern Deciduous Forest

A forest of mainly broad-leaved, deciduous trees is the native vegetation of much of eastern North America. Narrow fingers of this forest, growing along rivers, penetrate westward into the interior grasslands. Early settlers from Europe cut most of the eastern forest, but second-growth forest now covers considerable areas. The plants are closely related to plant species of the temperate deciduous forests in Europe and Asia. In contrast, the plants of other biomes in North America are generally not closely related to the plants that occur in the same biomes elsewhere in the world, although they look similar.

In the eastern deciduous forest, maple and oak are widespread—maples especially in the north, oaks in the south. There are major subdivisions within the forest. These include oak and hickory forests in Illinois, Missouri, Arkansas, eastern Texas, and also in the east—Pennsylvania, Virginia, and West Virginia—where oak and chestnut forest formerly predominated; beech and maple forest in Michigan, Indiana, and Ohio; and maple and basswood forest in Wisconsin and Minnesota. The forest in parts of Michigan, Wisconsin, Minnesota, and New England contains not only deciduous trees but also evergreen conifers, including pines and hemlock. Vast native pine stands in the Great Lakes states have been cut for lumber.

Plant diseases have changed the composition of the eastern forest. American chestnut was once an important tree but has now nearly disappeared as a result of an introduced fungal disease. Dutch elm disease is similarly devastating American elms.

Other Forests

The southeastern United States, excluding the peninsula of Florida, once supported open stands of pine and also mixed evergreen and deciduous forest. The *mixed forest* included a variety of pines, evergreen oaks, and deciduous trees. In much of Florida, the native vegetation is a mixture of deciduous and evergreen trees that are subtropical rather than temperate. In many parts of the Southeast, people have replaced the native vegetation with fast-growing species of pines for timber production. In Mexico, tropical rain forests are prominent on the west coast, in the south and east, and in Yucatán. On the south coasts of Mexico and Florida, swamps of mangrove trees are common.

Central Grasslands

The central plains of North America, a wide swath from the Texas coast north to Saskatchewan, Canada, were once a vast *grassland*, the prairie. The climate there is too dry to support trees, except along rivers. From west to east, there is a transition from the more desertlike short-grass prairie (the Great Plains), through the mixed-grass prairie, to the moister, richer, tall-grass prairie. This change is related to an increase in rainfall from west to east. Grasses shorter than 1.5 feet (0.5 meter) dominate the short-grass prairie. In the tall-grass prairie, some grasses grow to more than 10 feet (3 meters). Colorful wildflowers brighten the prairie landscape.

Grassland soil is the most fertile in North America. Instead of wild prairie grasses, this land now supports agriculture and the domesticated grasses corn and wheat. The tall-grass prairie, which had the best soil in all the grasslands, has been almost entirely converted to growing corn. Much of the grassland that escaped the plow is now grazed by cattle, which has disturbed the land and aided the spread of *invasive*, nonnative plants.

Other outlying grasslands occur in western North America. Between the eastern deciduous forest and the prairie is *savanna*, a grassland with scattered deciduous trees, mainly oaks. Savanna also occurs over much of eastern Mexico and southern Florida.

Scrub and Desert

In the semiarid and arid West, the natural vegetation is grass and shrubs. Over a large part of California, this takes the form of a fire-adapted *scrub community* called *chaparral* or *Mediterranean scrub*, in which evergreen, often spiny shrubs form dense thickets. The climate, with rainy, mild winters and hot, dry summers, is like that around the Mediterranean Sea, where a similar kind of vegetation, called *maquis*, has evolved. However, chaparral and maquis vegetation are not closely related genetically. Humans have greatly altered the chaparral through *overgrazing* of livestock and other disturbances.

The North American deserts, which are located between the Rocky Mountains and the Sierra Nevada, cover less than 5 percent of the continent. Shrubs are the predominant vegetation, although there are many species of annuals. Desert plants,


PhotoDisc

Wildflowers grow along a trail at the Grand Canyon in Arizona.

commonly cacti and other *succulents*, are sparsely distributed.

In Southern California, Arizona, New Mexico, West Texas, and northwestern Mexico, there are three distinct deserts. The Sonoran Desert stretches from Southern California to western Arizona and south into Mexico. A characteristic plant of the Sonoran is the giant saguaro cactus. To the east of the Sonoran, in West Texas and New Mexico, is the Chihuahuan Desert, where a common plant is the agave, or century plant. North of the Sonoran Desert, in southeastern California, southern Nevada, and northwestern Arizona, is the Mojave Desert, where the Joshua tree, a tree-like lily, is a well-known plant. It can reach 50 feet (15 meters) in height. Creosote bush is common in all three deserts. To the north, the Mojave Desert grades into the Great Basin Desert, which is a cold desert, large and bleak. The dominant plant of the Great Basin Desert is big sagebrush. Plant diversity there is lower than in the hot American deserts.

Deserts dominated by grasses rather than shrubs once occurred at high elevations near the Sonoran and Chihuahuan Deserts. Much of this area has been overtaken by desert scrub, including creosote bush, mesquite, and tarbush. Cattle grazing may have been a factor in this change. Desert is very fragile; even one pass with a heavy vehicle causes lasting damage.

Tundra

Tundra vegetation grows to the northern limits of plant growth, above the Arctic Circle, in Canada. The flora consists of only about six hundred plant species. In contrast, tropical regions that are smaller in area support tens of thousands of plant species. *Arctic tundra* is dominated by grasses, sedges, mosses, and lichens. Some shrubby plants also grow there. Most tundra plants are perennials. During the short Arctic growing season, many of these plants produce brightly colored flowers. Like desert, tundra is exceptionally fragile, and it takes many years for disturbed tundra to recover. Tundra also occurs southward, on mountaintops, from southern Alaska into the Rocky Mountains, the Cascades, and the Sierra Nevada. This *alpine tundra* grows at elevations too high for mountain coniferous forest.

Coastal Vegetation

Along the coasts of the Atlantic Ocean and the Gulf of Mexico, the soil is saturated with water and is very salty. Tides regularly inundate low-lying vegetation. The plants in these *salt marsh* areas consist mainly of grasses and rushes. Marshes are a vital breeding ground and nursery for fish and shellfish. They play an important role in absorbing and purifying water from the land. Coastal marshes are being lost to development at a rapid rate.

Jane F. Hill

See also: Arctic tundra; Biological invasions; Biomes: types; Forests; Deserts; Grasslands; Grazing and overgrazing; Mediterranean scrub; North American agriculture; Savannas and deciduous tropical forests; Taiga; Tundra and high-altitude biomes.

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NUCLEAR ENVELOPE

Categories: Anatomy; cellular biology; physiology; transport mechanisms

The nuclear envelope is the outer covering of the nucleus in plant and other eukaryotic cells that acts as a barrier separating the nuclear contents from the surrounding cytoplasm.

The nuclear envelope is a double membrane system, consisting of two concentric membranes. The membranes are separated by a fluid-filled space called the perinuclear cisterna that measures about 20 to 40 nanometers. Like other plant cell membranes, the nuclear envelope consists of two bilayers, both made of phospholipids, in which numerous proteins are embedded. Attachment sites for protein filaments are stitched on the innermost surface of the nuclear envelope. These protein filaments anchor the molecules of deoxyribonucleic acid (DNA) to the envelope and help to keep them organized. The network of filaments that enmesh the nuclear envelope provides stability.

Large numbers of ribosomes are located on the outer surface of the envelope. The outermost membrane is continuous with the organelle called *rough endoplasmic reticulum* (RER) in the *cytoplasm* of the plant cell, which also has ribosomes attached to it. The space between the outer and inner membranes is also continuous with the rough endoplasmic reticulum space and can fill with newly synthesized proteins, just as the RER does. When the nuclear envelope breaks down during cell division, its fragments are similar to portions of the endoplasmic reticulum. This can be commonly observed at the root and shoot apices of a plant, where active mitosis (regular cell division for growth) occurs. Both bilayers of the envelope are fused at intervals to form many nuclear pores, which consist of protein complexes in clusters. The two membranes enclose a flattened sac and are connected at the nuclear pore sites.

Functions

The nuclear envelope surrounds the fluid portion of the nucleus, called the *nucleoplasm*, in all plant cells. The ribosomes on the outer surface of the envelope serve as sites for protein synthesis in addition to ribosomes located in the cytoplasm. The envelope is selectively permeable and therefore regulates the passage of materials and energy between the nucleoplasm and the cytoplasm. The envelope allows certain cell activities to be localized within the nucleus or outside in the cytoplasm. It also permits many different activities to go on simultaneously within and outside of the nucleus.

Like other membranes of the plant cell, the nuclear envelope membranes serve as important work surfaces for many chemical reactions in plants that are carried out by enzymes bound to the membranes. These functions are essential in the plant for the transport and use of minerals and water from the roots to cells of the stem and leaves. They are also important for the movement and use of carbohydrates, proteins, lipids, nucleic acids, and other chemical compounds in plant cells after photosynthesis, protein synthesis, and other biochemical activities have occurred.

Nuclear Pores

Nuclear pores, of about 100 nanometers in diameter, perforate the nuclear envelope. These pores look like wheels with eight spokes when observed from the top. Each contains eight subunits over the region where the inner and outer membranes join. They form a ring of subunits that are 15 to 20 nanometers in diameter. At the lip of each pore, the inner and outer membranes of the nuclear envelope are fused.

Each nuclear pore serves as a water-filled channel, and the arrangement allows transport in and out of the nucleus to occur in several ways. The nuclear pores allow the passage of materials to the cytoplasm from the interior of the nucleus, and vice versa, but the process is highly selective, permitting only specific molecules to pass through these openings. An intricate protein structure called the pore complex lines each pore and regulates the entry and exit of certain large macromolecules and particles. Large molecules, including the subunits of ribosomes, cross the bilayers at the pores in highly controlled ways. Ions and small, water-soluble molecules cross the nuclear envelope at the pores.

Studies show that the pore can actually dilate more when it gets the appropriate signal. Studies have also shown that the signal is in the peptide sequences of the molecules. These signals are recognition sequences rich in the amino acids lysine, arginine, and proline. Nuclear pores in plants therefore exert control over the movement of materials. This is, for example, demonstrated in the fact that if a nucleus is extracted from a cell and placed into water, it swells; this can happen only if the pores prevent material from oozing out as the nucleus absorbs water.

Nuclear Lamina

The *nuclear lamina* is a layer of specific proteins, called lamins, attached to inside membrane of the nuclear envelope. The layer consists of thin filaments (intermediate filaments) that are 30 to 40 nanometers thick. Each filament is a polymer of lamin. There are two types of lamin: A-type lamins are inside, next to the nucleoplasm, and B-type lamins are near the inner part of the nuclear membrane. The nuclear lamina surrounds the nucleus, except at the nuclear pores. The lamina serves as a skeletal framework for the nucleus. It may be involved in the functional organization of the nucleus and may also play an important role in the breakdown and reassembly of the nuclear envelope during mitosis.

Samuel V. A. Kisseadoo

See also: Cell cycle; Cell wall; Cytoskeleton; Cytosol; Endoplasmic reticulum; Eukaryotic cells; Liquid transport systems; Membrane structure; Mitosis and meiosis; Nucleus; Plasma membranes; Water and solute movement in plants.

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NUCLEIC ACIDS

Categories: Cellular biology; genetics; reproduction and life cycles

Nucleic acids are the genetic material of cells, including DNA and the various types of RNA.

Nucleic acids were discovered in the mid-nineteenth century, but their role as genetic material was not substantiated until the mid-twentieth century. When chromosomes were discovered at the beginning of the twentieth century, they were quickly identified as the genetic material of the cell. Chromosomes were found to be composed of nucleic acids and proteins. Through the experiments of Fred Griffith on transformation in pneumonia bacteria and the work of Alfred Hershey and Martha Chase on bacteriophages, by 1952 most biologists recognized *deoxyribonucleic acid* (DNA) as containing the genes. James Watson and Francis Crick provided the capstone to science's initial understanding of nucleic acids when they determined the double helix structure of DNA in 1953.

Heredity is the process by which the physical traits of an organism are passed on to its offspring. At the molecular level, DNA contains the information necessary for the transmission of genetic characteristics from one generation to the next, as well as the information required for the new organisms to grow and to live. DNA is the chemical basis of heredity and provides the synthesis of new proteins, such as enzymes.

DNA and RNA

There are two types of nucleic acids within cells, the single-stranded *ribonucleic acid* (RNA) and the double-stranded DNA. Each kind has specific roles. DNA was isolated in 1869 by German chemist Friedrich Miescher. The substance that Miescher found was white, sugary, and slightly acidic, and it contained phosphorus. Because it occurred only within the nuclei of cells, he called it "nuclein." The name was later changed to deoxyribonucleic acid, to distinguish it from ribonucleic acid, which is also found in cells.

In eukaryotic cells, DNA is present in the *chromosomes* of the nucleus and within the *mitochondria* and *chloroplasts*. Bacteria, yeasts, and molds, in addition to the chromosomes, contain circular strands of DNA, called *plasmids*, within the cytoplasm of their cells. Plasmids are relatively small, circular strands of DNA that exist independently of the chromosome. Plasmids typically have only twenty-five or thirty genes, which are not essential to the host cell but often confer antibiotic resistance, the ability to pass DNA to other bacterial cells, and other useful functions. Some plasmids are only found as single copies, whereas others occur as many copies. The mitochondria and chloroplasts of eukaryotic cells are self-replicating and contain a tiny circular chromosome (DNA) resembling a plasmid of a bacterium.

Viruses (minute parasites that infect specific hosts) contain only one type of nucleic acid—either DNA or RNA, never both, and the DNA or RNA can be single- or double-stranded. The DNA of some viruses can integrate into the DNA of the host cell. In this state, the viral DNA replicates as the host DNA replicates. The genetic apparatus of a virus, whether RNA or DNA, is much the same as that of bacteria but is far less complex. Even large viruses (such as the pox virus) have only a few hundred genes. Smaller viruses (such as the polio virus) have considerably fewer.

Chemical Structure

Both DNA and RNA are long-chained polymers made up of nucleotides. The nucleotides, in turn, are made up of a nitrogenous base, a ribose or deoxyribose sugar, and a phosphate. All the bases of DNA and RNA are heterocyclic amines. Two, adenine and guanine, are called *purines*; the other three, cytosine, thymine, and uracil, are called *pyrimidines*. The two purines and one of the pyrimidines, cytosine, occur in both RNA and DNA. Uracil is found only in RNA, while thymine occurs only in DNA.

The purines are nine-membered heterocyclic rings with nitrogen occurring in place of carbon at several positions. Adenine and guanine differ in the *functional groups* attached to them. The pyrimidines are six-membered heterocyclic rings, with nitrogen in place of two of the carbon atoms. Like the purines, the three pyrimidines also differ in the specific functional groups attached to them.

The ribose sugars are made up of a five-membered heterocyclic ring containing one oxygen atom between carbons one and four. A fifth carbon (number five) is not part of the ring and is bonded to carbon number four. Along with hydrogen atoms attached to each carbon, there is one hydroxyl group (OH) attached to each of the four heterocyclic carbon atoms in the ribose sugar of RNA. (The fifth carbon has a phosphate group attached to it.) The sugar of DNA is called *D-deoxyribose* because a hydroxyl group is missing from the second carbon, having been replaced by a hydrogen atom—thus the name deoxyribonucleic acid.

The sugar-base combination is called a *nucleoside*. The purines are linked to carbon one of the sugars with the nitrogen at position one. The nucleoside of guanine and ribose is guanosine; it is adenosine for adenine and D-ribose. The pyrimidines of RNA, when attached to ribose, are uridine and cytosine. In DNA the nucleoside names are deoxyadenine, deoxyguanosine, deoxythymidine, and deoxycytidine.

Nucleotides are phosphate esters of nucleosides. In these molecules, a phosphate group (phosphoric acid) is attached to carbon five (called the 5′ carbon) of the sugar (ribose or deoxyribose) in the nucleoside. Nucleotides are named by combining the name of their nucleoside with a word describing the numbers of phosphates attached to it. Guanosine monophosphate, for example, is the name of the phosphate ester of guanosine, which is often abbreviated as GMP.

Individual nucleotides also occur in cells. These free nucleotides usually exist as diphosphates or triphosphates. Examples of these are adenosine diphosphate (ADP) and adenosine triphosphate (ATP). ATP is the universal energy source for the anabolic processes of all cells, including the formation of the DNA and RNA.

DNA Structure and Function

DNA can be an extremely long molecule that is tightly wound within the nuclei of eukaryotic cells and within the cytoplasm of prokaryotic cells. Nuclear DNA is linear, whereas prokaryotic DNA is circular. (If the DNA in a human cell could be stretched out, it would measure roughly 2 meters, or 6 feet long; bacterial DNA would be about 1.5 millimeters long, or just over 0.5 inch.) Using a typical lily as a point of reference, DNA is packaged into twenty-four chromosomes, twelve of which are contributed by the pollen and twelve by the egg. Every cell derived from the fertilized egg (zygote) will have exactly the same amount of DNA containing exactly the same genetic information. Within the cytoplasm, several mitochondria (the sites of respiration) and chloroplasts (the sites of photosynthesis) are found, both of which contain their own DNA, which is circular and resembles prokaryotic DNA in many respects.

DNA is a double-stranded spiral; its shape is called the *double helix*. Structurally, it may be compared to a ladder, with the rails or sides of the ladder consisting of alternating deoxyribose sugar and phosphate molecules connected by phosphodiester bonds between the 5′ carbon of one sugar and the 3′ carbon of the other. The rungs of the ladder consist of purine (adenine and guanine, often abbreviated as A and G, respectively) and pyrimidine (cytosine and thymine, often abbreviated as C and T, respectively) building blocks from the opposite strands, held together by hydrogen bonds. The building blocks pair with each other consistently in what are called complementary pairs: Adenine always pairs with thymine with two hydrogen bonds, and cytosine always pairs with guanine with three hydrogen bonds. Consequently, the attraction between cytosine and guanine is stronger than that between adenine and thymine.

Because of this arrangement, the sequence of the purine and pyrimidine building blocks on one strand is complemented by the sequence of building blocks on the other strand. The specificity of the base pairing between the two strands allows strands to fit neatly together only when such pairing exists. Each DNA strand has a 5′ end with a hydroxyl group attached to the 3′ carbon of a deoxyribose sugar. When connected, the two strands are actually in an opposite orientation and are referred to as being *antiparallel*. This is best observed by looking at one end of the double-stranded molecule. One strand terminates with a 5′ phosphate group and the other with a 3′ hydroxyl group.

The specific nucleotide composition in a species is essentially constant but can vary considerably among organisms. Regardless, the amounts of adenine and thymine are always the same, as are the amounts of guanine and cytosine because of the required complementary pairing. Due to the greater strength of G-C bonds, organisms with a high GC content have DNA that must be heated to a higher temperature to *denature*, or separate, the strands. Some bacteria that live in hot springs have an especially high GC content.

The instructions contained within the DNA molecules occur in segments called *genes*. Most genes instruct the cell about what kind of *polypeptide* (molecule composed of amino acids used to make functional proteins) to manufacture. These polypeptides lead to the formation of enzymes and other proteins necessary for survival of the cell. Other genes are important in coding for the production of antibodies, RNA, and hormones.

RNA Types

The DNA acts as a template to make three kinds of RNA: *messenger RNA* (mRNA), *transfer RNA* (tRNA), and *ribosomal RNA* (rRNA). Each kind of RNA has a specific function. RNA is not found in chromosomes and is located elsewhere in the nucleus and in the cytoplasm.

The largest and most abundant RNA is rRNA. Between 60 and 80 percent of the total RNA in cells is rRNA, and it has a molecular weight of several million atomic mass units. The rRNA combines with proteins to form *ribosomes*, which are the sites for the synthesis of new protein molecules. About 60 percent of the ribosome is rRNA, and the rest is protein. Although single-stranded, rRNA molecules fold into specific functional shapes that involve the pairing of portions of the molecule to form double-stranded regions. The precise shape of rRNAs is important for their function, and some of them actually have catalytic properties, just as enzymes do. RNAs of this type are sometimes called ribozymes.

Molecules of mRNA carry the genetic information from DNA to the ribosomes. The process of converting the DNA code of a gene into an mRNA is called *transcription*. When attached to the ribosomes, mRNAs direct protein synthesis in a process called *translation*. The size of the mRNA molecule depends upon the size of the protein molecule to be made. In prokaryotes (such as bacterial cells), as well as in mitochondria and chloroplasts, mRNAs are ready to take part in translation even while transcription of the remainder of the mRNA is taking place. In eukaryotes (cells of most other forms of life), the mRNAs transcribed from nuclear DNA are initially much larger than they are later, when they participate in translation. These mRNAs must be processed to removed large pieces of noncoding RNA, called *introns*, and to modify both ends of the mRNA in specific ways. After introns are removed, the remaining codon regions, called *exons*, are spliced together by *splicesomes* (a complex system composed of proteins and small RNAs). Once all the modifications are complete, the mRNA is ready to be translated. A small number of mRNAs are translated in the nucleus, but most are transported to the cytoplasm first.

The smallest of the three main kinds of RNA is tRNA. Each of the tRNA molecules consists of about one hundred nucleotides in a single chain that loops back upon itself in three places, forming double-stranded regions that result in a structure that, when viewed in two dimensions, could be compared to a cross or clover leaf. The function of tRNA is to bring amino acids to the ribosomes to be used in the formation of new proteins. Each of the twenty amino acids found in proteins has at least one particular tRNA molecule to carry it to the site of protein synthesis.

The cloverleaf shape of the tRNA molecule is maintained by hydrogen bonds between base pairs. The other parts of the molecule that do not have hydrogen-bonded base pairs exist as loops. Two parts of every tRNA molecule have significant biological functions. The first is the place where the specific amino acid to be transferred is attached. This is located at the longest free end of the three-looped structure, often called the stem, where it is specifically attached to an adenine of an adenine monophosphate nucleotide. The second important site is the loop at the opposite end of the molecule from the stem. This loop contains a specific three-base sequence that represents a code for the amino acid that is being transferred by the tRNA. This three-base sequence is called an anticodon and plays an important role in helping place the amino acid in the correct position in the protein molecule under construction.

Jon P. Shoemaker, updated by Bryan Ness

See also: Chloroplast DNA; Chromosomes; DNA in plants; DNA replication; Extranuclear inheritance; Gene regulation; Genetic code; Genetic equilibrium: linkage; Mitochondrial DNA; Proteins and amino acids; RNA.

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NUCLEOLUS

Categories: Anatomy; cellular biology; physiology

The most prominent organelle of the eukaryotic cell is the nucleus. Within the nucleus, substructures called nucleoli are visible by light microscopy, each nucleolus as a small spot.

Generally, nucleoli are most prominent in nondividing cells, and they are not visible in dividing cells in which the nuclear membrane has disassembled. The nucleolus is composed of genes that encode the *ribonucleic acid* (RNA) molecules found in ribosomes (*ribosomal RNA*, or rRNA), the "working" copies or transcripts of these genes (the rRNA itself), and proteins. Nucleoli are the sites of ribosome synthesis in eukaryotic cells.

The *ribosome* is the site of protein synthesis in the cell. All proteins made by cells are made on ribosomes, so cells need an abundant supply of ribosomes to support the synthesis of all the cellular proteins. Mature ribosomes are found in the cytoplasm of eukaryotic cells, either attached to the membrane of the endoplasmic reticulum or "free" within the cytoplasm. Although ribosomes function outside the nucleus in the cytoplasm, they are synthesized in the nucleus at the nucleolus.

Nucleolar Structure

Nucleoli are clearly visible with light microscopy. They disassemble and reassemble with the cell cycle and exhibit different staining properties than the rest of the nucleus. They range in diameter from 1 micrometer in small yeast cells to 10 micrometers in larger cells, such as the root cells of pea plants and wheat.

When observed using electron microscopy, nucleoli appear to have roughly three distinct regions: the *fibrillar center* (FC), the *dense fibrillar center* (DFC), and the *granular component* (GC). In some plant cells, the nucleolus also has a centrally located clear region, sometimes called the *nuclear vacuole*. Although the precise molecular structures within nucleoli have not yet been thoroughly described, the regions of the nucleolus appear to correspond roughly to content and function, rRNA transcription, processing, and assembly.

rRNA Genes

A typical cell contains around one million ribosomes. To produce this number of ribosomes, a cell needs to be able to mass-produce the ribosomal components. To provide enough ribosomes for daughter cells produced from cell divisions, a cell must synthesize new ribosomes at the rate of several hundred per second. Additionally, these ribosomes must be exported from the nucleus into the cytoplasm, where proteins are synthesized.

In order to mass-produce the RNA components of ribosomes, the three rRNA genes that are transcribed (copied) in the nucleolus are present in multiple copies. The genes for the 5.8S, 18S, and 28S rRNAs (rRNAs are named for their sedimentation rate, "S," a measure of their size) are arranged in tandem repeats on the chromosomes of the cells. Typically, each repeat contains the 18S, the 5.8S, and the 28S genes, in that order, preceded by a region called a *nontranscribed spacer* (NTS) and separated by internal nontranscribed spacers. The NTS's are typically as small as two thousand to three thousand base pairs of deoxyribonucleic acid (DNA) in yeast and plants. These spacer regions may be involved in regulating gene expression in these regions of DNA or in attaching these areas of the chromosomes to protein structures inside the nucleolus.

Among different organisms, the number of copies of rRNA genes varies greatly. In fact, the number of copies of rRNA genes can even vary within different cells of a single organism. The human genome (haploid set) contains approximately one hundred copies of these genes, but many organisms, especially plants, have several thousand copies of the rRNA genes. By having hundreds or thousands of copies of the genes, the cells are able to mass-produce the rRNAs that these genes encode.

Nucleolar Organizing Regions

The genes that encode the rRNAs are found along metaphase chromosomes at constrictions called *nucleolar organizing regions*, or NORs. When the cell completes division and reenters interphase, NORs are the sites where the nucleoli will form. In plants, experiments to stain the specific rRNA genes reveal a complex organization of the genomic DNA. Large areas of inactive or untranscribed rRNA gene repeats appear at the periphery of the plant nucleoli, and several spots containing inactive rRNA genes also appear at the center of the nucleoli. However, many areas of active transcription of a single copy of the rRNA genes appear dispersed throughout the nucleolus. These areas of active rRNA gene transcription may correspond to the fibrillar center regions.

Ribosome Assembly and rRNA Processing

The three rRNA genes are initially copied as one large molecule of RNA, called the pre-rRNA. This large piece of RNA is processed to make the three smaller 18S, 5.8S, and 28s rRNAs that will become part of the ribosome. During processing the nontranscribed spacer sequences are removed. Each pre-rRNA molecule moves away from the genomic material as it is processed in several steps. Processing of the pre-rRNA molecule appears to require many accessory proteins and other RNA molecules, called small, nucleolar RNAs (snoRNAs).

The nucleolus contains many proteins that function in rRNA transcription and processing as well as transport of ribosome components into and out of the nucleus. One of these proteins, nucleolin, which is specific to the nucleolus, is found in the dense fibrillar center and appears to be involved in different stages of ribosome synthesis. Nucleolin travels between the nucleus and cytoplasm and therefore may also be involved in transport of ribosome components between the two cellular compartments.

For ribosome synthesis, ribosome proteins must be assembled with the three nucleolar rRNAs. The ribosomal proteins are synthesized, like other cellular proteins, on existing ribosomes in the cytoplasm. These proteins must be transported into the nucleus, where they associate with the pre-rRNA in the nucleolus even while it is being processed. A fourth rRNA, the 5S RNA, is transcribed in a separate part of the nucleus and transported to the nucleolus to be assembled with the other ribosomal components.

The ribosome consists of a small subunit and a large subunit. The small subunit, which contains the 18s rRNA and many proteins, is produced and exported from the nucleus separately from the large subunit, which contains the 28S, 5.8S, and 5S rRNAs. The two subunits continue to mature in the cytoplasm, and matured subunits recognize messenger RNA within the cytoplasm to assemble a functional protein-synthesizing ribosome.

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See also: DNA in plants; DNA replication; Nucleic acids; Nucleus; Plant cells: molecular level; Proteins and amino acids; RNA.

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NUCLEOPLASM

Categories: Anatomy; cellular biology; physiology

The nucleoplasm is the protoplasm contained within the plant cell nucleus and can best be described as the fluid-filled matrix that is contained within the nuclear membrane.

The nucleoplasm is a distinct entity of the plant cell *nucleus*, bounded, protected, and separated from the cytoplasm by the double-membrane *nuclear envelope*. Connections between the *cytoplasm* and nucleoplasm are closely regulated by nuclear pores that penetrate the nuclear envelope at intervals. Interiorly, these *nuclear pores* connect to a complex of nucleoplasmic channels that lead into the pores and serve simultaneously to direct and regulate exchange of materials between the nucleoplasm and the cytoplasm.

The nucleoplasm consists of a viscous mix of water, in which various substances and structures are dissolved or carried, and an underlying intranuclear ultrastructure. Comparisons of the aqueous phase of nucleoplasm with that of cytoplasm using a technique called the Stokes-Einstein equation reveal that diffusion rates are 1.2 times slower through cytoplasm than nucleoplasm, indicating that nucleoplasm is a less viscous fluid than cytoplasm. Substances in the nucleoplasm include ions, enzymes, minerals, and some organic molecules and macromolecules. The nucleoplasm is especially rich in protein enzymes and protein constituents involved in the synthesis of deoxyribonucleic acid (DNA) and the various types of ribonucleic acid (RNA), the precursor molecules of RNA, and the nucleotides from which they are assembled. Some of these proteins direct initial transcription, while others function in the further modification of the RNA molecules for packaging and transport to the cytoplasm.

Prominent structures located within the interphase nucleoplasm (the resting cell or the nonreplicating cell) include organelles called *nucleoli* and the unwound DNA, called *chromatin*. The nucleoli resemble miniature nuclei and are the sites of synthesis of precursor RNA molecules and their assembly.

The other major components in nucleoplasm include the DNA chromosomes seen during mitosis. During cell interphase most of the DNA chromosomes exist as unwound chromatin that extend through the nucleoplasm. Two distinct types of chromatin are recognized. Diffuse, or uncondensed, chromatin is called *euchromatin* and exists as thin threads that extend throughout much of the nucleoplasm. Small sections of DNA that remain uncondensed during cell interphase are called heterochromatin. The chromatin can be further subdivided into gene-rich R bands concentrated within the nucleus and gene-poor G bands found in the peripheral regions of the nucleus.

The space between these chromatin elements is called the *interchromatin space*. Ultrastructure studies have revealed a surprisingly complex structure within this interchromatin space. It consists of several components, including a nuclear lamina, nuclear matrix, thousands of highly organized sites called foci, and nuclear speckles.

The *nuclear lamina* and *nuclear matrix* consist of protein microfilaments—fine tubular structures—which apparently provide structural support for the interior of the nucleus as well as a framework for further nuclear structure and function. The lamina consists of lamin proteins that help shape and maintain the inner membrane of the nuclear envelope. The nuclear matrix functions in pore formation and may also be continuous with the nuclear lamina in conferring an interior structure or shape to the nuclear envelope. The nuclear matrix also binds chromosomes, or parts of chromosomes, to specific sites on the inner nuclear membrane.

Foci and *nuclear speckles* are both involved in the production of the several types of RNA molecules manufactured by the nucleus. Foci are apparently sites that are functionally associated with gene-rich chromatin. Some scientists argue, in fact, that foci are actually functional domains on active chromatin. Whether active chromatin sites or separate entities, the foci contain protein enzymes and assembly components involved in the transcription and splicing of ribonucleoprotein (RNP) molecules associated with the production of RNA precursor or subassembly molecules. The production of a specific RNP molecule may involve the activity of hundreds or thousands of discrete foci. Once completed, the molecular products of the foci are transported to nuclear speckles for further modification.

Nuclear speckles appear to be clusters of RNP. They are highly organized sites that are separated from other nuclear compartments by nucleoplasm. Their role and importance is still uncertain, but they are probably nuclear structures directly involved in the final assembly and modification of the various types of RNA molecules from RNP molecules supplied by the foci.

Although much of the structure and role of the nucleoplasm remains to be investigated, it is increasingly clear that the nucleoplasm has a complex ultrastructure underlying and facilitating its myriad functions.

Dwight G. Smith

See also: Chromatin; Cytoplasm; Cytosol; Mitosis and meiosis; Nuclear envelope; Nucleic acids; Nucleolus; Nucleus; Plant cells: molecular level.

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NUCLEUS

Categories: Anatomy; cellular biology; physiology

A eukaryotic cell's nucleus directly or indirectly controls virtually all cellular physiological activities, including initiation, regulation, and termination of enzymatic events. It is also the repository of genetic information (the genome), housing and protecting the chromosomes and the genes that they carry. In all eukaryotic cells the nucleus is generally the largest and most centrally located cell structure, although in plant storage cells certain kinds of vacuoles may be larger and more conspicuous.

The nucleus, from the Greek word *nucle* (meaning "pit" or "kernel") is the command and control center of the cell. The six basic functions of the nucleus are, first, to protect and store genes, ultimately protecting the deoxyribonucleic acid (DNA) on which the genes are organized from the rest of the cell; second, to organize genes into chromosomes to facilitate their movement and distribution during cell division; third, to organize the uncoiling of DNA during the copying of genes for the production of thousands of proteins; fourth, to manufacture and transport regulatory molecules, mostly enzymes and other gene products, into the cytoplasm; fifth, to manufacture subunits of ribosomes; and sixth, to respond to hormones and other chemical signals received via the nuclear pores.

Components

Structurally, the nucleus consists of several distinct parts: a *nuclear envelope*, *nucleoplasm*, *chromatin*, and one or more suborganelles called *nucleoli*.

The nuclear envelope forms a protective barrier that isolates the nucleus from the cytoplasm of the cell. The envelope consists of two unit membranes (a double-unit membrane) which are structurally similar to other membranes of the cell. The outer membrane is closely associated with the cell's endoplasmic recticulum (ER) and may be continuous with it. Like the rough ER of the cytoplasm, the outer nuclear membrane has ribosomes embedded in it. Some scientists, in fact, suggest that the nuclear envelope is just a localized and specialized version of the ER. The inner nuclear membrane is lined with a fibrous layer, called the nuclear lamina, which provides strength and structure to the nucleus shape and may also serve as a binding site for some chromatin.

At intervals, the nuclear envelope is perforated by small pores which function as communication channels for the controlled exchange of materials between the nucleus and the cytoplasm. Collectively, the *nuclear pores* cover about 10 percent of the surface of the nucleus. Each nuclear pore is a complex consisting of a central pore that has been estimated at 30-100 nanometers in diameter. The selectively permeable nuclear pores function as entry and exit ways for a variety of water-soluble molecules, mostly nuclear products, such as ribosome subunits, messenger RNA (ribonucleic acid) molecules, and chromosomal proteins.

The protoplasm within the nucleus is called nucleoplasm. Like cytoplasm, it consists of a jellylike mix of substances and organelles but differs in having a higher concentration of nucleotides and other organic molecules that are used in the synthesis of DNA and RNA.

Major structures within the nucleoplasm include the DNA and usually one organelle—but sometimes several—called the nucleolus. Except during cell division, the molecules of DNA occur as a network of unwound fibers called chromatin. During cell division molecular strands of DNA coil and supercoil around histone proteins to condense and form the chromosomes. The number of chromosomes found within the nucleus are specific for each species of plant and animal. Humans, for example, have forty-six chromosomes, tobacco has forty-eight, corn has twenty, carrots have eighteen, and peas have fourteen chromosomes.

The nucleolus is the largest visible organelle within the nucleus. It is typically associated with specific regions of chromosomes, called nuclear organizer regions, which contain genes that direct synthesis of ribosomal subunits. The main products of nucleolus activity are the units of ribosomal RNA (rRNA). These subunits are eventually complexed with ribosomal proteins and transported from the nucleus into the cytoplasm by special carrier proteins. Other sites within the nucleus called *functional domains* control the synthesis of messenger (pre-mRNA), transfer (tRNA) molecules. Once formed, these molecules are then complexed with proteins and transported as nucleoproteins to the cytoplasm.

Cell Division

Although seemingly both stable and durable, the nucleus disappears from normal view and is reformed during cell division in almost all plants except yeasts, which retain a clearly defined nucleus throughout the division process. In other eukaryotic plant cells the nucleus disappears early during the prophase of mitosis, when the nuclear envelope is enzymatically fragmented into small, nearly invisible vesicles. These are not reassembled until the final events of telophase, when they reform around the chromosomes and are controlled by the lamina of the daughter cells.

Dwight G. Smith

See also: Chromosomes; Chromatin; Cytoplasm; Cytosol; DNA in plants; DNA replication; Eukaryotic cells; Mitosis and meiosis; Nuclear envelope; Nucleolus; Nucleoplasm.

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NUTRIENT CYCLING

Categories: Biogeochemical cycles; ecosystems; nutrients and nutrition

Within an ecosystem, nutrients move through biogeochemical cycles. Those cycles involve chemical exchanges of elements among the earth's atmosphere, water, living organisms, soil, and rocks.

All biogeochemical cycles have a common structure, sharing three basic components: inputs, internal cycling, and outputs.

Input of Nutrients

The input of nutrients to an ecosystem depends on the type of biogeochemical cycle. Nutrients with a gaseous cycle, such as carbon and nitrogen, enter an ecosystem from the atmosphere. For example, carbon enters ecosystems almost solely through photosynthesis, which converts carbon dioxide to organic carbon compounds. Nitrogen enters ecosystems through a few pathways, including lightning, nitrogen-fixing bacteria, and atmospheric deposition. In agricultural ecosystems, nitrogen fertilization provides a great amount of nitrogen influx, much larger than by any other influx pathways.

In contrast to carbon and nitrogen with input from the atmosphere, the input of nutrients such as calcium and phosphorus depends on the weathering of rocks and minerals. Soil characteristics and the process of soil formation have a major influence on processes involved in nutrient release to recycling pools. Supplementary soil nutrients come from airborne particles and aerosols, as wet or dry depositions. Such atmospheric deposition can supply more than half of the input of nutrients to some ecosystems.

The major sources of nutrients for aquatic ecosystems are inputs from the surrounding land. These inputs can take the forms of drainage water, detritus and sediment, and precipitation. Flowing aquatic systems are highly dependent on a steady input of detrital material from the watershed through which they flow.

Internal Cycling

Internal cycling of nutrients occurs when nutrients are transformed in ecosystems. Plants take up mineral (mostly inorganic) nutrients from soil through their roots and incorporate them into living tissues. Nutrients in the living tissues occur in various forms of organic compounds and perform different functions in terms of physiology and morphology. When these living tissues reach senescence, the nutrients are usually returned to the soil in the form of dead organic matter. However, nitrogen can be reabsorbed from senescent leaves and transferred to other living tissues. Various microbial decomposers transform the organic nutrients into mineral forms through a process called *mineralization*. The mineralized nutrients are once again available to the plants for uptake and incorporation into new tissues. This process is repeated, forming the internal cycle of nutrients. Within the internal cycles, the majority of nutrients are stored in organic forms, either in living tissues or dead organic matter, whereas mineral nutrients represent a small proportion of the total nutrient pools.

Output of Nutrients

The output of nutrients from an ecosystem represents a loss. Output can occur in various ways, depending on the nature of a specific biogeochemical cycle. Carbon is released from ecosystems to the atmosphere in the form of carbon dioxide via the process of *respiration* by plants, animals, and microorganisms. Nitrogen is lost to the atmosphere in gaseous forms of nitrogen, nitrous oxide, and ammonia, mostly as by-products of microbial activities in soil. Nitrogen is also lost through leaching from the soil and carried out of ecosystems by groundwater flow to streams. Leaching also results in export of carbon, phosphorus, and other nutrients out of ecosystems.

Output of nutrients from ecosystems can also occur through surface flow of water and soil erosion. However, loss of nutrients from one ecosystem may represent input to other ecosystems. Output of organic matter from terrestrial ecosystems constitutes the majority of nutrient input into stream ecosystems. Organic matter can also be transferred between ecosystems by herbivores. For example, moose feeding on aquatic plants can transport nutrients to adjacent terrestrial ecosystems and deposit them in the form of feces.

Considerable quantities of nutrients are lost permanently from ecosystems by harvesting, especially in farming and logging lands, when biomass is directly removed from ecosystems. Fire usually results in the loss of large amounts of nutrients. Fire kills vegetation and converts portions of biomass and organic soil matter to ash. Fire causes loss of nutrients through volatilization and airborne particulate. After fire, many nutrients become readily available, and nutrients in ash are subject to rapid mineralization. If not taken up by plants during vegetation recovery, nutrients are likely to be lost from ecosystems through leaching and erosion.

The Hubbard Brook Example

Nutrient cycling has been studied in several intact ecosystems. One of the most notable experiments was conducted in the Hubbard Brook experimental forest in New Hampshire. The experimental forest was established initially for forest hydrology research. Begun in the early 1960's, one of the longest-running studies of water and nutrient dynamics of forest ecosystems has been on the Hubbard Brook site. Both water and nutrient concentrations in precipitation inputs

PhotoDisc

Supplementary soil nutrients come from airborne particles and aerosols, as dry or wet depositions, such as this fog. Such atmospheric deposition can supply more than half of the input of nutrients to some ecosystems.

and stream outputs were regularly monitored, allowing estimations of nutrient balances over the watershed ecosystems.

One of the major findings from the Hubbard Brook study was that undisturbed forests exhibit regularity and predictability in their input-output balances for water and certain chemical elements. Nitrogen, however, shows a more complex, but still explicable, pattern of stream concentrations. Losses of nitrates from the control watershed are higher in the dormant season, when biological activity is low. Losses are near zero during the growing season, when biological demand for nitrogen by plants and microbes are high. Removal of vegetation in the Hubbard Brook forest had a marked effect on water and nutrient balances. Summer stream flow during the devegetation experiment was nearly four times higher than in the control watershed. The increase in stream flow, combined with increases in the concentration of nutrients within the stream, resulted in increases in loss rates of nitrate much higher than those of undisturbed areas. Similarly, loss of potassium used in large quantities by plants showed a great increase.

Nutrient Uptake and Competition

Ecosystem nutrient cycling is critical for plant growth and ecosystem productivity. Plant uptake of essential nutrient elements is related to nutrient availability, root absorption surface, rooting depth, and uptake kinetics of roots. A nutrient-rich site usually supports more plants of different species than a site with fewer available nutrients. Nutrient competition among plants is usually manifested through physiological, morphological, and ecological traits. Usually grasses and forbs can coexist in one grassland ecosystem, for example, through different rooting depth. To compete for less soluble nutrients such as phosphorus, plants usually extend their root surfaces using symbiotic relationships with mycorrhizae. Differential seasonality in nutrient uptake and rooting depth become more critical to compete limited nutrients.

Yiqi Luo

See also: Carbon cycle; Ecosystems: studies; Erosion and erosion control; Hydrologic cycle; Nitrogen cycle; Nutrients; Nutrition in agriculture; Phosphorus cycle; Root uptake systems; Soil.

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NUTRIENTS

Categories: Cellular biology; nutrients and nutrition

Plant nutrients are the molecular compounds necessary to maintain plant life.

Plants, like animals and other forms of life, require a great diversity of compounds. Molecules of these compounds are used to build and maintain cells and to perform other necessary life processes, such as growth and reproduction, as well as respiration and photosynthesis.

Plants manufacture, by the process of photosynthesis, simple sugars. From these are formed polysaccharides (starches, cellulose) and, eventually, a variety of lipids (fats, oils, and waxes), hundreds of different protein molecules, and many other organic compounds. Normal functioning of plants re-

Plant Nutrients

Nutrient	*Functions*
Macronutrients	
Calcium	Formation of cell walls, regulator of membrane permeability, enzyme regulator
Carbon	Basic to all structures and functions
Hydrogen	Basic to all structures and functions
Magnesium	Chlorophyll component, enzyme activator
Nitrogen	Formation of amino acids, proteins, nucleotides, nucleic acids, chlorophyll, coenzymes
Oxygen	Basic to all structures and functions
Phosphorus	Formation of ADP and ATP, nucleic acids, coenzymes, phospholipids
Sulfur	Component of proteins, coenzyme A, thiamine, biotin
Micronutrients	
Boron	Calcium metabolism, nucleic acid synthesis, cell membranes, carbohydrate synthesis
Chlorine	Osmosis, photosynthesis
Copper	Redox enzymes
Iron	Chlorophyll synthesis, electron transport system, cellular respiration
Manganese	Enzyme activator, chloroplast membrane activity, photosynthesis
Molybdenum	Nitrogen fixation
Zinc	Enzyme activator, auxin synthesis
Some species need:	Aluminum, cobalt, silicon, sodium

quires that they absorb, usually by roots from soil, a variety of chemical elements. From these elements, which are combined with water, carbon dioxide, and other compounds, the more complex compounds are formed.

Plant Nutrition

Plant nutrition involves the uptake from the environment of the raw materials needed for performing a variety of biochemical processes, the conduction of these substances to all parts of the plant, and their use in growth and metabolic processes. Most of these materials are in the form of ions dissolved in soil water. The water occupies the spaces between solid soil particles and is absorbed through the roots and then conducted upward by means of *xylem* tissue located in roots, stems, and leaves.

Present in soil water, and therefore in a plant growing in that soil, are more than sixty chemical elements. Some of these, however, are present only incidentally and perform no known function. Others, known as *essential elements*, are used in some particular way by the plant. These elements have been the object of study by many plant physiologists.

Essential Elements

By the mid-1800's, chemistry had become sufficiently advanced that botanists could analyze the chemical content of plants. They discovered that in the ash remaining after a plant had been burned were a variety of minerals. In order to be considered an essential element, that element must be necessary for normal metabolic processes, growth, and reproduction; another element cannot replace it. Essential elements are classified as either *macronutrients* or *micronutrients*. Although both types of nutrients are required, macronutrients are needed in much larger amounts.

To recognize the difference between the two categories of minerals, one may consider the following. When freshly harvested plants are heated in an oven to remove the water, the dry matter remaining can be analyzed. Macronutrients are those required in concentrations of at least 1,000 milligrams per kilogram of dry plant matter. In contrast, micronutrients are required in much smaller or even trace amounts, generally less than 100 milligrams per kilogram of dry matter.

Among the macronutrients, nitrogen is a key element needed in large amounts to form proteins, nucleotides, chlorophyll, and coenzymes. Phosphorus is also required to build nucleic acids, but it is also necessary to form adenosine triphosphate (ATP) and adenosine diphosphate (ADP), energy-carrying compounds vital to all cells. Among the several functions of calcium are its roles as a component of cell walls and in changing the permeability of cell membranes. Magnesium is necessary to activate certain enzymes; also a single atom of magnesium occupies a central position in each molecule of chlorophyll. Sulfur is essential to synthesizing proteins, coenzyme A, thiamine, and biotin.

Among the micronutrients, iron functions in the electron transport system, playing a role in cellular respiration; also it is vital for chlorophyll synthesis. Chlorine helps to maintain an ionic balance by controlling osmosis. Manganese is involved in activating many enzymes. Boron is believed to be involved in carbohydrate synthesis; also it is required for nucleic acid synthesis. Zinc is required for the synthesis of the plant hormone auxin; it also is involved in enzyme activation. Copper is present in the active site of redox enzymes and electron carriers. Nickel plays a role in enzyme functioning in the metabolism of nitrogen. Molybdenum is required for nitrogen fixation, the process by which free nitrogen (N_2) in the air is converted into nitrates.

Identifying Essential Elements

To identify a particular mineral as essential, a classic *protocol* (series of steps) is followed. The method used today was developed by Julius von Sachs, an early German plant physiologist, in 1860: Two seedlings of the same kind of plant are grown in separate containers. One container contains what is considered to be a complete growth medium. The other container contains all but a single mineral. If the growth of the seedling in the latter container is abnormal, or if its normal flowering and seed production are not successful, the missing element is determined to be essential.

Just as animals suffer symptoms when certain vitamins or minerals are absent in their diets, so plants are affected when they suffer a deficit in a particular essential element. Such symptoms are used by farmers and gardeners to determine which types of fertilizer need to be added to the soil in order to correct the problem. Some of the more common mineral deficiencies include nitrogen, iron, magnesium, calcium, and phosphorus deficiencies. For example, because plants require large amounts of nitrogen for growth, this mineral is often not present in sufficient amounts. A typical symptom is a uniform yellowing of the older leaves, a condition called chlorosis. An iron deficiency is diagnosed when the youngest leaves turn yellow. In the case of a magnesium deficiency, the older leaves are yellow between the veins. A calcium deficiency causes the growing points to die back; young leaves are yellow and crinkly. Plants with a phosphorus deficiency turn dark green and have leaves with purple veins.

Alternative Nutrient Sources

Whereas most plants, both wild or cultivated, absorb required nutrients from soil water, some plants obtain nutrients by other means. Plants such as Venus's fly trap, the pitcher plant, and various other carnivorous plants supplement soil nutrients by trapping insects or other small animals. Once an animal is caught, its protein is digested, yielding nitrogen that is made available to the plant. Intricate traps and other means of attracting and capturing insects have evolved over long periods of time. The traps are commonly modified leaves. Carnivorous plants generally inhabit sunny habitats with soils that have low levels of nitrogen. Thus nitrogen from animal protein is necessary to supplement that obtained in the more usual way from the soil.

Because of the special role of the proteins in plant (and animal) cells, nitrogen, a key element required to form proteins, is of special concern. Many plant species, especially those of the pea or legume family (*Fabaceae*) have root nodules, or mycorrhizae, filled with bacteria that are able to convert free nitrogen into compounds of nitrogen called nitrates. This process, called *nitrogen fixation*, makes nitrates available to the plant (as well as to the bacteria) as a usable source of nitrogen. Also, the surrounding soil is enriched, making nitrogen available to other plants growing in the soil. Thus, nitrogen taken from the soil in large quantities, especially by cultivated crops, is replaced. The common agricultural practice of rotating crops, in which a leguminous crop such as alfalfa or clover is alternated with corn or wheat, which removes large amounts of nitrogen from the soil, takes advantage of the nitrogen that has been fixed by legumes.

Hydroponic cultures allow for the growing of plants without soil. The plants survive on solutions that contain water and essential minerals. Plants are typically grown in greenhouses with their roots bathed in circulating water containing the minerals. Provision must be made to keep the water aerated. Hydroponic plants can be grown year-round, but the added expense of hydroponic culture limits its use to fruits and vegetables made available to specialty markets.

Thomas E. Hemmerly

See also: Biofertilizers; Carbohydrates; Carnivorous plants; Fertilizers; Hydroponics; Lipids; Nitrogen fixation; Nutrition in agriculture; Photosynthesis; Proteins and amino acids; Root uptake systems; Soil; Water and solute movement in plants.

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NUTRITION IN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; nutrients and nutrition

Extensive research has been conducted to investigate the nutritional requirements of different crops and ways to enhance soil fertility, which has greatly benefited agricultural production.

Even though people have known for more than two thousand years that adding mineral elements, such as plant ash or lime, to the soils can improve plant growth, the systematic study of plant nutrition is a relatively young science, considering humanity's long history of cultivating crops. About 250 years ago, farmers and gardeners started to ask the question, "What makes plants grow?" It was widely believed that soil humus, a brown or black organic substance resulting from the partial decay of plant and animal matter, provided plants with carbon for making sugar and starch, and substances such as saltpeter, lime, and phosphates simply helped the humus to be more useful. It was not until around 1840 that the German chemist Justus von Liebig (1803-1873) helped to compile and summarize the scattered information on the importance of mineral elements for plant growth, and plant nutrition began to be established as a scientific discipline. Since then, great progress has been made in the study of plant nutrition.

It is now known that, aside from carbon, hydrogen, and oxygen, which plants get from air and water, about a dozen other nutrients are needed for plant growth. They can be divided into three classes. The primary (or major) nutrients, including *nitrogen*, *phosphorus*, and *potassium*, are needed in larger quantities than are the secondary nutrients, *calcium*, *magnesium*, and *sulfur*. These in turn are required in greater quantity than the trace (or minor) nutrients iron, boron, manganese, copper, zinc, molybdenum, chloride, and nickel. These nutrients are contained in the minerals and organic matter in the soil. Many more elements are found in both soils and plants—for instance, aluminum, cobalt, fluorine, iodine, and sodium. They may not be needed by all plants and may be either beneficial or toxic to plant growth. Silicon, sodium, and cobalt are beneficial to some plants.

Soil and Plant Nutrients

Soil is the natural medium in which crops grow. The nutrient content of a soil and the availability of the nutrients to crops are important factors that determine a soil's productivity. Soil nutrients are mostly present in forms not immediately available to plants, such as being adsorbed onto or as constituents of soil mineral particles, or in organic matter. They become available through slow processes, such as biological decomposition of organic matter called *mineralization*, chemical reactions on soil minerals called *weathering*, and release from soil particles.

Soil nutrients in agricultural land may be gradually lost with the removal of harvested products, such as grain and straw, which take with them considerable amounts of all nutrients. In addition, nutrients may be lost from the soil through *leaching* and *erosion*. Therefore, it is common for field crops to suffer from nutrient deficiencies. On the other hand, certain soils may present the crops with problems of mineral toxicity, that is, excess amounts of particular elements. To maintain healthy growth of crops, it is necessary to correct these problems.

Soil testing, visual diagnosis of the plant, and plant tissue analysis can all be used to evaluate the fertility status of the soil and detect deficiencies and toxicities in soil nutrients. The results of such tests provide the basis for recommendations on the application of fertilizer and soil amendments.

Coping with Nutrient Deficiencies

Based on knowledge of plant nutrition and experience accumulated over a long period of time, nutrient management practices have been established to enhance soil fertility and overcome crop nutritional problems by balancing the use of mineral fertilizers combined with organic and biological sources of plant nutrients. In practice, different methods may have both advantages and disadvantages, depending on the particular set of local conditions.

Organic sources of plant nutrients include farmyard manure (animal waste products), green manure (plant products), and compost. They contain small amounts of nutrients and are often bulky in nature. When added to the soil, their main value is to provide organic matter that promotes microbial activity and improves soil structure, aeration, and water-holding capacity, enabling the soil to respond better to fertilizers and irrigation. The organic matter may also supply micronutrients and help to make the phosphate in the soil more available to crops. The disadvantages of applying organic manures are that they may be expensive, difficult to handle, or likely to release excess nutrients into the environment.

Nitrogen availability is one of the most limiting factors in crop productivity. Although nitrogen is abundantly available in the air, this form of it is not directly usable by the plants. Some crops, such as legumes, can form a beneficial relationship called *symbiosis* with certain bacteria capable of converting atmospheric nitrogen to ammonia, a process known as biological *nitrogen fixation*. The bacteria supply the plant with nitrogen (ammonia), while the plant provides the bacteria with organic compounds for use as energy. Legumes can be used as a source of nitrogen when planted with cereals. Fast-growing legumes can be grown early in the season and then ploughed under to provide nitrogen for the main crop. Recent research has identified the mechanisms controlling the expression of the nitrogen-fixation genes at the molecular level, and one of the goals of ongoing research is to explore various approaches to constructing a viable nitrogen-fixing system for use with nonlegumes.

Low soil phosphorus availability is another constraint on plant growth. Phosphorus is progressively lost from soil through weathering, and reactions with various soil constituents substantially reduce phosphorus available to plants. One research effort has been directed toward investigating various root characteristics that are useful in phosphorus uptake by plants. The findings may help farmers to breed for crops that are better able to grow in soils with low phosphorus.

Nutrient removal from cultivated land usually exceeds the natural rate of nutrient input. One remedy is to add appropriate and balanced fertilizers back to the soil. Mineral fertilizers are widely used to supply either single nutrients or multiple nutrients in combination. Foliar spray is effective for correcting deficiencies in micronutrients. Timing and dosage of applications is important, because the nutritional requirements of a crop vary with its stage of growth. Insufficient supply reduces crop yields, but applying too much or at a wrong time is not only wasteful but also potentially harmful to the environment.

Overcoming Nutrient Toxicities

Soil can become acidified as a result of its own physical properties, microbial activity, climate, vegetation, and the addition of acidifying fertilizers. As a result, important nutrients can be lost, and toxicities from aluminum and manganese may occur. Liming, the application to land of a material containing calcium, usually chalk or limestone, is often used as a standard measure in order to reduce problems of soil acidity.

Salts introduced in irrigation water, blown inland from oceans, or produced by weathering may accumulate in topsoil and cause toxicity to crops. This is normally controlled by applying more water than the crop can use, so that excess salts are leached downward below the root zone. It is important, however, that the irrigation water does not have high salt content and that drainage is not a problem. The addition of calcium salts, such as calcium sulfate, together with organic manures, is also effective in treating salt-affected soils.

One focus of research in the field of plant nutrition has been the study of the mechanisms plants employ in avoiding or tolerating toxic elements, such as aluminum, manganese, and salts, and accessing scarce nutrients, such as phosphorus, in the soil. Knowing how plants cope with various nutrient stresses will help the effort of breeding crops that are better able to withstand adverse soil nutrient conditions and achieve high yields by making use of their own genetic potential.

Zhong Ma

See also: Agriculture: modern problems; Agriculture: traditional; Agriculture: world food supplies; Agronomy; Biofertilizers; Composting; Eutrophication; Fertilizers; Green Revolution; High-yield crops; Hydroponics; Nitrogen cycle; Nitrogen fixation; Nutrients; Organic gardening and farming; Phosphorus cycle; Roots; Root uptake systems; Slash-and-burn agriculture; Soil management; Sustainable agriculture.

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OIL BODIES

Categories: Anatomy; cellular biology; physiology

Oil bodies, also called oleosomes, are plant cell organelles that serve as storage structures for lipids, primarily triacylglycerols.

Oil bodies are found in many plant seeds and represent an efficient storage form of energy for a germinating embryo. Other, non-oilseed, plants rely primarily on starch as a storage form of energy in their seeds. On a weight basis, oils contain more the twice the amount of energy as starches, because they contain more carbon and hydrogen atoms and fewer oxygen atoms than starch. Oil thus represents a more compact storage form of energy. Some high oil content species include castor beans, canola, safflower, peanuts, sunflower, macadamia nuts, and hazelnuts. All of these contain about 50 percent or more oil on a dry-weight basis. Despite the ubiquitous presence of corn and soybean oil in the marketplace, these oils contain only 5 percent and 17 percent oil, respectively. Although oil bodies are found predominantly in seeds, they may also be present in fruits, such as olives and avocados.

Structure

Oil bodies are unique in structure. They are surrounded by single-layer phospholipid membrane, as opposed to the bilayer membrane found around most other plant organelles. The single-layer membrane is derived from the endoplasmic reticulum (ER), from which oil bodies are believed to originate. *Triacylglycerols* are synthesized in the ER and accumulate within the two layers of its phospholipid membrane. Eventually the two layers are separated as oil accumulates and pinches off to form the oil body. The hydrophobic (water-avoiding) tails of the resulting phospholipid monolayer are associated with the oily interior, and the polar heads face outward. In addition, proteins called *oleosins* are present in the single-layer membrane and are thought to prevent fusion with other oil bodies. Oleosomes appear to be consistent in size, about 1 micron. Thus, a cell with a large amount of oil will have more oil bodies present.

Function

When seeds imbibe water and germination is initiated, many metabolic activities are activated. In order for a germinating seed to utilize the energy in an oil body, the triacylglycerols must be converted to a form of sugar, typically sucrose, that can be used by the growing embryo. The sequence of enzymatic events that makes this possible involves the close coordination of three organelles: the oleosome, the mitochondrion, and the highly specialized *glyoxysome*. It is in the glyoxysome where the many carbon atoms present in the fatty acids of the triacylglycerols are removed, two at a time, in a process called oxidation. These reactions, together with those of the mitochondria, are often referred to as the *glyoxylate cycle*. The end products allow for *reverse glycolysis*, which produces sugars that can be metabolized by typical respiratory pathways in the growing seedling.

Thomas J. Montagno

See also: Cytoplasm; Endoplasmic reticulum; Glycolysis and fermentation; Lipids; Membrane structure; Mitochondria; Plasma membranes; Respiration.

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OLD-GROWTH FORESTS

Categories: Forests and forestry; ecosystems; environmental issues

Ancient ecosystems, old-growth forests consist of trees that have never been harvested. These forests are, in some cases, the only habitat for a number of plant and animal species.

The timber industry views the large, old trees as a renewable source of fine lumber, but environmentalists see them as part of an ancient and unique ecosystem that can never be replaced. In the 1970's scientists began studying the uncut forests of the Pacific Northwest and the plants and animals that inhabited them. In a U.S. Forest Service publication, *Ecological Characteristics of Old-Growth Douglas-Fir Forests* (1981), Forest Service biologist Jerry Franklin and his colleagues showed that these forests were not just tangles of dead and dying trees but rather a unique, thriving ecosystem made up of living and dead trees, mammals, insects, and even fungi.

Old-Growth Forest Ecosystem

The forest usually referred to as old growth occurs primarily on the western slope of the Cascade Mountains in southeast Alaska, southern British Columbia, Washington, Oregon, and Northern California. The weather there is wet and mild, ideal for the growth of trees such as Douglas fir, cedar, spruce, and hemlock. Studies have shown that there is more biomass, including living matter and dead trees, per acre in these forests than anywhere else on earth. Trees can be as tall as 300 feet (90 meters) with diameters of 10 feet (3 meters) or more and can live as long as one thousand years. The forest community grows and changes over time, not reaching *biological climax* until the forest primarily consists of hemlock trees, which are able to sprout in the shade of the sun-loving Douglas fir.

One of the most important components of the old-growth forest is the large number of standing dead trees, or *snags*, and fallen trees, or *logs*, on the forest floor and in the streams. The fallen trees rot very slowly, often taking more than two hundred years to decompose completely. During this time they are important for water storage, as wildlife habitat, and as "nurse logs" where new growth can begin. In fact, seedlings of some trees, such as western hemlock and Sitka spruce, have difficulty competing with the mosses on the forest floor and need to sprout on the fallen logs.

Another strand in the complex web of the forest consists of mycorrhizal fungi (mycorrhizae), which attach themselves to the roots of the trees and enhance their uptake of water and nutrients. The fruiting bodies of these fungi are eaten by small mammals such as voles, mice, and chipmunks, which then spread the spores of the fungi in their droppings. There are numerous species of plants and animal wildlife that appear to be dependent on this ecosystem to survive.

Protecting the Forest

By the 1970's most of the trees on timber industry-owned lands had been cut. Their replanted forests, known as second growth, would not be ready for harvest for several decades, so the industry became increasingly dependent on public lands for their raw materials. Logging of old growth in the national forests of western Oregon and Washington increased from 900 million board feet in 1946 to more than 5 billion board feet in 1986.

Environmentalists claimed that only 10 percent of the region's original forest remained. Determined to save what was left, they encouraged the use of the evocative term "ancient forest" to counteract the somewhat negative connotations of "old growth." Then they were given an effective tool in the northern spotted owl. This small bird was

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found to be dependent on old growth, and its listing under the federal Endangered Species Act in 1990 caused a decade of scientific, political, and legal conflict.

Under law, the U.S. Forest Service was required to protect enough of the owl's habitat to ensure its survival. An early government report identified 7.7 million acres of forest to be protected for the bird. Later, the U.S. Fish and Wildlife Service recommended 11 million acres. In 1991 U.S. District Court judge William Dwyer placed an injunction on all logging in spotted owl habitat until a comprehensive plan could be finalized. The timber industry responded with a prediction of tens of thousands of lost jobs and regional economic disaster. In 1993 President Bill Clinton convened the Forest Summit conference in Portland, Oregon, to work out a solution. The Clinton administration's plan, though approved by Judge Dwyer, satisfied neither the industry nor the environmentalists, and protests, lawsuits, and legislative battles continued.

As the twentieth century came to an end, timber harvest levels had been significantly reduced, the Northwest's economy had survived, and additional values for old-growth forests were found: habitat for endangered salmon and other fish, a source for medicinal plants, and a repository for benefits yet to be discovered. The decades-long controversy over the forests of the Northwest had a deep impact on environmental science as well as natural resource policy and encouraged new interest in other native forests around the world, from Brazil to Malaysia to Russia.

Joseph W. Hinton

See also: Conifers; Forests; Forest management; Logging and clear-cutting; Mycorrhizae; Sustainable forestry; Timber industry.

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OOMYCETES

Categories: Molds; *Protista*; taxonomic groups; water-related life

Oomycetes are a diverse group of fungus-like eukaryotic microorganisms that form the phylum Oomycota. *First classified within the kingdom* Fungi, *oomycetes are now unambiguously recognized as distinct from fungi and more closely related to heterokonts, such as brown algae, phylum* Phaeophyta.

The more than five hundred species of oomycetes, commonly known as water molds, white rusts, or downy mildews, are essentially saprophytic but include pathogens of plants, insects, crustaceans, fish, vertebrate animals, and various microrganisms. Plant pathogenic oomycetes cause devastating diseases on several crop, ornamental, and native plants. Animal pathogenic oomycetes can cause severe losses in aquaculture and fisheries. Both have had a significant impact on human history.

Evolutionary History

Traditionally, and due essentially to their filamentous growth habit, oomycetes have been classified in the kingdom *Fungi*. However, modern molecular and biochemical analyses as well as morphological features suggest that oomycetes share little taxonomic affinity with filamentous fungi but are more closely related to brown algae (phylum *Phaeophyta*) in the kingdom *Protista*. This position is supported by molecular phylogenies based on ribosomal RNA (ribonucleic acid) sequences, compiled amino acid data for mitochondrial proteins, and protein encoding chromosomal genes. The oomycetes also display a number of biochemical and morphological characteristics that distinguish them from the fungi and confirm their affinity to brown algae and other heterokonts.

The cell walls of oomycetes are composed mainly of glucans and cellulose and, unlike fungal cell walls, contain little or no chitin. The zoospores display two flagella, with an ultrastructure similar to that of the flagella of the motile spores of heterokont algae. The oomycetes also contain the energy storage chemical mycolaminarin, a molecule that is also found in kelps and diatoms.

Taxonomic Classes

The subdivison of oomycetes into taxonomic classes remains under debate. Typically four classes of oomycetes are identified. These include *Saprolegniales*, *Leptomitales*, *Lagenidales*, and *Peronosporales*. Some authors elevated the plant pathogenic genera *Phytophthora* and *Pythium* to a separate class, named *Pythiales*. Recent molecular phylogenetic studies using ribosomal and mitochondrial sequences have started to unravel the evolutionary relationships between the different classes of oomycetes. The *Peronosporales* and

Pythiales, which together account for the majority of plant pathogenic genera, form an ancient monophyletic group, suggesting that acquisition of plant pathogenicity probably occurred early in the evolution of this lineage. Most of the saprophytic and animal pathogenic species are restricted to the other classes. *Aphanomyces*, a genus with strong affinity to the *Saprolegniales*, includes both animal and plant pathogenic species.

General Features

The oomycetes inhabit primarily aquatic and moist soil habitats. They are often very abundant and can be easily cultured from both freshwater and saltwater ecosystems, as well as from a variety of agricultural or natural soils. However, several species are mainly terrestrial, including obligate biotrophic pathogens of plants that depend on air currents to disperse their spores.

The basic somatic structure of a majority of oomycete species is an extending funguslike thread, the *hypha*, that grows into a branched network of filaments, the *mycelium*. Oomycetes are known as *coenocytic* organisms; that is, their mycelium lacks septa or crosswalls that divide the hypha, except to separate it from the reproductive organs.

Both asexual and sexual reproductive structures occur. The primary asexual reproductive organ is the sporangium that differentiates at the tip of a vegetative hypha to produce and release motile zoospores with two flagella. The zoospores can germinate directly or indirectly to produce a vegetative mycelium or can differentiate into secondary zoospores. Sexual reproduction involves the interaction of a male antheridia with a female oogonia through a fertilization tube that allows the male nuclei to migrate into the oogonium. Some oomycetes are self-fertile or homothallic, whereas others are self-sterile or heterothallic and require that strains with different mating types come into contact to achieve sexual reproduction. The sexual spores are the oospores, which can survive desiccation and starvation over long periods of time. Under favorable environmental conditions, the oospores germinate to form vegetative mycelium or to release zoospores. Oospores are also the structures that gave the oomycetes their name of egg fungi. Oomycetes are diploid in the dominant vegetative phase with meiosis occurring only during gametogenesis.

Economic Importance

Saprophytic oomycetes play an important role in the decomposition and recycling of decaying matter in aquatic and soil environments. In addition, both plant and animal pathogenic oomycetes can cause serious economic impact by destroying crop, ornamental, and native plants as well as fish and other aquatic organisms.

Typically, oomycete diseases are difficult to manage and require the use of specific chemicals (fungicides or oomycides). Sources of sustainable genetic resistance in plants to oomycetes are limited. In addition, most oomycetes, such as *Phytophthora*, exhibit tremendous ability to adapt to chemical and genetic resistance through the development of new resistant strains. For example, the appearance in the 1990's of *Phytophthora infestans* strains resistant to the chemical metalaxyl resulted in potato late blight epidemics in the United States that were severe and destructive. Most modern research focuses on innovative approaches for the management of oomycete diseases, including the use of plant breeding, genetic engineering, and genomic technologies.

Plant-Pathogenic Oomycetes

Plant-associated oomycetes may be facultatively or obligately pathogenic. Pathogenic oomycetes form specialized infection structures, also found in fungi, such as *appressoria* (penetration structures) and *haustoria* (feeding structures). Plant-pathogenic oomycetes include about sixty species of the genus *Phytophthora*, several genera of the biotrophic downy mildews, and more than one hundred species of the genus *Pythium*. *Phytophthora* species cause some of the most destructive plant diseases in the world and are arguably the most devastating pathogens of dicotyledonous plants.

The most notable plant-pathogenic oomycete is *Phytophthora infestans*, the Irish Potato Famine pathogen, which causes late blight, a disease of potato and tomato. Introduction of this pathogen to Europe in the mid-nineteenth century resulted in the potato blight famine and the death and displacement of millions of people. Today, *Phytophthora infestans* remains a prevalent pathogen causing multibillion dollar losses in potato production worldwide.

Other economically important *Phytophthora* diseases include root and stem rot caused by *Phytophthora sojae*, which hampers soybean production in several continents, and black pod of cocoa caused by *Phytophthora palmivora* and *Phytophthora megakarya*, a recurring threat to worldwide chocolate production. The introduction of exotic plant pathogenic oomycetes to natural ecosystems can also cause devastating effects. For example, *Phytophthora cinnamomi* has decimated native plants in Australia and South America. More recently, sudden oak death, a disease caused by a new species, *Phytophthora ramorum*, has emerged as a severe disease of oak trees along the Pacific Coast of the United States. Other notorious oomycete pathogens include the obligate biotrophs *Plasmopara viticola*, the agent of downy mildew of grapevine, as well as *Albugo* and *Peronospora* species, which cause white rust and downy mildews on several crops.

Animal-Pathogenic Oomycetes

Animal-pathogenic oomycetes are common. At least one oomycete species, *Pythium insidiosum*, is known to infect mammals, sometimes including humans, fatally. However, most economic impact on animals is caused by oomycetes that infect fish, fish eggs, and crustaceans. Examples include *Saprolegnia parasitica*, a ubiquitous pathogen of fish that is common in aquaria and can cause severe losses in aquaculture, particularly when fish density is too high or fish diet is unbalanced. Another important animal pathogenic oomycete is *Aphanomyces astaci*, the agent of crayfish plague that decimated European crayfish populations following its introduction from North America. Animal-pathogenic oomycetes can also have beneficial effects. At least one species of oomycetes, the insect pathogen *Lagenidium giganteum*, has been commercialized by a California company as a biocontrol agent for mosquitoes.

Sophien Kamoun

See also: Algae; Biopesticides; Brown algae; Cladistics; Diseases and disorders; Eukaryotic cells; Flagella and cilia; Fungi; Heterokonts; Molecular systematics; *Protista*; Resistance to plant diseases.

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ORCHIDS

Categories: Angiosperms; economic botany and plant uses; gardening; taxonomic groups

Orchids are the largest family of monocots among the angiosperms (flowering plants), with between twenty-five thousand and thirty thousand species, and new species are continually being described.

There are numerous natural and artificial hybrids of orchids (family *Orchidaceae*). The floral and vegetative variation in this family is enormous, and most orchid specialists consider the orchids to be undergoing a great deal of evolutionary activity as well. Orchids follow the general monocot pattern of having flower parts in three's. They differ from other monocots in several ways, however.

First, the stamens are fused together. Orchids are divided into two major groups based on their anthers and stamens: the *diandrous* orchids, which have two functional anthers and a sterile stamen, which in the lady's slipper orchids (such as *Cypripedium*, *Selenipedium*, *Paphiopedilum*, and *Phragmipedium*) becomes modified into a staminode, and the *monandrous* orchids (all other orchids), which have one functional anther.

Second, the stamens are fused with the pistil to form a structure called a *column*, which has at its tip a *rostellum*, a gland that separates the pollinia from the stigmatic surface. The fusion of the stamens and pistils into a column also occurs in the milkweed family (*Asclepiadaceae*) in the dicots.

Third, the pollen grains are formed together into packets called *pollinia*.

Fourth, flowers have bilateral symmetry or asymmetry, as in *Tipularia*.

Fifth, *resupination* is the most common condition for orchid flowers. In resupinate orchids, the pedicel and ovary undergo a 180 degree twisting process so that as the flower matures the lip is lowermost and the column uppermost. Although some orchids (such as *Calopogon*, *Polystachya*, *Malaxis*, and *Platanthera nivea*) are nonresupinate, most are resupinate.

Image Not Available

Sixth, the third petal, or lip, is usually highly modified in size, shape, or color when compared to the other two petals.

Seventh, the ovary is inferior.

Eighth, orchids produce large numbers of tiny seeds that lack endosperm. Most orchids have bisexual flowers; however, some (*Catasetum*, *Cycnoches*, *Mormodes*) produce unisexual (male or female) flowers. Flowers may last only a day (*Sobralia*), or for more than a month (some *Paphiopedilium* and *Dendrobium*).

Pollination

Pollination ranges from promiscuous to pseudocopulation. Promiscuous pollination occurs when almost any appropriate insect can transfer the pollinia successfully from one flower to another. Pseudopollination involves flowers which mimic the size, shape, smell, or movements of female wasps or bees (*Ophrys*, *Caladenia*, *Drakaea*). These flowers attract the male wasp or bee, which attempts to mate with the flower. Pollinia are thereby attached to the insect's body. Eventually the frustrated male leaves the flower and finds another flower, again trying to mate with it but succeeding only in depositing the pollinia from the first flower onto the second flower's stigmatic surface.

Mycorrhizae and Seed Germination

To germinate, orchid seeds, which lack endosperm, must form a symbiotic relationship with the mycelium of an appropriate fungus (mycorrhiza) which provides the seeds with nutrients and water.

Vegetative Plant Structure

Vegetative plants are herbs or, rarely, vines (*Vanilla*), perennials or, rarely, annuals (*Zeuxine strateumatica*). Vegetative parts are normally roots, stems, and leaves, which can undergo many different modifications. The roots of terrestrial orchids are similar to other terrestrial monocots and are nonphotosynthetic. Some are modified into food storage structures (tuberoids). Roots of epiphytic orchids have a specialized outer multilayered tissue called the velamen, which forms a spongy, whitish sheath around the root. The velamen allows absorption of water and dissolved mineral nutrients.

Stems are frequently modified into creeping rhizomes and often into water- and food-storage structures, such as corms, tubers, or pseudobulbs. These structures are usually aboveground and photosynthetic. Plants may be minute (some *Bulbophyllum* and *Platystele*) or gigantic (about 44 feet tall, such as *Sobralia altissima*) or may form large clusters of pseudobulbs weighing several hundred pounds (*Grammatophyllum*).

Growth Patterns, Distribution, and Habitats

There are two basic growth forms in orchids. In the *sympodial* form, successive new stem growth originates from the base of the preceding stem growth (as in *Cattleya* and *Cypripedium*). In the *monopodial* form, new growth comes from an apical meristem; these plants often become quite tall (such as *Vanda*).

Orchids occur worldwide, from the Arctic to the tropical rain forests but do not grow wild in Antarctica. Most tropical orchids are epiphytic (growing on other plants) or epilithic (growing on rock surfaces), and a relatively small number, including the temperate and Arctic orchids, are terrestrial. The genus *Rhizanthella* in Australia is subterranean.

Economic Uses

Uses include a complex starch (called salep) used as food in Turkish and other Middle-Eastern confections. Salep is made from the dried tuberoidal roots of *Dactylorhiza*, *Eulophia*, and *Orchis*. In the Americas, the Mayans and the Aztecs cultivated *Vanilla* vines for the fleshy fruit, or bean, which was fermented to make vanilla for use as food flavoring and perfume. Some orchids have been used as sources of fibers for weaving or basket making. Currently, many different orchids are important as cut flowers or as potted plants, including *Cattleya*, *Dendrobium*, *Cymbidium*, *Paphiopedilium*, and *Laelia*. Advances made during the 1990's in mericloning have greatly reduced the cost of producing high-quality plants.

Lawrence K. Magrath

See also: Angiosperm evolution; Animal-plant interactions; Garden plants: flowering; Monocots vs. dicots; *Monocotyledones*; Mycorrhizae.

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ORGANIC GARDENING AND FARMING

Categories: Agriculture; economic botany and plant uses; environmental issues; food; gardening

Organic growing strives to produce healthy soils and plants through practices that replenish and maintain soil fertility. Organic farmers avoid the use of synthetic and often toxic fertilizers and pesticides.

At the beginning of agricultural history, farmers believed that plants "ate the soil" in order to grow. During the nineteenth century, German chemist Justus von Liebig discovered that plants extracted nitrogen, phosphorus, and potash from the soil. His findings dramatically changed agriculture as farmers found they could grow crops in any type of soil, even sand and water solutions, if the right chemicals were added.

By the late twentieth century, diversified family farms in industrialized nations had given way to huge, specialized operations. Crop yields were raised with the use of chemicals, but farms and their soil and water were not being used efficiently. Over time, the organic quality of the soil was lost, even though the agricultural chemicals remained in the soil.

Chemicals were found to leach into the water supply. In 1988 the U.S. Environmental Protection Agency (EPA) found that groundwater in thirty-two states was contaminated with seventy-four different agricultural chemicals. Leaching causes once-friable and fertile soils to become nonproductive. Further, the use of chemical insecticides was having toxic effects on both the foods grown and the farmworkers encountering them. About forty-five thousand accidental pesticide poisonings occur in the United States each year; in 1987 the EPA ranked pesticides as the third leading environmental cancer risk. A National Academy of Science study estimated that twenty thousand people each year get cancer because of pesticides alone. Growing public awareness of the effects of the traditional agricultural reliance on synthetic chemicals is reflected in a growing demand for organically produced foods.

Tenets of Organic Farming

Organic farming represents the use of diversified farming practices that emphasize working with nature to create an ecologically sound and sustainable system of agriculture. Certified organic farmers are bound by practices that are free of synthetic chemicals and genetic engineering. Lands must be chemical-free for at least three years before products grown on them can be certified as organic. The organic certification further requires that both plants and livestock be raised without the use of chemicals, antibiotics, hormones, or synthetic feed additives.

Certified organic farmers must comply with both organic regulations in their state and the 1990 Organic Foods Production Act (OFPA). In the late 1990's the U.S. Department of Agriculture (USDA), through the National Organic Standards Board (NOSB), began working to develop standards and regulations that would ensure consistent national standards for organic products. There are six areas of standards that the NOSB is examining: crops; livestock and livestock products; processing, packaging and labeling; accreditation; international issues; and materials. There is interest in developing global standards for the importation and exportation of organic products.

Soil Fertility

Like all farmers, organic farmers must ensure soil fertility and control unwanted plants and pests. Organic farmers build organic materials in the soil by the addition of *green manure*, *compost*, or *animal manure*. Green manure is the term used for crops that are grown to introduce organic matter and nutrients into the soil. Such crops are raised expressly for the purpose of being plowed under rather than sold to the consumer. Green manure crops protect soil against erosion, cycle nutrients from lower levels of the soil into the upper layers, suppress weeds, and keep much-needed nutrients in the soil.

Legumes are an excellent green manure crop because they are efficient at extracting nitrogen from the air and transferring it into the soil, leaving a supply of nitrogen for the next crop. The legumes have nitrogen nodules on their roots; when the legumes are tilled under and decompose, they add more nitrogen to the soil. As plants decay, they also make insoluble plant nutrients such as carbon dioxide and organic acids available in the soil.

Much of the organic material derived from green manure comes in the form of decaying roots. Alfalfa, one type of legume, sends its roots several feet down into the soil. When alfalfa plants are turned, the entire root system decomposes into organic material. Thus they help improve water retention and soil quality at the same time. Some examples of legumes used for green manure are sweet clover, ladino clover, and trefoil. Grasses used for green manure include rye, redtop, and timothy grass.

Greater fertility can be achieved if green manure is grazed by animals and animal manure is deposited on the soil. When grass is grazed, a proportion of the roots die and rot to form *humus*. This humus is the stable organic material that acts as a catalyst for allowing plants to find nutrients.

Animal manure is also used as an organic fertilizer. Rich in nitrogen, the best animal manures come from animals with high-protein diets. For ex-


PhotoDisc

A farmer tends organically grown cucumber plants.

ample, beef cattle being fattened for market consume a higher level of protein than dairy cattle that are producing milk for market. The application of manure to fields improves the structure of the soil, raises organic nitrogen content, and stimulates the growth of soil bacteria and fungi necessary for healthy soils.

Compost is particularly useful to the small-scale farmer or gardener who does not raise livestock or have the acreage to grow a green manure crop to plow under. Composting is a natural soil-building process that began with the first plants that existed on earth. It continues to be employed as a natural process today. As leaves and dead plants, animals, and insects decompose into the soil, they form a rich, organic layer. Compost can be made by farmers and gardeners by using alternating layers of carbohydrate-rich plant cuttings and leaves, animal manure, and topsoil and allowing it to decay and form a rich, organic matter to be added to the soil.

Crop Rotation

Planting the same crop year after year on the same piece of ground results in depleted soil. Crops such as corn, tobacco, and cotton remove nutrients, especially nitrogen, from the soil. In order to keep the soil fertile, a legume should be planted the year after a cash crop in order to add nitrogen and achieve a balanced nutrient level. Planting a winter-cover crop such as rye grass will help protect land from erosion and will, when plowed under in the spring, provide a nutrient-rich soil for the growth of a cash crop. *Crop rotation* also improves the physical condition of the soil because different crops vary in root depth and respond to either deep or shallow soil preparation.

Organic Insect and Weed Control

Monoculture puts a large amount of the same crop in proximity to pests that are destructive to that particular crop. Insect offspring can multiply out of proportion when the same crops are grown in the same field year after year. Because insects are drawn to the same home area, they are less able to proliferate if the crop is changed to one they cannot eat. For this reason, organic farmers rely on crop rotation as one aspect of insect control. Rotating crops can also help control weeds. Some crops and cultivation methods inadvertently allow certain weeds to thrive. Crop rotation can incorporate a successor crop that eradicates those weeds. Some crops, such as potatoes and winter squash, work as "cleaning crops" because of the different styles of cultivation that are used on them.

Organic farmers and gardeners believe that plants within a balanced ecosystem are resistant to disease and pest infestation. Therefore, the whole premise of organic farming is working with nature to help grow healthy, unstressed plants. Rather than using chemicals, which often create resistant generations of pests and thus the need for newer and stronger chemicals, organic farmers have found natural ways to diminish pest problems.

Organic farmers strive to maintain and replenish soil fertility to produce healthy plants resistant to insects. They also try to select plant species that are naturally resistant to insects, weeds, and disease. Crop rotation, as already discussed, is one method of keeping infestation down. Rows of hedges, trees, or even plants that are not desirable to insects planted in and around the crop field can act as barriers to pests. They can also provide habitat for pests' natural enemies, including birds, beneficial insects, and snakes.

Beneficial insects can be ordered through the mail to help alleviate insect pests. The ladybug and the praying mantis are two insects that can help rid farms or gardens of aphids, mites, mealy bugs, and grasshoppers. Just one ladybug can consume fifty or more aphids per day. Because most people order ten thousand to twenty thousand ladybugs for their garden, and one ladybug can lay up to one thousand fertile eggs, the overall cost of *biopesticides* is much less than that of buying *insecticides*. Trichogramma, also available by mail order, is a small wasp that will destroy moth eggs, squash borers, cankerworms, cabbage loopers, and corn earworms.

Organic farmers and gardeners also rely on what is called an *insecticide crop*. Garlic planted near lettuce and peas will deter aphids. Geraniums or marigolds grown close to grapes, cantaloupes, corn, and cucumbers will deter Japanese and cucumber beetles. Herbs such as rosemary, sage, and thyme planted by cabbages will deter white butterfly pests. Potatoes will repel Mexican bean beetles if planted near beans, and tomatoes planted near asparagus will ward off asparagus beetles. Natural insecticides such as red pepper juice can be used for ant control, while a combination of garlic oil and lemon may be used against fleas, mosquito larvae, houseflies, and other insects.

Organic farming relies on the physical control of weeds, especially through the use of cutting (cultivation) or smothering (mulching and hilling). Cultivation is the shallow stirring of surface soil to cut off small developing weeds and prevent more from growing. Cultivating tools include tractors, wheel hoes, tillers, or, for small gardens, hand hoes.

Mulch is a soil cover that prevents weeds from getting the sunlight they need for growth. Mulching with biodegradable materials can help build soil fertility while controlling weeds. Plastic mulches can be used on organic farms as long as they are removed from the field at the end of the growing or harvest season.

Dion Stewart and Toby R. Stewart

See also: Agriculture: modern problems; Biopesticides; Composting; Herbicides; Hydroponics; Legumes; Monoculture; Nitrogen cycle; Nitrogen fixation; Nutrients; Nutrition in agriculture; Pesticides.

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OSMOSIS, SIMPLE DIFFUSION, AND FACILITATED DIFFUSION

Categories: Cellular biology; transport mechanisms

Osmosis, simple diffusion, and facilitated diffusion are the processes by which water and other substances—usually small molecules and ions—cross cell membranes.

Transport of materials across cellular membranes is essential to the functioning of plants and other living organisms. It is the movement of materials across these semipermeable barriers that provides the conditions necessary for life, not only for the plasma membrane separating a cell from its environment but also for membranes surrounding organelles within cells.

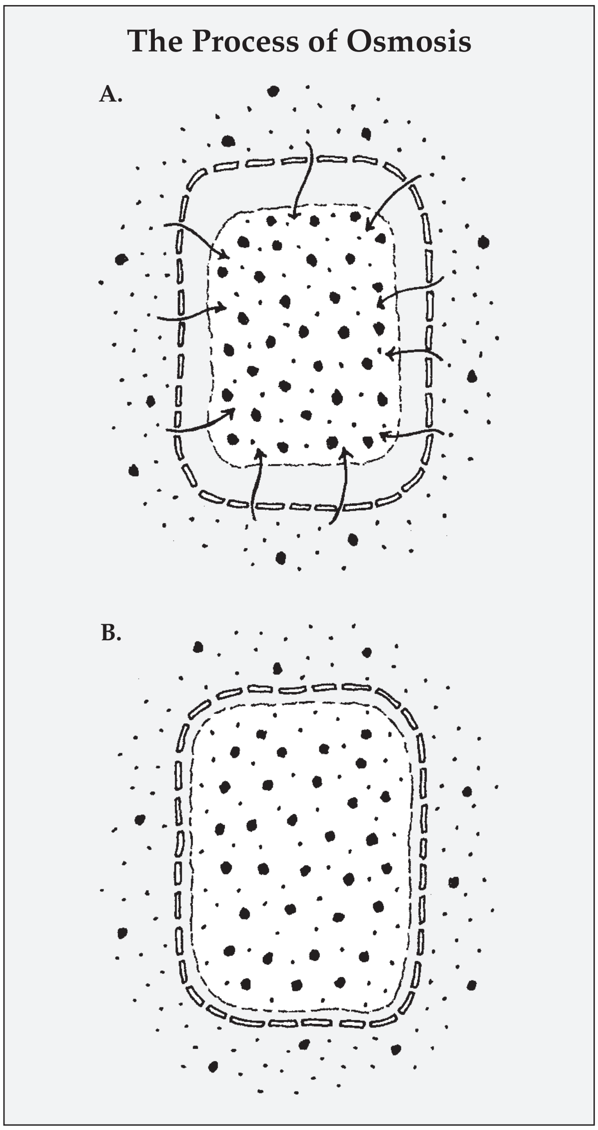
Unless cells are able to maintain a stable internal environment (homeostasis), growth, development, and metabolism are not possible. Thus, understanding how substances move across membranes and how membranes select which substances to admit and exclude leads to a better understanding of homeostasis and its maintenance.

Some substances require metabolic energy to cross membranes in a process called *active transport*. All other movement across membranes, however, is through either simple or facilitated diffusion. Osmosis is a special case of simple diffusion involving just the movement of water.

Cell Membranes

Cell membranes, typically about eight nanometers thick, serve as barriers between the cell's cytoplasm and the extracellular environment. The cell membrane's lipid constituents (primarily phospholipids) make it fundamentally insoluble in water and therefore impermeable to all but the smallest uncharged polar molecules and a variety of lipid soluble molecules. It is necessary, though, for some of these substances to cross this barrier.

The currently accepted structure of the cell membrane was proposed by Jonathan Singer and Garth Nicolson in 1972. According to their *fluid mosaic model*, a membrane consists of a double layer of phospholipids, called a *lipid bilayer*. Phospholipids are more or less linear molecules with a hydrophilic end (water-soluble or, literally, "water-loving"), often called the "head," and a hydrophobic end (water-insoluble or "water-fearing"), often called the "tail." Within the bilayer, the lipids naturally orient themselves with their hydrophilic heads facing toward the aqueous fluid on each side—the cytoplasm on one side, the extracellular fluid on the other—and their hydrophobic tails touching one another within the bilayer. Phospholipids on each side of the membrane are free to move around, a property called fluidity. Among thephospholipids float various proteins. They, too, are free to move unless constrained by anchors to cytoplasmic or extracellular structures or by limits on the fluidity of the lipid. Lipids and proteins that are exposed to the outside of the cell may also have oligosaccharides (short chains of sugar molecules) attached to them, making them glycolipids and glycoproteins. The carbohydrate portion recognizes and is recognized by specific binding substances on other cells or in the environment.



Kimberly L. Dawson Kurnizki

A. In osmosis, water (small dots) outside the plant cell moves from a region of greater concentration, outside, across the cell wall and the cell membrane to a region of less concentration initially occupied by more solutes (large dots) inside the cell.
B. The cell's uptake of water increases the volume of the cytoplasm and presses the cell membrane against the cell wall. The resulting turgor pressure or turgidity keeps the plant from wilting. The opposite occurs in dry conditions and causes the plant to wilt.

Concentration and Electrochemical Gradients

Substances crossing the membrane barrier by osmosis or diffusion will cross only from the side of the membrane with a higher concentration of the substance to the side with a lower concentration of the substance. If the substance is an ion (all of which are electrically charged), the concentration gradient of the ion and the difference in electrical charge across the membrane (called the *membrane potential*) together determine the direction of diffusion. The concentration gradient and the membrane potential together are referred to as an *electrochemical gradient*. Ions will only go down their electrochemical gradient.

If the concentration gradient and the membrane potential are lined up in the same direction, it is easy to determine which way the ion involved will travel. For example, if chloride ions (Cl^-), which have a negative charge, are in higher concentration outside the cell than inside the cell, they will be able to move into the cell by facilitated diffusion. This is because all cells have a negative membrane potential, which is to say, the electrical charge in the cytoplasm is more negative than the electrical charge on the outside. Thus, for this Cl^- example, both the concentration gradient and the membrane potential are aligned in the same direction. On the other hand, if the Cl^- concentration is higher inside the cell than outside, Cl^- could potentially travel in either direction. If the concentration gradient is very large and the membrane potential is only slightly negative, Cl^- would likely move out of the cell, whereas if the concentration gradient is small, and the membrane potential is very negative, Cl^- will likely move into the cell.

Routes Across the Membrane

Regardless of the direction substances will potentially be able to travel across the membrane, they will be able to do so by only one of three different processes: osmosis, simple diffusion, or facilitated diffusion. Water molecules, which are very small, can penetrate the lipid bilayer by passing between the phospholipids in a process called osmosis, although the exact mechanism is poorly understood. A few other hydrophilic molecules, such as methanol and ethanol, can cross a lipid bilayer. Apparently they, too, can penetrate the otherwise inhospitable hydrophobic environment of the membrane because of their small size and lack of charge. Hydrophobic substances, including dissolved gases such as oxygen, can also cross the membrane essentially unrestrained, and because they are lipid-soluble they simply "dissolve" into the membrane and through to the other side.

Hydrophilic substances, particularly charged molecules (ions), however, cannot cross a lipid bilayer by simple diffusion. They can cross membranes only with assistance from specialized *transport proteins*. These proteins penetrate both sides of the bilayer, with one part exposed to the cytoplasm and the opposite part to the extracellular fluid. Many transport proteins appear to work by a "shuttle" type of mechanism, binding to recognized substances on one side of the membrane and releasing them on the other side. Like many other processes involving proteins, the activity of transport proteins depends critically on the shape of the protein itself and on its ability to recognize a limited group of substances. Some membrane proteins form complexes of several proteins that form aqueous channels of the proper dimensions and charge distribution to serve as pores for specific molecules or ions.

Osmosis

Because living cells occupy an aqueous environment, water will always be present on both sides of a membrane. If one side has a higher concentration of *solutes* (dissolved material) in it than the other side, it will have a correspondingly lower concentration of water. Driven by random molecular movement, more water molecules will bump into one another and move out of the region of lower solute concentration than move into it, until eventually the water is uniformly distributed on both sides and the solute concentrations are the same. This net movement driven by the difference in solute concentration is called osmosis.

Osmosis is of fundamental importance in a variety of living systems. Organisms originally evolved in the ocean, so the cytoplasm of most cells has a solute concentration similar to seawater. Even terrestrial organisms have evolved mechanisms that maintain proper solute concentrations in tissue fluids. If the balance deviates from relatively narrow limits, there can be serious consequences.

For example, the freshwater green alga *Spirogyra* has a higher solute concentration than the surrounding water. Consequently, the net movement of water is from outside the algal cells to the cytoplasm. If this movement of water were to continue indefinitely, it would eventually cause such a buildup of pressure inside the algal cells that they would burst, except that algal cells (as well as all plant cells) are surrounded by a rigid cell wall. As the pressure builds, the cytoplasm swells in volume and presses the cell membrane against the cell wall, and the cell is said to be *turgid*. This same process occurs in terrestrial plants when roots absorb water from the soil, and this enables stem and leaf cells to maintain the turgidity required to keep the plant from wilting. In these examples, the cytoplasm is said to have a lower (more negative) water potential than the water outside. A solution with a lower water potential than another solution across a semipermeable membrane is said to be *hypertonic* (or hyperosmotic), while the other solution is said to be *hypotonic* (or hypo-osmotic). If the solute concentrations are the same on both sides of a semipermeable membrane, they are said to be *isotonic* (or iso-osmotic).

If the same green algae is placed in concentrated saltwater, the cytoplasm will now be hypotonic (and the saltwater will be hypertonic), and the net flow of water will be out of the algal cells. When this occurs in plants, the cytoplasm shrinks in volume, and the cell membrane pulls away from the cell wall in a process called plasmolysis. As a result, turgor pressure drops, and in the case of terrestrial plants in salty or dry soil, they begin to wilt. Some freshwater protozoa have specialized structures called contractile vacuoles that serve as pumps to maintain hypertonic conditions in the cytoplasm.

Diffusion

Both simple and facilitated diffusion involve the movement of a substance down a concentration or electrochemical gradient between the two compartments separated by a membrane The main difference between the two mechanisms is that substances moving by simple diffusion move through the lipid portion of the membrane, while substances using facilitated diffusion require specialized membrane proteins to allow their transport.

In simple diffusion, dissolved gases, such as oxygen and carbon dioxide, can cross membranes, as can lipid soluble substances. One type of important small molecule that crosses membranes by free diffusion are steroid hormones. These extremely potent regulators of cell metabolism readily diffuse through cellular membranes because their hydrophobic nature makes them dissolve readily in lipids. Within cells, they bind to specific receptors, which pass messages on to other proteins that control various biochemical events.

Facilitated Diffusion

All other materials that enter and leave cells down their chemical or electrochemical gradients do so by facilitated diffusion. Forming this pathway is the role of the particular membrane proteins, called carrier proteins, transport proteins, or *permeases*. Such proteins allow larger, polar molecules such as sugars and amino acids to be taken up by cells. They control the response of cells to certain growth factors and hormones, whose binding to the cell membrane causes channels for facilitated diffusion to open or close selectively.

Extremely specific recognition by the transport protein enables material to be transported. For this reason, membranes may readily transport one type of molecule but be completely impermeable to another molecule, even a closely related one. Membranes with selective permeability probably represent one of the most important innovations in living organisms. Without membranes, separate compartments could not be maintained to separate the various incompatible biochemical reactions of living systems. Without the semipermeability of biological membranes, the environment within the various compartments could not be continuously replenished and would be unable to respond to a continuously changing environment.

Mary Lee S. Ledbetter, updated by Bryan Ness

See also: Active transport; Cell wall; Cells and diffusion; Liquid transport systems; Membrane structure; Plasma membranes; Vesicle-mediated transport; Water and solute movement in plants.

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OXIDATIVE PHOSPHORYLATION

Categories: Cellular biology; transport mechanisms

Oxidative phosphorylation is the sequence of reactions in mitochondria that convert energy from food into cellular energy by synthesizing ATP, the primary energy currency of cells. To drive the second step in oxidative phosphorylation, electrons must be passed to one of the electron carrier molecules of the electron transport system.

The ability to convert the energy from food molecules into cellular energy efficiently is crucial to cell survival. The central conversion system is oxidative phosphorylation, a sequence of reactions that take place in mitochondria (a type of organelle found in plant cells). These reactions take high-energy electrons and use them to make *adenosine diphosphate* (ADP) and inorganic phosphate (P_i). The name "oxidative phosphorylation" derives from the fact that organic molecules are oxidized to provide the electrons that are used as an energy source to facilitate the phosphorylation of ADP.

Oxidative phosphorylation may be divided into four general steps:

- obtaining high-energy electrons
- transferring energy from the electrons into cellular energy, accomplished via the electron transport system
- using the cellular energy from the electron transport system to establish a proton (H^+) gradient across the inner mitochondrial membrane
- using the stored energy of the proton gradient to drive the synthesis of *adenosine triphosphate* (ATP)

Finding Electrons: Oxidation

The main source of the electrons for the first step of oxidative phosphorylation is the chemical oxidation of organic molecules. Sources can include *glycolysis*, *fatty acid oxidation*, and the *Krebs cycle* (citric acid cycle). Chemical oxidation results in a loss of electrons by the oxidized molecule; when the electrons are removed from a molecule they are picked up by an electron acceptor, or *electron carrier*. Electron carriers are molecules that can transport electrons between molecules in the cell, much as a package delivery service will carry a box between two addresses. The most common electron carriers are *nicotinamide adenine dinucleotide* (NAD^+) and *flavin adenine dinucleotide* (FAD). Each one of these molecules can carry two electrons at a time. Once NAD^+ or FAD molecules accept electrons, they are said to be chemically reduced and are denoted as NADH or $FADH_2$.

Electron Transport

To drive the second step in oxidation phosphorylation, the electrons carried by NADH and $FADH_2$ must be passed to one of the electron carrier molecules of the electron transport system. The carriers that receive the electrons then pass them to other carriers in the system. Every time one carrier gives a pair of electrons to another, a small amount of energy is released. This energy is used by the *mitochondrion* to pump H^+ across the inner mitochondrial membrane. The electron pair continues to be transferred through a series of electron carriers until any extra energy they carry has been used for pumping H^+. The last carrier transfers what are now low-energy electrons to oxygen, which is the final electron acceptor in the series. When the electrons are accepted by the oxygen, it combines with two H^+ to form a molecule of water.

The components of the electron transport system are embedded in the inner mitochondrial membrane, and they are arranged in four large complexes. Each complex contains a component responsible for picking up the electrons and a protein portion that delivers the electrons to the next carrier in the chain. Each complex also contains additional proteins—in some cases as many as twenty—that attach the complex to the inner mitochondrial membrane.

In addition to these four complexes, there are two smaller electron carriers that can transport electrons between the larger complexes. One of these, *cytochrome c*, is a small protein. The other electron carrier is called *ubiquinone*, or coenzyme Q. Every time an electron pair is delivered to a new carrier, it loses a certain amount of energy, and each of the carriers can only accept electrons that have a particular amount of energy. Therefore, an electron pair moves through the electron transport system in an exact order, going only to carriers that are able to accommodate electrons of a precise energy level.

The order in which electrons move through all the components of the electron transport system has been determined by Britton Chance and several other investigators. An electron pair entering the system would proceed as follows. (The four complexes are identified by Roman numerals I-IV.)

$$\text{NADH} \rightarrow \text{complex I} \rightarrow \text{ubiquinone} \rightarrow \text{complex III} \rightarrow \text{cytochrome c} \rightarrow \text{complex IV} \rightarrow \text{oxygen}$$

Complex II accepts electrons directly from $FADH_2$, found in the matrix of the mitochondrion, then passes them to ubiquinone.

Establishing the Proton Gradient

The energy harvested during electron transport is used in the third step of the process to create an H^+ gradient. Three of the complexes (I, III, and IV) contain an additional protein component that is able to use the harvested energy to move protons from the matrix across the inner membrane, into the space between the inner and outer membranes, which is called the intermembrane space. The accumulation of protons in this intermembrane space results in proton concentration gradient across the inner membrane, from a high proton concentration in the intermembrane space to a low proton concentration in the matrix of the mitochondrion. The proton concentration gradient represents a stored form of energy, much like the capacitor in an electronic device.

ATP Synthesis

Finally, in the fourth and final step of oxidative phosphorylation, the proton gradient is used to drive the synthesis of ATP. The energy from the proton gradient is used by an ATP-synthesizing enzyme, also found in the inner membrane of the mitochondrion called *ATP synthase*. ATP synthase is a very large molecule. At very high magnification, the ATP synthase molecule looks like a lollipop sticking out from the inner membrane into the matrix of the mitochrondrion.

In 1961 Peter Mitchell proposed that the stepwise transfer of electrons by the electron transport system and the proton gradient worked together to synthesize ATP. His proposal, called the *chemiosmotic hypothesis*, represented a radical departure from other ideas at the time. At first the chemiosmotic hypothesis found little support among scientists, but the chemiosmotic hypothesis has stood the test of time. Although some details remain to be worked out, the experimental evidence accumulated by Mitchell, as well as by many other investigators since 1961, overwhelmingly supports this model. Mitchell received the Nobel Prize in Chemistry in 1978 for his proposal of the chemiosmotic hypothesis and the elegant research he performed in its support.

Work from the laboratory of scientist Efraim Racker has demonstrated that there are different functions for the two parts of the lollipop. The spherical part of the lollipop can be removed by mechanical shaking and has been found still to be able to synthesize ATP. Racker called the sphere F_1, or coupling factor 1. The "stick" portion of the lollipop is embedded in the inner mitochondrial membrane. This part of the enzyme acts as a tunnel for protons to travel back into the mitochondrion. The stick portion of the enzyme can be inactivated by the antibiotic oligomycin, so it is called the F_o, or oligomycin-sensitive factor. Another name for the ATP synthase is thus F_oF_1ATPase.

The fine details of how the movement of protons through the channel in the stick drives ATP synthesis have not been completely worked out. The spherical portion of the molecule can make ATP without the proton gradient. Once synthesized, however, the ATP remains tightly attached, so no additional ATP can be made by the enzyme. The large concentration of protons in the intermembrane space causes a net flux of protons back into the matrix through the tunnel provided by the ATP synthase. Paul Boyer suggested that when protons move through the lollipop stick into the mitochondrion, the sphere changes its shape. This shape change, in turn, causes the enzyme to release newly synthesized ATP. The ATP can now be used by the cell, and the enzyme can now make more ATP. Boyer's proposal, which has gradually gained acceptance among researchers, is reasonable. Many biological enzyme reactions work by using similar shape changes to attach and release the substrates. A molecule of ATP is released for every three hydrogen ions that are returned to the matrix.

Alina C. Lopo

See also: ATP and other energetic molecules; Carbohydrates; Cell-to-cell communication; Energy flow in plant cells; Exergonic and endergonic reactions; Glycolysis and fermentation; Krebs cycle; Lipids; Mitochondria; Proteins and amino acids.

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OZONE LAYER AND OZONE HOLE DEBATE

Categories: Environmental issues; pollution

Ozone, a form of the element oxygen, forms naturally in the stratosphere and provides the earth with a filter from ultraviolet radiation. Some human activities have been linked to a decrease in the amount of ozone present, an effect that has been described as a hole in the ozone layer. The size of the hole located over Antarctica fluctuates with the seasons but over the past several decades has steadily increased in average size.

Ozone is a highly reactive form of oxygen. It is composed of three oxygen atoms in a molecule (O_3) rather than the more usual two atoms (O_2). Ozone is formed from the more common diatomic oxygen where high energy is present. Near the earth, ozone forms in high-temperature combustion processes, such as in automobile engines and in electrical sparks.

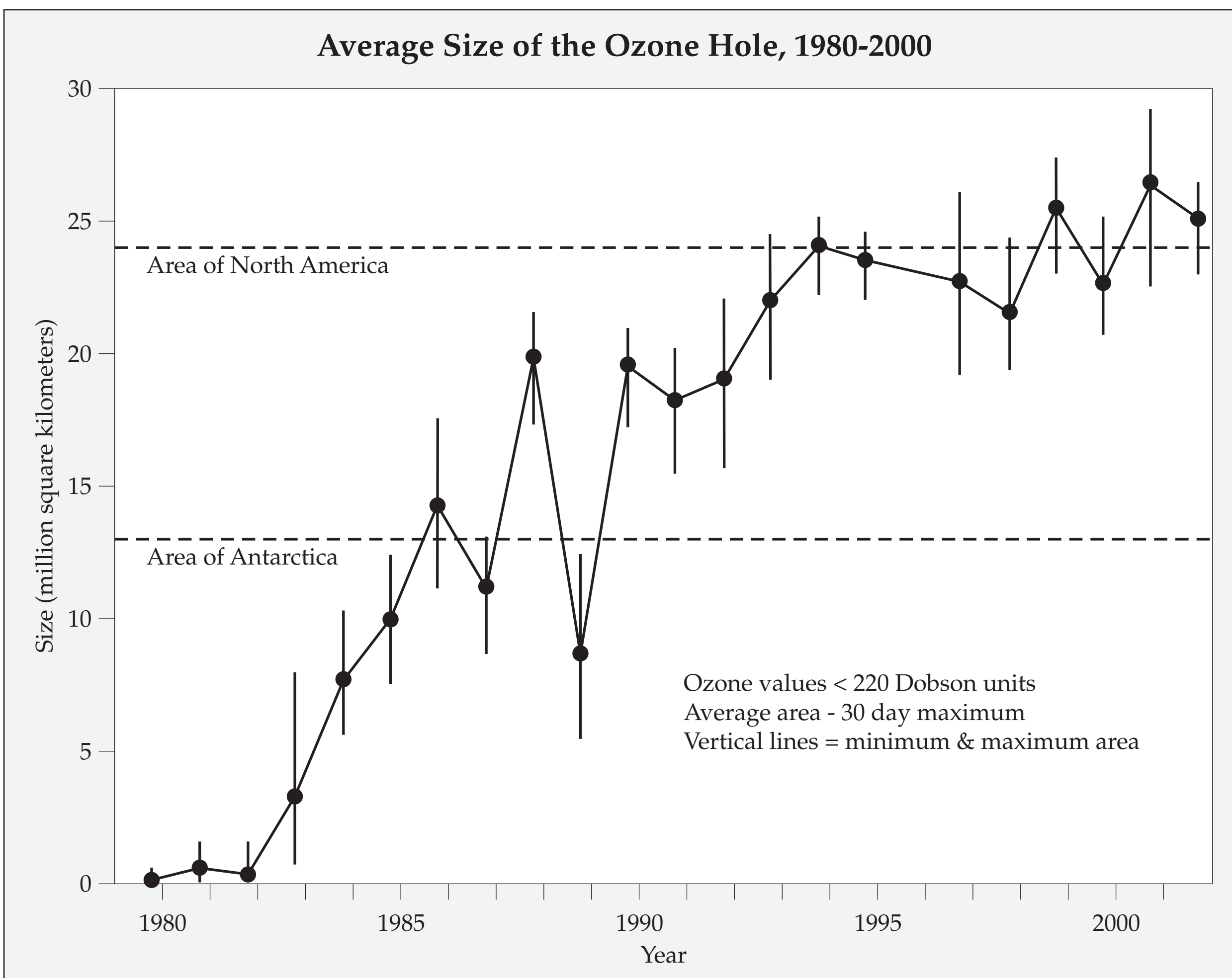
In the stratosphere, ozone forms because of high-energy ultraviolet radiation. Once formed, it is quick to react with other molecules. Near the earth there are many molecules with which to react, and the ozone concentration remains low. In the stratosphere there are few molecules present, so ozone concentration builds up and forms what is known as the ozone layer. Ozone also disappears naturally by decomposing to ordinary oxygen, so there is a natural limit to the concentration that accumulates, and equilibrium, or a "steady state," occurs. The ozone layer is actually quite diffuse, and the ozone concentration is never very high.

Changes in the Ozone Layer

Since the mid-1950's, measurements of ozone concentrations in the atmosphere have been made regularly. In the early 1970's analysis of the measurements suggested that something new was causing a reduction in the concentration of ozone in the stratosphere, particularly in the region over the South Pole. Continued measurements established a similar change above the North Pole and a spreading of the effect over a larger area. Laboratory experiments show that molecular fragments containing unpaired electrons are very effective in speeding the decomposition of ozone. This catalytic effect is particularly strong in the presence of small ice crystals, as are present in the stratosphere in the polar regions in winter.

Chlorofluorocarbons

Chlorofluorocarbons (CFCs) are a class of chemicals that have found wide use as propellants in aerosol cans, cleaning solvents for electronic circuit boards, and working fluids in air conditioning and refrigeration. These molecules are very stable, which is a prime factor in their utility, but this property also allows the molecules to drift into the stratosphere after they are released. Most other es-



Source: Goddard Space Flight Center, National Aeronautics and Space Administration, http:\\toms.gsfc.nasa.gov\multi\oz_hole_area.jpg; accessed April 15, 2002.

caping molecules react or are washed out by precipitation before they gain much height in the atmosphere.

In the stratosphere, CFCs decompose by irradiation and form molecular fragments to which ozone is sensitive. CFCs are not the only artificial cause of ozone depletion, but they have been recognized as a major contributor. Much of what is known about the way that the ozone layer forms and decomposes comes from the work of Paul Crutzen, Mario J. Molina, and F. Sherwood Rowland, who received the 1995 Nobel Prize in Chemistry for their work on this subject.

The Importance of Ozone

Ozone is decomposed when the energy available in part of the ultraviolet region of the spectrum is absorbed by the molecule. When the energy is used in such a fashion it is no longer present in the sunlight that comes through the stratosphere to the earth. Thus, the ozone layer acts as a filter to limit the earth's exposure to high-energy light. This type of energy, if it does make it to the earth, is capable of causing the reaction of other molecules, including those of biological importance. The evidence is overwhelming that the primary cause of nonmelanoma skin cancers is chronic long-term exposure to ultraviolet light. Increased ultraviolet levels also cause cellular modifications in plants, including food crops, which may lead to their death. Of particular concern is the inhibition of photosynthesis in the phytoplankton, the photosynthetic organisms that form the base of the ocean food chain. With a diminishing level of filtering, one would expect that there would be a global increase in the effects of overexposure to ultraviolet radiation.

Image Not Available

The Ozone Debate

Some scientists believe that ozone depletion is part of a natural cycle related to sunspot activity. Knowledge of what has happened in the distant past is circumstantial and not easy to interpret, but most scientists agree that human activities play a significant role in the current decrease in the ozone layer. In terms of the human contribution, CFCs have received the major attention, and their production was severely limited by international agreement in the 1987 Montreal Protocol and later revisions.

CFCs are no longer used as propellants, and their role as cleaners is all but over. However, their use as refrigerant fluids continues while economically viable, safe substitutes are being sought. People in developed countries have become extremely dependent on air conditioning; nearly all large buildings are designed to be air-conditioned rather than open to the outside. Part of the controversy concerning banning CFCs is based on ethical considerations. The developed countries used CFCs to help build their economies, so prohibiting CFC use in developing countries is considered inequitable by some. The search for substitutes has proved difficult, with economic, safety, and environmental concerns all placing limits on what is acceptable.

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See also: Air pollution; Greenhouse effect; Photosynthesis; Phytoplankton; Rain forests and the atmosphere.

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PACIFIC ISLAND AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

Agricultural practices in the Pacific Islands have an unsettled history. Typhoons, storms, drought, and volcanic activity can cause havoc to these islands' agriculture. For some, the rise of sea level can be devastating.

Throughout history, attempts by foreigners to encourage commercial agriculture in the Pacific Islands through *monoculture* (single cropping) have threatened fragile island environments. Large-scale land clearing and the use of fertilizers and pesticides have caused erosion, pollution, loss of biodiversity, and depletion of precious soils. Introducing new crops to these communities has resulted in the loss of native crops, harm to native species, and the elimination of traditional mixed farming methods.

The Pacific Islands have unique and fragile ecosystems, many of which are endangered by modern agricultural practices. The islands can be divided into two main types: the high islands, which are generally volcanic islands, and the *atolls*, or low islands. Volcanic lava wears down rapidly and provides fertile soil for cultivation. Atolls are low-lying coral reefs, which generally have an inadequate supply of fresh water and poor soils.

Coconuts, which can grow in poor soil and ripen throughout the year, are one of the few crops that thrive on the low islands. Coconuts are an important source of nutritious food and are easy to store. The meat of the coconut can be dried into a product called copra, which is pressed to make multipurpose oils.

Islands vary greatly in the amounts of rainfall they receive, the steepness of their slopes, and their varieties of plant life. Differences in rainfall and vegetation also exist on different parts of the same island. For example, one side of the island of Hawaii has one of the driest deserts on earth, whereas a few miles away on the other side of the island is a tropical rain forest.

Melanesian Islands

These fairly large islands are located to the northeast of Australia. They are quite damp, have a hot climate, and display a mountainous terrain covered with dense vegetation. Papua New Guinea is the largest island in Melanesia, slightly larger in size than California. It has a mountainous interior with rolling foothills that are surrounded by lowlands along the coastal areas. Its highest point is Mount Wilhelm, which rises to 14,795 feet (4,509 meters). Permanent crops occupy only 1 percent of the land. Crops are terraced in areas having steep slopes and extreme vegetation. Irrigation water is often brought to the crops through bamboo pipes. Approximately 64 percent of the labor force is involved in subsistence agriculture. Products grown include coffee, cocoa, coconuts, palm kernels, tea, rubber, fruit, sweet potatoes, vegetables, poultry, and pork. Palm oil, coffee, and cocoa are exported. In 1997 droughts brought on by the El Niño weather cycle caused extreme damage to coffee, cocoa, and coconut production.

Vanuatu, which includes eighty islands in the South Pacific due east of Australia's Cape York Peninsula, covers a total area a bit larger than the state of Connecticut. Its mostly mountainous terrain provides minimal arable land. Approximately 2 percent of the land is arable, and another 2 percent is used for pasture. About two-thirds of the population is involved in subsistence or small-scale agriculture. The main agricultural products are coconuts, cocoa, yams, coffee, fruits, vegetables, fish, and beef. Copra, beef, cocoa, and coffee are exported.

New Caledonia, located east of Australia in the South Pacific, is almost the size of New Jersey. It consists of coastal plains with interior mountains that range up to 5,340 feet (1,628 meters) in height. New Caledonia, which is known for its nickel resources, imports much of its food supply. A few vegetables are grown, but raising livestock is more common. Of New Caledonia's land, 12 percent is in permanent pasture, used for raising beef cattle.

The Fiji Islands include 332 islands, 110 of which are inhabited, located east of Vanuatu in the South Pacific. These islands are volcanic in origin. Approximately 10 percent of the land is arable, and 10 percent is in permanent pasture. About 67 percent of the labor force is involved in subsistence agriculture. Sugarcane is an important crop in Fiji and constitutes 32 percent of Fiji's exports. Other products grown in Fiji are coconuts, cassava, rice, sweet potatoes, cattle, pigs, and goats.

The Solomon Islands are a cluster of small islands that collectively cover an area almost the size of Maryland. They are located in the Solomon Sea between Papua New Guinea and Vanuatu. Some of the islands have rugged mountainous terrain; others are low coral atolls. Only 1 percent of the land is arable and 1 percent devoted to pastures. Approximately 24 percent of the working population is involved in agriculture, forestry, or fishing. Beans, cocoa, coconuts, palm kernels, rice, potatoes, fruit, and vegetables are grown on the islands. Cattle and pigs are the primary livestock raised there. Palm oil, cocoa, copra, and tuna are exported.


PhotoDisc

Tropical fruits like these on display at a market are a major export from many Pacific islands.

Micronesian Islands

Micronesia comprises thousands of relatively small islands located along the equator in the central Pacific Ocean and up to 1,200 miles (2,000 kilometers) north of the equator in the western Pacific Ocean. The region covers 1.54 million square miles (4 million square kilometers) and is subdivided into four areas: the Kiribati group, which lies around the intersection of the equator (0 degrees latitude) and the international date line (longitude 180 degrees); the Marshall Islands, which are about 900 miles (1,500 kilometers) to the northwest of Kiribati; the Federated States of Micronesia, which extend westward from the Marshall Islands for another 900 miles; and Guam, a U.S. territory located within the western cluster of islands of the Federated States of Micronesia.

The Kiribati group includes the Gilbert, Line, and Phoenix Islands, which are primarily low-lying atolls encircled by extensive living reefs. Of the thirty-three islands in the group, twenty are inhabited. Agriculture is mainly subsistence, with copra being one of Kiribati's few exports. Grown on the island for local consumption are taro, breadfruit, sweet potatoes, vegetables, and coconuts. Taro is one of the oldest cultivated plants in Pacific Island history and was once a staple food of the island people. This starchy, edible tuber can be cultivated by clearing or partially clearing a patch in the tropical rain forest and planting the taro in the moist ground.

The Marshall Islands contain two island chains of 30 atolls and 1,152 islands. Agriculture exists as small farms that provide commercial crops of tomatoes, melons, coconuts, and breadfruit. Coconuts, cacao, taro, breadfruit, pigs, and chickens are produced for local consumption.

Leading Agricultural Crops of Pacific Island Nations

Country	*Products*	*Percent Arable Land*
Fiji	Sugarcane, coconuts, cassava, rice, sweet potatoes, bananas	10
Micronesia	Black pepper, tropical fruits and vegetables, coconuts, cassava, sweet potatoes	—
New Zealand	Wheat, barley, potatoes, pulses, fruits, vegetables	9
Palau	Coconuts, copra, cassava, sweet potatoes	—
Papua New Guinea	Coffee, tea, cocoa, coconuts, palm kernels, tea, rubber, sweet potatoes, fruit, vegetables	—
The Philippines	Rice, coconuts, corn, sugarcane, bananas, pineapples, mangoes	19
Polynesia	Coconuts, vegetables, fruits, vanilla	—
Solomon Islands	Coconuts, palm oil, rice, cocoa, yams, vegetables, timber, beans, potatoes	1
Vanuatu	Copra, cocoa, coffee, coconut, taro, yams, fruits, vegetables	2

Source: Data are from *Time Almanac 2000*. Boston: Infoplease, 1999.

The Federated States of Micronesia include Pohnpei, the Truk Islands, the Yap Islands, and Kosrae. There are a total of 607 diverse islands, some high and mountainous, others low-lying atolls. Volcanic outcroppings are found on Kosrae, Pohnpei, and Truk. Agriculture on the islands is mainly subsistence farming. Products grown include black pepper, coconuts, tropical fruits and vegetables, cassava, and sweet potatoes. Pigs and chickens are the main livestock raised. Bananas and black pepper are exported.

Guam, the largest island in the Mariana archipelago, is of volcanic origin and surrounded by coral reefs. It has a flat coral limestone plateau that serves as a source of fresh water for the islands. In Guam, 15 percent of the land is used as permanent pasture. and another 11 percent is arable. Although fruits, vegetable, copra, eggs, poultry, pork, and beef are raised on the island, much of its food is imported because the economy relies heavily on U.S. military spending and the tourist trade.

Polynesia

Polynesia comprises a diverse set of islands lying within a triangular area having corners at New Zealand, the Hawaiian Islands, and Easter Island. French Polynesia is at the center of the triangle, 15 degrees south latitude and longitude 140 degrees west, and includes 118 islands and atolls.

The five archipelagoes of French Polynesia include four volcanic island chains (the Society Islands, the Marquesas, the Gambiers, and the Australs) and the low-lying atolls of the Tuamotus. The mountainous volcanic islands contain fertile soils along their narrow coastal strips. The atolls have little soil and lack a permanent water supply. Permanent pasture covers 5 percent of French Polynesia, and 6 percent of the land is used for permanent crops. Agricultural products raised include coconuts, vegetables, fruits, vanilla, poultry, beef, and dairy products. Coconut products and vanilla are exported. Thirteen percent of the population is involved in agriculture. On Tahiti, the largest island in French Polynesia, less than 10 percent of the land is arable. Exports include vanilla and coffee, but the main export from French Polynesia is pearls.

Samoa is a chain of seven islands lying several thousand miles to the west of Tahiti. Collectively, the islands are almost the size of Rhode Island, and they are covered with rugged mountains with a narrow coastal plain. Approximately 24 percent of the land sustains crops of bananas, taro, yams, and coconuts. Taro is a crop that can be used in land reclamation by building mud ridges or mounds in swampy ponds between the beach rampart and the foothills. Coconuts grown on the island are processed into creams and copra for export.

Tuvalu is a group of nine coral atolls located almost halfway between Hawaii and Australia. The soil is poor on these islands, and there are no streams or rivers. Water is captured in catchment systems and put into storage. Islanders live by subsistence farming and fishing. Coconut farming allows the islanders to export copra.

The Cook Islands comprise a combined area almost the size of Washington, D.C. Located halfway between Hawaii and New Zealand, the northern islands are primarily low coral atolls, and the southern Cook Islands are hilly volcanic islands. Permanent crops occupy about 13 percent of the land; 29 percent of the labor force is involved in agriculture. The Cook Islands produce a wide diversity of crops, including pineapple, tomatoes, beans, papayas, bananas, yams, taro, coffee, and citrus fruits. Agriculture is an important part of the economy, and copra, fresh and canned citrus fruit, and coffee are major exports.

The Hawaiian Islands are a volcanic chain of more than 130 islands, centered near 25 degrees north latitude and longitude 160 degrees west. Hawaii, with more than one million people, has the largest population in the Polynesian Island group. Lanai, one of the seven largest islands in Hawaii, is privately owned, and almost all its cultivated land is planted in pineapples. There are more than fifty-five hundred farms in Hawaii, and more than forty crops are grown commercially.

Because of the absence of adequate water on some sides of the Hawaiian Islands, water is brought through aqueducts from the wet sides of the islands to the dry sides, then kept in lined reservoirs to be used for irrigation, ranching, and tourism. Sugarcane requires enormous amounts of water to grow, and most pineapple crops are grown under irrigation. Hawaii is the second-largest producer of macadamia nuts in the world. The islands of Hawaii, Kauai, Maui, Molokai, and Oahu produce 7.6 million pounds of green coffee a year. Hawaii is also a prime producer of pineapple, cane from sugar, greenhouse and nursery plants, and dairy products. The main exports are fruits, coffee, and nuts.

New Zealand

About the size of Colorado, New Zealand is divided into two large islands and numerous smaller islands. About 50 percent of its land is in permanent pasture. A mountainous country with large coastal plains, 9 percent of the land in New Zealand is arable, and 5 percent is planted in permanent crops. Agriculture accounts for 9 percent of the gross national product and employs approximately 10 percent of the labor force.

In New Zealand, livestock outnumber people twenty-three to one. Wool, lamb, mutton, beef, and dairy products account for more than one-third of New Zealand's exports, and New Zealand is one of the world's top exporters of these products. New Zealand exports 90 percent of its dairy products. Other exports include cheese, fruits, and vegetables. Industry in New Zealand is primarily based on food products, including processed fruit, wines, and textiles.

Toby R. Stewart

See also: Caribbean agriculture; Monoculture; Pacific Island flora.

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PACIFIC ISLAND FLORA

Category: World regions

Pacific Island ecosystems are unique and fragile, but with extensive wildlife management, many native species can be saved from extinction.

The vast region of the Pacific Ocean collectively called Oceania holds thousands of islands. Oceania spreads across the Pacific from 20 degrees north latitude to 50 degrees south latitude and from longitude 125 degrees east to 130 degrees west. The major groupings of islands are Melanesia, Micronesia, Polynesia, and New Zealand. Melanesia ("black islands") is a group of large islands immediately north and east of Australia, from New Guinea to New Caledonia. Micronesia ("little islands") is made up of hundreds of tiny atolls in the western Pacific. Polynesia ("many islands") covers

Digital Stock

Hawaiian palm trees.

a huge region in the central Pacific. New Zealand lies east and south of Australia. For botanical purposes, these islands can be categorized by climate and formation type. Climates range from tropical to sub-Antarctic, dry to very rainy. Types include volcanic (Fiji, Guam, and Hawaii), tectonic (New Zealand and New Guinea), and low coral atolls (nearly all of Micronesia's islands).

Unique Ecosystems

Organisms have a hard time reaching islands across the broad expanses of the Pacific Ocean. The islands' isolation leads to trends in the number of species on any given island. Bigger islands have more species; those farthest from continents have fewer species. To reach the islands, plants must be carried by animals or rely on wind or water currents. Birds are usually the first visitors, bringing with them hitchhiking insects and plant seeds in their digestive tracts.

Island plants and animals evolve together, affected by difficult conditions. Soil is often poor and food limited. Harsh environments and isolation contribute to the formation of new and unique species. Island ecosystems are sensitive to disturbances, whether from natural causes, such as severe storms, or human activities, such as construction, agriculture, logging, and introduced species.

Introduced species (exotics), both accidental and deliberate, are a serious problem. Rats and feral animals (domestic animals that have gone wild) can devastate island ecosystems. Pigs, rats, and goats are particularly devastating to vegetation. Introduced plants may overgrow native ones. Exotics also bring diseases or other problems to which native plants and animals have no resistance. For example, a Hawaiian bee crawls headfirst into native, barrel-shaped flowers, gathers the nectar, and then backs out. A plant that was introduced in Hawaii by landscapers attracted bees, but the flowers were smaller than those of the native plants. Once a bee crawled in, it became stuck like a cork in a bottle. This led to thousands of these plants, each with hundreds of flowers, becoming stoppered with dead bees.

Many tropical and temperate islands have coastal wetlands and mangrove swamps growing at the edge of the sea. Mangroves are low-growing, salt-tolerant trees that form dense tangles virtually impenetrable to humans. Wetlands and mangrove swamps are important breeding grounds for many types of fish and crabs and also trap sediment, stabilize shorelines, and protect coastlines from storms. When humans fill in the wetlands and cut down the mangroves, it causes coastal erosion and the loss of food fish.

Fiji Islands

The Fiji Islands are mostly volcanic in origin and lie in the South Pacific Ocean between longitudes 175 degrees east and 178 degrees west and 15 degrees and 22 degrees south latitudes, about 1,300 miles (2,100 kilometers) north of Auckland, New Zealand. Some parts of the islands receive up to 13 feet (4 meters) of rain per year, while other parts remain dry. A range of volcanic peaks divides the islands. The differences in weather and elevation create a variety of habitats—dense rain forests, grassy savanna, and mangrove swamps—and a large diversity of species.

Human disruption on Fiji has been moderate. About half the total area is still forested, and less than one-fourth of the land is suitable for agriculture. Trees include mahogany, pine, pandanus, coconut palms, mangoes, guava, and figs. Banyan figs are difficult to cut down and are responsible for some of the lack of forest clearing. The figs are an important food for many birds and animals. Other rain-forest plants include orchids, ferns, and epiphytes (plants that grow upon other plants).

There are nearly fifteen hundred endemic Fijian plant species, including ten species of palm tree on the island of Viti Levu. Grassy savannas are found higher on the volcanic slopes and in the dry zones. They are often planted with coconut palms and taro, a plant with potato-like tubers that grows on many Pacific Islands.

There are twelve reserve areas in the Fijian islands, but several are being logged and provide little sanctuary to native plants and animals. The government is interested in increased logging of mahogany and pine. The Fiji Pine Commission hopes to encourage the development of pine forests. Pines grow quickly and could form a sustainable logging industry, unlike the valuable but slow-growing mahogany trees. Increased world interest in herbal remedies has created a market for Fiji's traditional crop, kava root, and for ginger processing. The University of the South Pacific is located in Fiji and is a center of serious research into South Pacific species. Tourism is important to Fiji's economy and, with management, could be a source of income to Fijians while preserving native wildlife.

New Guinea

The world's largest tropical island, New Guinea is located north of Australia, just south of the equator. It is tectonic in origin, with large changes in elevation and many different habitats. Because of its size and varied terrain, New Guinea has a greater variety of habitats than any similar-sized land area in the world. In fact, New Guinea is so rugged that it is one of the least explored or developed places on earth. It provides the best remaining example of the types of organisms that can develop in island isolation.

New Guinea habitats include cold tundra, tropical rain forests, grassy savannas, coastal zones, montane rain forests, cloud forests, and bogs. There are at least twenty thousand species of flowering plants, including more than twenty-five hundred species of orchids, and hundreds of birds and animals. Many New Guinea species are unusual. Endemic Klinki pines are the tallest tropical trees in the world, reaching 295 feet (90 meters) tall. Many forests host "ant-plants," warty looking epiphytes that have hollow mazes inside their tissues. Ants live in the maze, safe from predators. The ants provide nutrition for the plant in the form of droppings, scraps of food, and dead ants.

Even though New Guinea is rugged and isolated, human impact is increasing. The population is rising, which means that more forests are being logged and grasslands plowed for agriculture, roads, and development. Humans have brought in food plants such as the sago palm, which can be cultivated in areas where traditional crops will not survive. They also cultivate pandanus trees, several varieties of fruiting vine, breadfruit, fungi, tubers, sugarcane, bananas, taro, and yams. Gold, silver, and copper have been discovered, which encourages destructive mining.

It has proven difficult to develop New Guinea economically without destroying the unique life of the island. It is hoped that lessons learned on other islands, such as Guam and New Zealand, may be applied to New Guinea. The government has tried incentives to keep wild areas wild, including encouraging ecologically friendly businesses, such as crocodile and butterfly farms and ecotourism. The National Park reserve that includes Mount Jaya is the only place in the world where it is possible to visit a glacier and a coral reef in the same park.

New Zealand

Located off the eastern edge of Australia, New Zealand has a fairly moderate climate that comes from conflicting warm, humid Pacific and colder Antarctic weather. It is similar to New Guinea, with rugged terrain, high mountains, and habitats from grassy open plains to dense forests, wet areas to near-deserts. Unlike New Guinea, however, New Zealand has been occupied and developed by humans for hundreds of years. Before large-scale agriculture, about half of New Zealand was covered with forests and one-third with grassland communities. Now half is pasture for grazing, and one-quarter is forest, mostly introduced species. Much of the remaining native forest is maintained as national parks and reserves. Pastureland usually consists of a single species of grass and does not support the wide variety of bird and animal life of the original grassland communities. There are more than four thousand species of beetles, two thousand species of flies, and fifteen hundred species of butterflies and moths. In a reversal of the usual ecological concerns, some native insects are destroying introduced pasture grasses.

Coral Atolls

The Federated States of Micronesia consist mainly of small atolls. Coral atolls are found only in tropical latitudes because coral (small, colonial animals) grow only in warm water. Coral reefs support a tremendous variety of fish, crabs, and mollusks. Atolls tend to have porous, infertile soil and to be very low in elevation. The inhabited state of Tokelau, three small islands located at 9 degrees south latitude, longitude 172 degrees west, has a maximum elevation of 16 feet (5 meters). Due to the low profile, poor soil, and occasional scouring by typhoons, flora are mostly limited to hardy root crops and fast-growing trees such as coconut and pandanus. Other vegetation may include native and introduced species such as papaya, banana, arrowroot, taro, lime, breadfruit, and pumpkin. Common fauna are lizards, rodents, crabs, and other small creatures. Pigs, ducks, and chickens are raised for food.

Human disturbances on coral atolls often have been particularly violent; several nuclear test bombs were exploded on Bikini Atoll and other islands in the 1940's and 1950's. Kwajalein, the largest atoll in the world, is used by the U.S. military for intercontinental ballistic missile target practice. Johnston Atoll, about 820 miles (1,320 kilometers) southwest of Honolulu, is a U.S. military base and storage facility for radioactive and toxic substances. It is also designated as a protected area and bird-breeding ground.

Future Prospects

Island ecosystems are unique and fragile. Some, like those in Guam and New Zealand, can never be returned to their original state, but with extensive wildlife management, many native species can be saved from extinction. New Guinea, Fiji, and many smaller islands are in earlier stages of development, and wildlife destruction can still be controlled. Conservationists sometimes do not realize that islands are not small, geographical zoos and gardens; people live there and want to improve their lives. Development cannot be stopped, but it can be managed so that the humans can improve their standard of living as they wish and the original, amazing island dwellers can still survive.

Kelly Howard

See also: Biological invasions; Caribbean flora; Invasive plants; Pacific Island agriculture.

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PACLITAXEL

Categories: Economic botany and plant uses; medicine and health

Also known by the brand name Taxol, paclitaxel is a potent cancer-fighting drug originally derived from the bark of the Pacific yew tree, a small- to medium-sized understory tree that occupies Pacific coastal forests from southwestern Alaska to California.

Development of paclitaxel as a drug began in 1962 with the collection in Washington State of the reddish-purple bark of the Pacific yew tree (*Taxus brevifolia nutt*) by Kurt Blum, then a technician with the National Cancer Institute (NCI). The NCI was employing a "shotgun" approach to cancer research: A wide variety of plant parts of various species were being screened for anticancer activity. Thereafter, several scientists, including Monroe Wall and M. C. Wani at Research Triangle Institute in North Carolina and Susan Horwitz and Peter Schiff of the Albert Einstein College of Medicine in New York, recognized the potential of paclitaxel and became intensely interested.

Image Not Available

After years of delay, the pharmaceutical company Bristol-Myers Squibb continued tests and production on a larger scale. Paclitaxel was found to arrest the growth of cancer cells by attaching to their microtubules, thus preventing cell division. By the late 1980's Taxol had become the drug of choice, despite its high cost, for the treatment of a wide range of cancers, especially ovarian and breast cancer.

In spite of Taxol's prominence as a success story in the "herbal renaissance" of the twentieth century, several problems involved in production and medicinal use have persisted. For one, the cost of Taxol treatment has been prohibitive for many who desperately need it. The large amount of bark required (all the bark from a one-century-old tree yields only enough paclitaxel for a 300-milligram dose) raised fears among conservationists that continued harvest could threaten the species. While occurring over a wide area, the Pacific yew tree exists only in relatively small numbers. Furthermore, it is a slow-growing species that rarely reaches a height of more than 18 meters (60 feet); stripping the bark kills the tree. Plantations of the Pacific yew tree could be established, but it would take years for them to become productive.

Several means of producing paclitaxel without the destruction of wild yew trees have been proposed. Attempts have been made to produce paclitaxel from tissue cultures. Efforts to identify other *Taxus* species that may contain paclitaxel have been only marginally successful. In 1993 Bristol-Myers Squibb announced that it had found a semisynthetic method of producing paclitaxel that does not require yew bark. Paclitaxel-like compounds have been found in extracts from needles of the European yew tree (*Taxus baccata*) and those of several yew shrub species. An important advantage is that needles can be harvested without killing the trees or shrubs. Similar compounds have also been found in a fungus that grows on *Taxus* species.

Thomas E. Hemmerly

See also: Endangered species; Medicinal plants; Mitosis and meiosis.

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PALEOBOTANY

Categories: Classification and systematics; disciplines; evolution; paleobotany

The study of plants in the fossil record, in order to understand both the evolution of plant life and the ecology of ancient eras, is known as paleobotany.

Only a small percentage of the plants that ever lived left a record of their existence, surviving as *fossils*: mineralized wood, flowers in amber, leaf imprints in coal, or other indicators of life in an earlier era. Paleobotanists document this fossil record and use it to interpret the past evolution of plants.

Importance of Plant Fossils

Paleontology (or paleobiology) is the science concerned with fossils, the physical evidence of prehistoric life—including plants, animals, and microorganisms—on the earth. Paleobotany focuses on plant fossils, including algae, fungi, and related organisms, as well as mosses, ferns, and seed plants. As most organisms decompose rapidly after death, their preservation in nature is a rare event. Most individuals are not represented in the fossil record, and even many species that must have existed have vanished without a trace.

As a branch of botany, paleobotany is of importance primarily because the record of fossil plants helps scientists understand the long process of plant evolution. Especially since the 1940's, fossil evidence has helped to explain the origin of major classes of organisms, such as *algae* and *fungi*. Researchers now also have evidence for the origin of the earliest vascular plants and the formation of reproductive structures, such as cones of gymnosperms (evergreen trees and relatives) and flowers of angiosperms (flowering plants). The location of fossils, including both their temporal (age) and their spatial (geographical) arrangement, is used to determine past climates.

The climates of the world have changed continuously as continents have shifted over the earth's surface. For example, the location of coal deposits (which are the remains of giant tree ferns) in what is now Pennsylvania indicates the warmer climate that must have existed then. Although perhaps most of the contributions to paleobotany have been made by professionally trained scientists with a solid background in geology, botany, and related sciences, amateurs have also made significant discoveries. Many valuable specimens of university and museum collections were made by people interested in paleobotany as a hobby.

How Fossils Form

The formation of a fossil is an exceptional event, one that requires a special combination of favorable environmental conditions. In the most common fossilization process, the plant becomes covered by a soft sediment that then hardens to form a sedimentary rock. This type of rock forms gradually, over long periods of time, as particles produced by erosion are compacted on the bottom of the body of water.

The large-scale process by which plant parts become impregnated with minerals produces what has traditionally been called *petrified wood*. The modern term for this process is *permineralization*. Soluble carbonates, silicates, and other compounds infiltrate plant cells and the spaces between them. Eventually, the mineral deposits may completely replace the naturally occurring organic matter, preserving the details of the plant's microscopic architecture. Well known are the petrified forests of western United States, many of which are protected within national parks, such as Petrified Forest National Park in Arizona.

Being trapped in a sedimentary rock does not automatically guarantee that the organism will be preserved. The environment must be an *anaerobic* one—that is, one in which oxygen is excluded—thus preventing the decay that would otherwise result. The process may be interrupted by the action of waves or other erosive forces which re-expose the developing fossil before the process of fossilization is completed. Even after the process is completed, the well-preserved specimen may become distorted or altered in appearance because of the combined effects of time, pressure, and high temperatures that convert sedimentary rocks into metamorphic rocks.

As one would expect, the harder cells and tissues of plants are more likely to be preserved as fossils than are softer ones. For example, the thick-walled cells of wood and bark (called xylem) are more often preserved than are those of the pith (center of a stem) or cortex (found in stems and roots beneath the bark or outer covering). Other cells that are often fossilized are pollen grains and spores, both of which have outer shells that are highly resistant to decay.

Limestone and dolomite are among the most common types of rocks that form in such a way that they trap plants and form fossils. Coal, a combustible sedimentary rock, is formed in much the same way as other rocks but is distinctive because the sediment involved is of plant, rather than mineral, origin. Within this matrix of plant-derived material is often embedded a variety of plant parts.

Special Types of Fossils

Two special kinds of rock that may contain plant and animal fossils are diatomite and amber. Diatomite is a rock that forms from the silica cell walls of a group of unicellular algae known as *diatoms*. Because silica is the same material that sand and quartz are composed of, it is unusually permanent. Diatoms are found in both fresh water and salt water in great numbers and diversity. When they die, their cell walls accumulate underneath the water and become compacted over time into diatomite. The rock, itself formed by fossilization, may have fossil remains of various kinds of plants and animals preserved within it.

Amber, considered a semiprecious stone by gemologists and valued because of its beauty and distinctive appearance, is also of interest to paleobotanists. Amber is basically the fossilized resin produced by ancient cone-bearing evergreen trees. Sticky resins ooze from trees in response to injuries. Before such resins harden, various small animals, floral parts, pollen grains, fungal spores, and other plant parts may become trapped and be preserved intact. Deposits of amber valued for their use as jewelry and as fossils are recovered mainly from two world areas: the Baltic region of northern Europe and the Dominican Republic in the Caribbean Sea.

Paleobotanists are sometimes challenged by puzzling specimens. Outright fakes are sometimes presented by pranksters, but more common are various mineral structures that bear a superficial resemblance to a plant. Such specimens are called *pseudofossils*. Mineral deposits called dendrites found in rock crevices bear a resemblance to fern leaves. A coprolite (fossilized feces) from the upper Cretaceous period in Alabama was initially mistaken for the cone of a conifer (cone-bearing evergreen tree); these specimens may be referred to as pseudo-plant fossils, as they are true fossils of animals. During the formation of flint, bands are sometimes formed that suggest fossil mollusks or coral. Suspicious specimens require careful analysis by a specialist. In general, plants and animals, and therefore their remains, possess details and a characteristic regularity of form absent in pseudofossils.

Naming and Classifying Fossils

In order to prevent confusion, fossils, like living species, need to be named and classified in a consistent, systematic fashion recognized by paleobiol-

The Geologic Time Scale

MYA	*Eon*	*Era*	*Period*	*Epoch*	*Developments*
0.01	Phanerozoic Eon (544 mya-today)	Cenozoic (65 mya-today)	Quaternary (1.8 mya-today)	Holocene (11,000 ya-today)	Ice Age ends. Human activities begin to impact biosphere.
1.8				Pleistocene (1.8 mya-11,000 ya)	Ice Age in northwest Europe, Siberia, and North America. Plants migrate in response. New speciations lead to modern plants. Modern humans evolve.
5			Tertiary (65-1.8 mya)	Pliocene (5-1.8 mya)	Cooling period leads to Ice Age.
23				Miocene (23-5 mya)	Erect-walking human ancestors
38				Oligocene (38-23 mya)	Primate ancestors of humans
54				Eocene (54-38 mya)	Intense mountain building occurs (Alps, Himalaya, Rockies); modern mammals appear (rodents, hoofed animals); diverse conferous forests
65				Paleocene (65-54 mya)	Cretaceous-Tertiary event leads to dinosaurs' extinction c. 65 mya; seed ferns, bennettites and caytonias die off; ginkgoes decline; deciduous plants rise.
146		Mesozoic (245-65 mya)	Cretaceous (146-65 mya)		Breakup of supercontinents into today's form; birds appear. Cycads, other gymnosperms still widespread, but angiosperms dominate by 90 mya; animal-aided pollination begins to evolve.
208			Jurassic (208-146 mya)		Earliest mammals; ginkgoes thrive in moister areas; drier climates in North and South America, parts of Africa, central Asia; rise of modern gymnosperms, such as junipers, pine trees. Earliest angiosperm fossil (from China) dates from end of this period.
245			Triassic (245-208 mya)		Diminished land vegetation, with lack of variation reflecting global frost-free climate; gymnosperms dominate, bennettites and gnetophytes appear; dinosaurs develop.
286		Paleozoic (544-245 mya)	Permian (286-245 mya)		Permian extinction event initiates drier, colder period; supercontinent Pangaea has formed; tree-sized lycophytes, club mosses, cordaites die off; horsetails, peltasperms, cycads, conifers dominate.
325			Carboniferous (360-286 mya)	Pennsylvanian (325-286 mya)	Gymnosperms, ferns, calamites, lycopods thrive (first seed plants); reptiles appear. Plant life diverse, from small creeping forms to tall forest trees. Coal beds form in swamp forests from the dominant seedless vascular plants.
360				Mississippian (360-325 mya)	
410			Devonian (410-360 mya)		Club mosses, early ferns, lycophytes, progymnosperms; amphibians, diverse insects; horsetails, gymnosperms present by end of period.
440			Silurian (440-410 mya)		Early land plants: nonvascular bryophytes (mosses, hornworts), followed by seedless vascular plants in now-extinct phyla *Rhyniophyta*, *Zosterophyllophyta*, *Trimerophytophyta*.
505			Ordovician (505-440 mya)		Life colonizes land; earliest vertebrates appear in fossil record.
544			Cambrian (544-505 mya)	Tommotian (530-527 mya)	Cambrian diversification of life
900	Precambrian Time (4,500-544 mya)	Proterozoic (2500-544 mya)	Neoproterozoic (900-544 mya)	Vendian (650-544 mya)	Age of algae, earliest invertebrates
1600			Mesoproterozoic (1600-900 mya)		Eukaryotic life established.
2500			Paleoproterozoic (2500-1600 mya)		Transition from prokaryotic to eukaryotic life leads to multicellular organisms.
3800		Archaean (3800-2500 mya)			Microbial life (anaerobic and cyanobacteria) as early as 3.5 bya
4500		Hadean (4500-3800 mya)			Earth forms 4.5 bya.

Notes: bya = billions of years ago; mya = millions of years ago; ya = years ago.
Source: Data on time periods in this version of the geologic time scale are based on new findings in the last decade of the twentieth century as presented by the Geologic Society of America, which notably moves the transition between the Precambrian and Cambrian times from 570 mya to 544 mya.

ogists throughout the world. The branch of biology devoted to the naming and classification of organisms is called *taxonomy*. The same system is applied to both living and fossilized plants.

According to the system of *binomial nomenclature*, each species is given a scientific name consisting of two parts: the genus name followed by the species name. The former is capitalized, whereas the latter is written in lower case; both are italicized. Often a name follows that belongs to the person who assigned that name. As example, the scientific name of an extinct redwood tree is *Sequoia dakotensis* Brown, while that of a stemless palm is *Nipa burtinii* Brongniart. The ginkgo tree, *Ginkgo biloba* L., is considered a "living fossil." Known from the fossil record, it persists as a commonly planted shade tree. The initial following its scientific name is that of Carolus Linnaeus, the Swedish botanist who established this binomial system of nomenclature in 1753.

Species, living or dead, are classified using a hierarchical system (also by Linnaeus), which reflects degrees of similarity or dissimilarity to other species. All three trees already mentioned, because they are (or were) vascular plants, are assigned to the division *Tracheophyta*. Within that division the redwood and ginkgo, because they produce uncovered seeds, are placed into the class *Gymnospermopsida* (naked seeded plants), whereas the palm, a flowering plant, is assigned to the class *Angiospermophytina*.

The plant fossil record is often used to establish natural relationships among various extant plant species and other taxa at higher levels. This is especially true of the vascular plants. In fact, the division *Tracheophyta* was established by A. J. Eames in 1936 to show the natural relationship between seed plants and ferns. The basis for this new category was the discovery, earlier in the twentieth century, of Devonian fossils of a group of primitive vascular plants known as *psilotophytes*. They were recognized as ancestral to both ferns and seed plants. Previously, ferns and seed plants had been assigned to a separate division of the plant kingdom.

As the plant fossil record becomes more complete, further revision of the classification system becomes necessary to allow the system to more nearly reflect the true or natural relationships among the various categories. This is, at least, the goal of both paleobotanists and those who study modern plants.

Thomas E. Hemmerly

See also: Angiosperm evolution; Cladistics; Coal; Cycads and palms; Dendrochronology; Diatoms; Evolution of plants; Ferns; Fossil plants; Ginkgos; Gymnosperms; Paleoecology; Petrified wood; Psilotophytes; Seedless vascular plants; Species and speciation; Systematics and taxonomy; Systematics: overview; *Tracheobionta*.

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PALEOECOLOGY

Categories: Disciplines; ecology; evolution; paleobotany

Paleoecology is the study of ancient environments. As a field of science, paleoecology is most closely related to paleontology, the study of fossils. It is also related to paleobotany and a number of other areas of study dealing with the distant past.

Because paleoecology and its related disciplines (paleontology, paleobotany, paleoclimatology, paleogeography, and others) deal with the past, scientists are unable to apply the usual scientific criteria of direct observation and measurement of phenomena. In order to make any conclusions about the past, scientists must assume at least one statement to be true without direct observation: The processes that exist in the modern universe and on the modern earth existed in the past.

Uniformitarianism and Catastrophism

Paleontologists must assume that ancient plants and animals had tolerances to temperature, moisture, and other environmental parameters similar to those of modern organisms. The belief that the present is the key to the past is called *uniformitarianism*. It has been a key concept of the biological and earth sciences since the early nineteenth century. Uniformitarianism does not include the belief that the ancient earth was like the modern earth in its life-forms or geography.

During the early part of the nineteenth century, another worldview dominated: *catastrophism*, the belief that the earth is relatively young and was formed by violent upheavals, floods, and other catastrophes at an intensity unlike those of modern earth. Many catastrophists explained the presence of fossils at high elevations by the biblical flood of Noah. The uniformitarian viewpoint prevailed and, although admitting that local catastrophes may be important, their long-term, earthwide importance was denied. Catastrophism was revived in the 1980's to explain certain important events. The rapid extinction of the large dinosaurs at the close of the Mesozoic era has been attributed to the climatic changes associated with an alleged encounter between the earth and a comet—certainly a catastrophic event.

Climatic Cycles

One of the most intensively investigated paleoecological problems has been the changing environments associated with the ice ages of the past million years. Analysis of pollen from bogs in many parts of the world indicates that there have been at least four advances and retreats of glaciers during that period. Evidence for this is the changing proportions of pollen from tree species found at the various depths of bogs. In North America, for example, spruces (indicators of cool climate) formerly lived much farther south than they do now. They were largely replaced almost eight thousand years ago by other tree species, such as oaks, which are indicative of warmer climates. This warming trend was a result of the latest glacial retreat.

Dendrochronology (tree-ring analysis) not only enables paleoecologists to date past events such as forest fires and droughts but also allows them to study longer-term cycles of weather and climate, especially those of precipitation and temperature. In addition, trees serve as accumulators of past mineral levels in the atmosphere and soil. Lead levels of tree wood showed a sharp increase as the automobile became common in the first half of the twentieth century because of lead additives in gasoline. Tree rings formed since the 1970's have shown a decrease in lead because of the decline in use of leaded fuels. Tree-ring analysis has also been a valuable tool for archaeologists' study of climatic changes responsible for shifting patterns of population and agriculture among American Indians of the southwestern United States.

Traces of Ancient Environments

Fossil evidence is the chief source of paleoecological information. A fossil bed of intact clamshells with both valves (halves) present in most individuals usually indicates that the clams were preserved in the site in which they lived (*autochthonous deposition*). Had they been transported by currents or tides to another site of deposition (*allochthonous deposition*), the valves would have been separated, broken, and worn. Similarly, many coal beds have yielded plant fossils that indicate that their ancient environments were low-lying swamp forests with sluggish drainage periodically flooded by water carrying a heavy load of sand. The resulting fossils may include buried tree stumps and trunks with roots still embedded in their original substrate and numerous fragments of twigs, leaves, and bark within the sediment.

Certain dome- or mushroom-shaped structures called *stromatolites* are found in some of the most ancient of earth's sedimentary rocks. These structures may be several meters in diameter and consist of layers of material trapped by blue-green algae (*cyanobacteria*). Such structures are currently being formed in shallow, warm waters. Uniformitarian interpretation of the three-billion-year-old stromatolites is that they were formed under similar conditions. Their frequent association with mud cracks and other shallow- and above-water features leads to the interpretation that they were formed in shallow inshore environments subject to frequent exposure to the air.

Relative oceanic temperature can be estimated by observing the direction in which the shells of certain planktonic organisms coil. The shell of *Globigerina pachyderma* coils to the left in cool water and to the right in warmer water. *Globigerina menardii* shells coil in an opposite fashion—to the right in cool water and to the left in warmer water. Uniformitarian theory leads one to believe that ancient *Globigerina* populations responded to water temperature in a similar manner. Sea-bottom core samples showing fossils with left- or right-coiling shells may be used to determine the relative water temperature at certain periods. Eighteen-thousand-year-old sediments taken from the Atlantic Ocean show a high frequency of left-handed *pachyderma* and right-handed *menardii* shells. Such observations indicate that colder water was much farther south about eighteen thousand years ago, a date that corresponds to the maximum development of the last ice age.

Interpreting Clues

Fossil arrangement and position can be clues to the environments in which the organisms lived or in which they were preserved. Sea-floor currents can align objects such as small fish and shells. Not only can the existence of the current be inferred, but also its direction and velocity can be determined. Currents and tides can create other features in sediments which are sometimes indicators of environment. If a mixture of gravel, sand, silt, and clay is being transported by a moving body of water such as a stream, tide, or current, the sediments will often become sorted by the current and be deposited as conglomerates—sandstones, siltstones, and shales. Such graded bedding can be used to determine the direction and velocity of currents. Larger particles, such as gravel, would tend to be deposited nearer the sediment source than smaller particles such as clay. Similarly, preserved ripple marks indicate current direction. Mud cracks in a rock layer indicate that the original muddy sediment was exposed to the atmosphere at least for a time after its deposition.

Certain minerals within fossil beds or within the fossil remains themselves can sometimes be used to interpret the paleoenvironment. The presence of pyrite in a sediment almost always indicates that the sedimentary environment was deficient in oxygen, and this, in turn, often indicates deep, still water. Such conditions exist today in the Black Sea and even in some deep lakes, with great accumulations of dead organic matter.

The method of preservation of the remains of the fossilized organism can be an indication of the environment in which the creature lived (or died). Amber, a fossilized resin, frequently contains the embedded bodies of ancient insects trapped in the resin like flies on flypaper. This ancient environment probably contained resin-bearing plants (mostly conifers) and broken limbs and stumps that oozed resin to trap these insects. Mummified remains in desert areas and frozen carcasses in the northern tundra indicate the environments in which the remains were preserved thousands of years ago.

Fossils and Fuels

One of the most immediately important applications of paleoecological data is in the search for increasingly scarce *fossil fuels*: petroleum, natural gas, and coal. Reconstruction of ancient environments and their paleogeographical distributions is probably the most accurate way to predict the presence of reservoirs of these natural resources. Because these substances are formed in environments that are biologically highly productive, with abundant plant and animal life, they are commonly found associated with reefs (petroleum, gas) and swamps (coal).

Index fossils and fossil assemblages can indicate such environments with a high degree of accuracy. Petroleum and gas reservoirs must be porous and permeable in order for the material to accumulate in high concentrations. Reef material and porous sandstones formed from ancient sandbars meet such criteria. Most of the historically famous oil-producing region of Pennsylvania lies within an area 40 to 100 kilometers west of a former shoreline near present-day Pittsburgh. Within this area, most oil pools are within the ancient offshore sandbar belt. Sediments forming this "Pocono formation" came from the east, from an area near present Atlantic City, New Jersey. These sediments, all deposited within the same time frame, grade from coarse, nonmarine conglomerates and sandstones in the east near their source to fine-grained sandstones and shales to the west in the oil-producing region.

P. E. Bostick

See also: Anaerobic photosynthesis; *Archaea*; Bacteria; Coal; Dendrochronology; Evolution: convergent and divergent; Evolution: gradualism vs. punctuated equilibrium; Evolution: historical perspective; Evolution of cells; Evolution of plants; Fossil plants; Paleobotany; Petrified wood; Prokaryotes; Stromatolites.

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PARASITIC PLANTS

Categories: Fungi; poisonous, toxic, and invasive plants

Parasitic plants are those symbiotic life-forms that form mutualistic relationships with other plants at their hosts' expense.

The more is learned about plants and other organisms, the more apparent it is that many, if not most, plants are involved in *symbiotic associations* in which one or more other organisms live in close interaction with the plant—almost as if they are one. Symbiosis is frequently thought of as being a *mutualistic* relationship in which both the plant and its symbiont benefit. Typical examples include the alga and fungus that make up a *lichen* and the bacteria living in a legume root nodule. *Commensalistic* relationships, such as Spanish moss hanging from a live oak, are less commonly thought of; in this relationship, one plant obviously benefits, while the other seems to be little affected.

Parasitism is the third symbiotic condition, in which one plant benefits, but the other is harmed. Fungi are by far the most common parasites of plants; the study of these fungi is a major component of the science of plant pathology. Less common, but frequently well known, are some flowering plants, such as mistletoe, that parasitize other plants.

Haustorium

The defining feature of parasitic plants is the presence of a *haustorium*. The concept of a haustorium is broadly defined as a structure formed by the parasite to connect it physiologically to its host—a morphological/physiological bridge. The haustorial organ may be a simple outgrowth and proliferation of tissue, or it may be an elaborate, highly organized structure. Its appearance is often a useful diagnostic feature. Typically, the haustorium serves three functions: to attach the parasite to the host (*adhesion*), to penetrate into the host tissue or even into individual host cells (*intrusion*), and to conduct water and nutrients from the host to the parasite (*conduction*).

Fungal Parasites

Fungal parasites are among the most destructive diseases of plants. (Some, such as athlete's foot, can affect animals.) Parasitic fungi occur in each of the fungal divisions. They can have tremendous economic impacts. For instance, rust fungi, members of the *Basidiomycetes*, infect every species of cereal grain and can reduce yields by as much as 25 percent.

In addition to their direct economic impact, parasitic fungi have historically had profound social effects. In the 1800's outbreaks of *Phytophthora infestans*, late blight, decimated the potato crops of Europe just prior to harvest. This *oomycete* first turned the potato leaves and stems to mush and then infected the tubers. As a result, millions of people who depended on potatoes as their primary source of food starved to death. Ireland was particularly hard-hit, and millions emigrated from there.

Some fungal parasites have a mixed impact on humans. The genus *Claviceps*, an *ascomycete*, infects cereal grains, producing structures called *ergots*. A variety of alkaloids are produced in the ergot tissue that causes ergotism in animals that eat infected grain. Symptoms include convulsions, psychotic delusions, and gangrene. It has been suggested that the Salem "witches" executed in colonial Massachusetts or their "victims" were suffering from the effects of eating ergotted grain. Today ergot is the source of vasoconstricting drugs used in medicine to control bleeding and relieve migraine headaches.

Angiosperm Parasites

Among vascular plants, parasites are limited to about twelve families of dicots. The best-known examples are the Christmas mistletoes, *Viscum album* in Europe and *Phoradendron serotinum* in North America. While most mistletoes are tropical, the two mentioned above are common in the temperate regions. Unlike many parasitic flowering plants, mistletoes are green and photosynthetic and can thus produce their own food. Many species, including the Christmas mistletoes, produce fleshy, rigid mature leaves, but in other species the leaves are reduced to scales. Most species are *epiphytic* and grow in the branches of a host tree. Some tropical species are terrestrial, and at least one forms a 30-foot-tall tree. Even these tree species form a characteristic *haustorium* connecting the parasite to the host. Mistletoes cause severe economic losses in many areas. For instance, dwarf mistletoe (*Anceuthobium*) attacks many gymnosperms in the southwestern United States, particularly ponderosa pine.

Another well-known flowering plant parasite is dodder (*Cuscuta*). Dodder is distributed worldwide. It is easily recognizable because its rapid growth can quickly cover a host plant with a network of yellowish stems and scalelike, yellow leaves. Although dodder seeds germinate on the ground, the root disintegrates as soon as haustoria make connections with a host, at which time the dodder becomes completely dependent on the host for nutrients. Dodder is designated as a noxious weed throughout the continental United States.

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Origin of Parasitism

It is generally believed that parasites evolved from "normal" plants. As haustoria developed and became more specialized, structural parts and physiological processes normally associated with support and nutrient assimilation were reduced until they were no longer capable of supporting the plant, which became dependent on its parasitic habit. For instance, within the mistletoe family there is a complete gradient from terrestrial root-parasites, in which the roots of the tree-mistletoe parasitize the roots of host plants, to epiphytic shoot parasites, which are completely dependent on their host. This gradient suggests that the epiphytic forms evolved from terrestrial species through increasing specialization of the haustorial organs and reduction of roots and leaves.

The visible effects of a parasite on its host ranges from spectacular malformations, such as "witches' brooms" (a proliferation of short branches by the host at the site of parasite attachment), to no discernable effect. The physiological effects are also variable. While all parasites weaken their host to some degree, in some cases the effect is hardly discernable. This makes sense because it would not be advantageous for the parasite to so weaken its host that the host dies. Nevertheless, this extreme is also evident, as described above for late blight of potato.

Marshall D. Sundberg

See also: Adaptations; Ascomycetes; Bacteria; *Basidiomycetes*; Basidiosporic fungi; Chytrids; Coevolution; Deuteromycetes; Diseases and disorders; Evolution of plants; Fungi; Mycorrhizae; Oomycetes; *Protista*; Rusts; *Ustomycetes*; Zygomycetes.

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PEAT

Category: Economic botany and plant uses

Peat is an unconsolidated accumulation of partly decomposed plant material, used as a fuel source, as a mulch, and for other uses.

Peat has been burned for heating and cooking or used as soil since the New Stone (Neolithic) Age, at least fifty-five hundred years ago. Peat has many uses in agriculture, industry, and energy generation because of its organic chemical content and combustion properties. Although abundant in the middle latitudes of the Northern Hemisphere, it has been exploited as fuel primarily in northwestern Europe.

Like crude oil and coal, peat is composed of the remains of dead organisms compressed underground, and it can be burned in home stoves and fireplaces or in factories and public power plants. Because peat is lightly compressed plant matter, it also works well as soil for agriculture and horticulture. Worldwide, reserves of peat are comparable to those of other fossil fuels. For example, according to some estimates, resources in the United States sur-pass the combined potential energy yield of the nation's petroleum and natural gas.

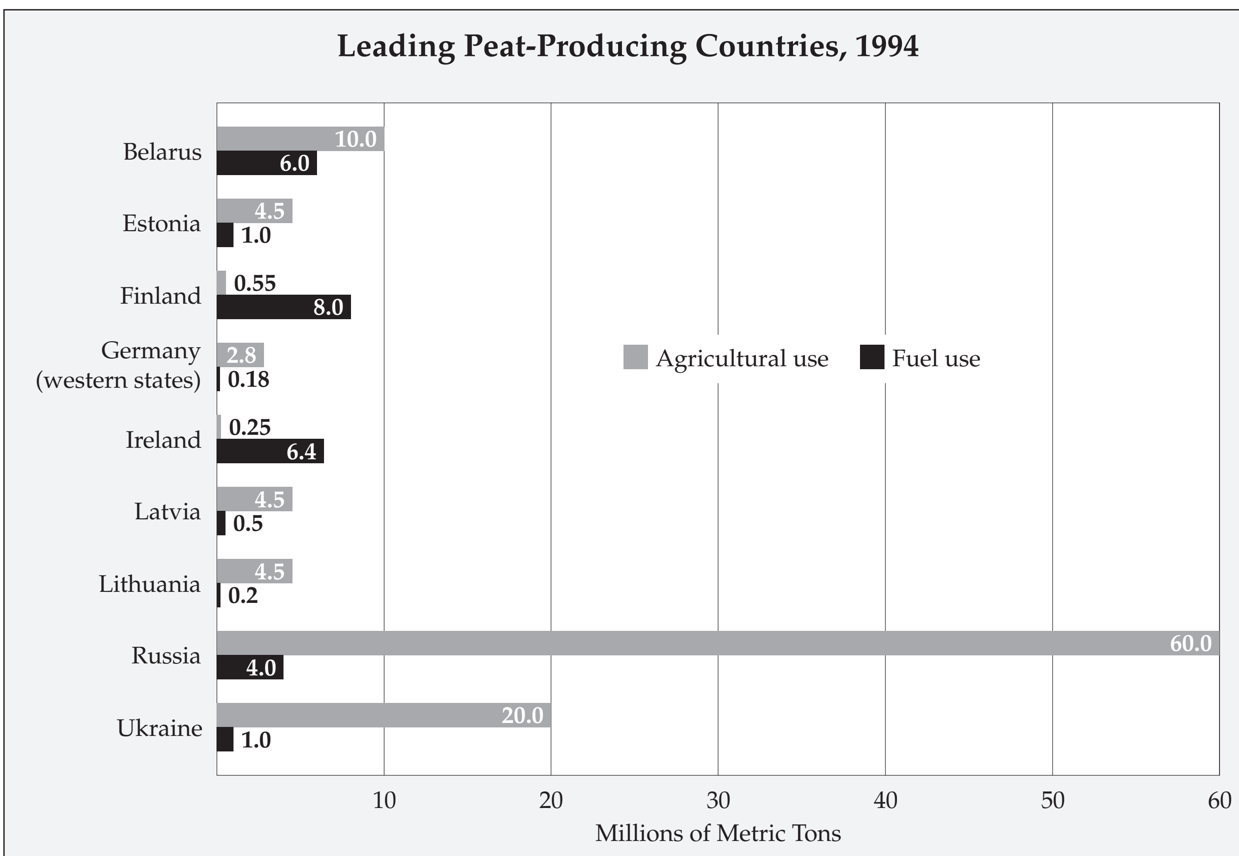
Peat forms in bogs, fens, sedge meadows, and some swamps as the debris of peat mosses (sphagnum), grasses, and sedges falls to the wet earth and becomes water-soaked. In the absence of oxygen underwater, the plant matter and microorganisms compact without completely decomposing, forming soft, usually fibrous soils that are tan to black in color. The organic component, which includes cellulose, lignin, and some humus, is greater than 20 percent, and in most peat soils plant fragments are visible. The ash content is less than 50 percent, usually as low as 10 percent. Although the rate varies widely, in general a peat field increases in depth about three centimeters yearly. The bottoms of large peat fields are typically about ten thousand years old and can be as much as 50 meters below the surface, although 3-meter to 6-meter fields are common.

Geographical Distribution

Most deposits lie between 40 and 65 degrees latitude of the Northern Hemisphere. World reserves of exploitable peat exceed 200 billion tons, of which more than half is in Russia. Canada, the United States, Great Britain, Ireland, Finland, Norway, Sweden, Germany, Iceland, France, and Poland also have substantial peat fields. In the United States, Alaska contains more than half the reserves, but peat is also abundant in Minnesota, Washington, Michigan, Wisconsin, Maine, New York, North Carolina, Florida, and Louisiana. Some countries well below the fortieth meridian have exploitable peat reserves, especially Indonesia, Cuba, and Israel.

Energy Potential and Uses

In northern Europe, peat has fueled fires since the New Stone Age. It provides one-half to two-



Note: Venezuela and the eastern German states are also major peat producers, but output is not reported, so no reliable estimates can be made concerning production. Reported world 1994 peat production was about 139 million metric tons.
Source: U.S. Bureau of Mines, *Minerals Yearbook, 1994*. U.S. Government Printing Office, 1996.

thirds as much energy as coal, or about 3.8 megajoules per dry kilogram, yet gives off far fewer pollutants such as sulfur and ash. It can be converted into coke, charcoal, or a synthetic natural gas.

Only in Ireland, Russia, Finland, and Great Britain is peat employed primarily as a fuel, where in fact it is a traditional domestic resource. Dried and pressed into briquettes, peat burns easily in fireplaces, stoves, and braziers. During the twentieth century the four countries burned increasing amounts of peat to generate electricity. Because it has very limited wood and fossil fuel resources, Ireland has consumed about three times as much peat for power generation as for domestic heating, whereas the other countries primarily rely on coal for that purpose.

Image Not Available

Agricultural and Horticultural Uses

The United States and Canada, as well as some European countries, process most of their peat as potting soil, lawn dressing, and soil conditioners. Because they are much lighter and fluffier than mineral soils, peat preparations let water and oxygen penetrate easily and increase water retention, and so can be soil supplements or mulch. Throughout the United States commercial nurseries and homeowners apply such products to gardens and tree beds. Farmers have raised grasses, clover, wild rice, cranberries, blueberries, strawberries, Christmas trees, and root and leafy vegetables on peat fields, and ranchers have used them for hay and grazing. However, peat fields are difficult to drain and clear and often remain wet, promoting rot and disease. They can be low in nutrients.

Other Uses

During the energy crisis of the 1970's, researchers investigated peat as an alternative to petroleum, although few of the efforts resulted in commercial products because oil again became cheaper than peat for industrial chemicals in the 1980's. Peat yields such mineral and organic substances as dyes, paraffin, naphtha, ammonium sulfate, acetic acid, ethyl and methyl alcohol, waxes, and phenols. Combined with clay, it forms lightweight blocks for construction. It can remove heavy metals from industrial waste and can be turned into coke for iron processing or into charcoal for purifying water. With its mildly antibiotic properties, peat served as a lightweight surgical dressing during World War I. Another of peat's well-known functions—and one of its oldest—is giving the smoky flavor to Scotch and Irish whiskeys as their malts slowly dry over open peat fires.

Because peat fields, once harvested, regenerate only after thousands of years, peat is not a renewable resource in any practical sense. Accordingly, intensive peat "mining" has caused concern among environmentalists. They worry that the rapid exploitation of peat fields, especially in Ireland and Great Britain, may permanently destroy bogs and fens and thereby threaten the wildlife dependent upon wetland habitats.

Roger Smith

See also: Coal; Wetlands.

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PEROXISOMES

Categories: Anatomy; cellular biology; physiology

Peroxisomes are distinct membrane-bound organelles within plant cells. A versatile microbody, the peroxisome plays key roles in photorespiration and in the conversion of stored fats to sucrose during the germination process in many seeds.

Peroxisomes are small, vesicle-like organelles that are found in virtually all eukaryotic plant cells. They are surrounded by a single lipid bilayer membrane and are spherically shaped microbodies with a granular interior containing proteins that usually function as enzymes. Many of these enzymes are important in the process of glycolic acid metabolism. Because peroxisomes contain no genome or ribosomes, their protein is imported from the cytosol. Peroxisomes reproduce by cycles of growth and fission and are not members of the endomembrane system.

Typically, peroxisomes vary in diameter from 0.2 to 2 micrometers. They are generally distributed throughout the cytosol, usually with more abundance around the nucleus and where the cell walls of two cells abut. Many researchers believe that peroxisomes are of primitive origin, predating the appearance of the mitochondria, and developed in response to the increased levels of oxygen in the environment that was generated by cyanobacteria.

Functions

In plants, peroxisomes perform many important roles in plant tissues and development. Their various functions are dictated by their enzyme content, which is constantly modified throughout the development of a plant. One function of peroxisomes is to remove hydrogen atoms from organic substrates by using oxygen, resulting in the production of hydrogen peroxide, a strong oxidizing agent.

In green leaves, peroxisomes play a vital role in photosynthesis by oxidizing glycolate to glyoxylate, a critical reaction that fixes carbon dioxide from the air into carbohydrate. The process is known as *photorespiration*. It provides a pathway for energy transfer to the bonds of sugar molecules. Photorespiration takes place during daylight, and, like normal cellular respiration, it requires oxygen and produces carbon dioxide and water.

In addition to photorespiration, a second function of peroxisomes that is unique to plants is the conversion of fatty acids to sugars by oxidation. It provides a vital pathway for young germinating seeds, particularly sunflower, watermelon, castor bean, and soy bean seeds, for the use of fatty acids as a source of food energy for germination and growth until they can carry out photosynthesis.

In seedlings and cotyledons, the specialized peroxisomes that carry out this function are called *glyoxysomes*. During this oxidation process glyoxysomes generate jasmonic acid, an important signaling molecule in plants. In leguminous plants, peroxisomes are vital in the formation of ureides, compounds that transport nitrogen to cellular locations, where it can be used in organic combination. Peroxisomes also function as sites of defense against activated oxygen species that produce oxidative stress in plants.

Alvin K. Benson

See also: Cell theory; Cytosol; Eukaryotic cells; Microbodies; Plant cells: molecular level; Proteins and amino acids; Respiration.

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PESTICIDES

Categories: Agriculture; environmental issues; pests and pest control

Pesticides are substances designed to kill unwanted plants, fungi, or animals that interfere, directly or indirectly, with human activities.

While the use of pesticides has mushroomed since the introduction of *monoculture* (the agricultural practice of growing only one crop on a large amount of acreage), the application of toxins to control pests is by no means new. The use of sulfur as an insecticide dates back before 500 B.C.E. Salts from heavy metals such as arsenic, lead, and mercury were used as insecticides from the fifteenth century until the early part of the twentieth century, and residues of these toxic compounds are still being accumulated in plants that are grown in soil where these materials were used. In the seventeenth and eighteenth centuries, natural plant extracts, such as nicotine sulfate from tobacco leaves and rotenone from tropical legumes, were used as insecticides. Other natural products, such as pyrethrum from the chrysanthemum flower, garlic oil, lemon oil, and red pepper, have long been used to control insects. *Biopesticides* are beneficial microbes, fungi, insects, or animals that kill pests.

The major types of pesticides in common use are *insecticides* (to kill insects), *nematocides* (to kill nematodes), *fungicides* (to kill fungi), *herbicides* (to kill weeds), and *rodenticides* (to kill rodents). Herbicides and insecticides make up the majority of the pesticides applied in the environment. In 1939 the discovery of dichloro-diphenyl-trichlorethane (DDT) as a strong insecticide opened the door for the synthesis of a wide array of synthetic organic compounds to be used as pesticides. *Chlorinated hydrocarbons* such as DDT were the first group of synthetic pesticides. Other commonly used chlorinated hydrocarbons have in the past included aldrin, endrin, lindane, chlordane, and mirex. Because of their low *biodegradability* and persistence in the environment, the use of these compounds was banned or severely restricted in the United States after years of use.

Organophosphates such as malathion, parathion, and methamidophos have replaced the chlorinated hydrocarbons. These compounds biodegrade in a fairly short time but are generally much more toxic to humans and other animals than the compounds they replaced. In addition, they are water-soluble and therefore more likely to contaminate water supplies. Carbamates such as carbaryl, maneb, and aldicarb have also been used in place of chlorinated hydrocarbons. These compounds rapidly biodegrade and are less toxic to humans than organophosphates, but they are less effective in killing insects.

Herbicides are classified according to their method of killing rather than their chemical composition. As their name suggests, contact herbicides such as atrazine and paraquat kill when they come in contact with a plant's leaf surface. Contact herbicides generally disrupt the photosynthetic mechanism. Systemic herbicides such as diuron and fenuron circulate throughout the plant after being absorbed. They generally mimic the plant hor-


PhotoDisc

Chemical pesticides are sprayed on this field of tulips.

mones and cause abnormal growth to the extent that the plant can no longer supply sufficient nutrients to support growth. Soil sterilants such as triflurain, diphenamid, and daiapon kill microorganisms necessary for plant growth and also act as systemic herbicides.

Pesticide Use

In the United States, approximately 55,000 different pesticide formulations are available, and Americans apply about 500 million kilograms (1.1 billion pounds) of pesticides each year. Fungicides account for 12 percent of all pesticides used by farmers, insecticides account for 19 percent, and herbicides account for 69 percent. These pesticides have been used primarily on four crops: soybeans, wheat, cotton, and corn. Approximately $5 billion is spent each year on pesticides in the United States, and about 20 percent of this is for nonfarm use. On a per-unit-of-land basis, homeowners apply approximately five times as much pesticide as do farmers. On a worldwide basis, approximately 2.5 tons (2,270 kilograms) of pesticides are applied each year. Most of these chemicals are applied in developed countries, but the amount of pesticide used in developing countries is rapidly increasing. Approximately $20 billion is spent worldwide each year, and this expenditure is expected to increase in the future, particularly in the developing countries.

Pesticide use has had a beneficial impact on the lives of humans by increasing food production and reducing food costs. Even with pesticides, pests reduce the world's potential food supply by as much as 55 percent. Without pesticides, this loss would be much higher, resulting in increased starvation and higher food costs. Pesticides also increase the profit margin for farmers. It has been estimated that for every dollar spent on pesticides, farmers experience an increase in yield worth three to five dollars.

Pesticides appear to work better and faster than alternative methods of controlling pests. These chemicals can rapidly control most pests, are cost-effective, can be easily shipped and applied, and have a long shelf life compared to alternative methods. In addition, farmers can quickly switch to another pesticide if *genetic resistance* to a given pesticide develops.

Perhaps the most compelling argument for the use of pesticides is the fact that pesticides have saved lives. It has been suggested that since the introduction of DDT, the use of pesticides has prevented approximately seven million premature human deaths from insect-transmitted diseases such as sleeping sickness, bubonic plague, typhus, and malaria. Perhaps even more lives have been saved from starvation because of the increased food production resulting from the use of pesticides. It has been argued that this one benefit far outweighs the potential health risks of pesticides. In addition, new pesticides are continually being developed, and safer and more effective pest control may be available in the future. In spite of all the advantages of using pesticides, their benefit must be balanced against the potential environmental damage they may cause.

Environmental Concerns

An ideal pesticide should have the following characteristics: It should not kill any organism other than the target pest; it should in no way affect the health of nontarget organisms; it should degrade into nontoxic chemicals in a relatively short time; it should prevent the development of resistance in the organism it is designed to kill; and it should be cost-effective. Since no currently available pesticide meets all of these criteria, a number of environmental problems have developed, one of which is broad-spectrum poisoning. Most, if not all, chemical pesticides are not selective; they kill a wide range of organisms rather than just the target pest. Killing beneficial insects, such as bees, lady bird beetles, and wasps, may result in a range of problems. For example, reduced pollination and explosions in the populations of unaffected insects can occur.

When DDT was first used as an insecticide, many people believed that it was the final solution for controlling many insect pests. Initially, DDT dramatically reduced the number of problem insects; within a few years, however, a number of species had developed genetic resistance to the chemical and could no longer be controlled with it. By the 1990's there were approximately two hundred insect species with genetic resistance to DDT. Other chemicals were designed to replace DDT, but many insects also developed resistance to these newer insecticides. As a result, although many synthetic chemicals have been introduced to the environment, the pest problem is still as great as it ever was.

Depending on the type of chemical used, pesticides remain in the environment for varying lengths of time. Chlorinated hydrocarbons, for example, can persist in the environment for up to fifteen years. From an economic standpoint, this can be beneficial because the pesticide has to be applied less frequently, but from an environmental standpoint, it is detrimental. In addition, when many pesticides are degraded, their breakdown products, which may also persist in the environment for long periods of time, can be toxic to other organisms.

Pesticides may concentrate as they move up the *food chain*. All organisms are integral components of at least one food pyramid. While a given pesticide may not be toxic to species at the base, it may have detrimental effects on organisms that feed at the apex because the concentration increases at each higher level of the pyramid, a phenomenon known as *biomagnification*. With DDT, for example, some birds can be sprayed with the chemical without any apparent effect, but if these same birds eat fish that have eaten insects that contain DDT, they lose the ability to metabolize calcium properly. As a result, they lay soft-shelled eggs, which causes deaths of most of the offspring.

Pesticides can be hazardous to human health. Many pesticides, particularly insecticides, are toxic to humans, and thousands of people have been killed by direct exposure to high concentrations of these chemicals. Many of these deaths have been children who were accidentally exposed to toxic pesticides because of careless packaging or storage. Numerous agricultural laborers, particularly in developing countries where there are no stringent guidelines for handling pesticides, have also been killed as a result of direct exposure to these chemicals. Workers in pesticide factories are also a high-risk group, and many of them have been poisoned through job-related contact with the chemicals. Pesticides have been suspected of causing long-term health problems such as cancer. Some of the pesticides have been shown to cause cancer in laboratory animals, but there is currently no direct evidence to show a cause-and-effect relationship between pesticides and cancer in humans.

D. R. Gossett

See also: Agriculture: modern problems; Agriculture: world food supplies; Biopesticides; Fertilizers; Green Revolution; Herbicides; Hormones; Monoculture.

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PETRIFIED WOOD

Categories: Evolution; paleobotany

Petrified wood is formed by the fossilized remains of ancient trees that were saturated with mineral-filled water which, over time, converted the woody tissues into stone.

Petrified wood is studied by scientists interested in prehistoric plants and their environments. The Latin word *petros*, meaning rock, is the source for the scientific term *petrification*. Petrified wood is actually the stone remnant of a prehistoric tree.

Formation

During the Triassic period, *gymnosperms*—seed-producing trees without flowers, such as gingkos and conifers—grew over much of the earth's landmass. Volcanic eruptions triggered tremors, lightning, and heavy rains, which washed trees from higher elevations down to swampy valleys. As they were pushed downhill, the trees were stripped of their bark, branches, and roots from the force of the water's impact and broke into pieces. Under normal circumstances, trees soaking in deep, muddy water would decay, but silt rapidly and completely covered these trees, preventing exposure to oxygen and inhibiting aerobic decomposition. Volcanic ash in the floodwater consisted of inorganic compounds such as magnesium carbonate and iron sulphide, and the trees also absorbed silicon dioxide (silica) that had dissolved in groundwater. The minerals filled the spaces between cells in the tree trunks and branches. Molecules of these inorganic materials replaced molecules of organic tissues. During the next millions of years, wood gradually became stone in the process of silicification. Assisted by extreme pressure and temperatures, the silica that was lodged in the wood was transformed into quartz. Plants that have undergone petrification are also referred to as being *permineralized*.

The trees remained preserved under the soil for millions of years until soil erosion and shifting plates exposed them. Manganese, lithium, copper, and iron created patterns of bright colors as the wood *fossilized*. Some petrified wood displays varying rings of vivid colors, resembling agates. Other pieces are brown and look like driftwood. More significant than its beauty, information about the history of plants on earth is revealed by petrified wood. Unlike other fossils that are seen as an impression or compression, petrified wood is a three-dimensional representation of its organic material that preserves its external shape and internal structure. The preserved tree trunk sections also indicate the size of the Triassic forest. Scientists have even seen chromosomes and stages of nuclear division in petrified cells. A termite nest was discovered in one petrified log, offering clues about that insect's communal evolution.

Identifying Petrified Wood

Geologists and paleobotanists analyze petrified wood samples to specify the type of ancient tree that became fossilized. The cell structure of hardwood fossils is more diverse than that of softwood trees, causing its source to be more easily identified. Scientists choose pieces that exhibit an intact cell structure and examine the specimen with a microscope to scrutinize how the wood's bands and pores are arranged, both of which are crucial identifying characteristics. Softwood samples require greater magnification of thin slivers only one or two cells thick in order to permit enough light to shine through when mounted on a slide.

Wood anatomists then describe the sample's cell structure, which they compare to records of previously identified petrified wood and existing trees. North Carolina State University and the International Association of Wood Anatomists created a computer database, the General Unknown Entry and Search System (GUESS), which can identify matching cell patterns. Other databases contain information about existing hardwood and softwood trees; one has information on at least 1,356 types of trees of more than twelve hundred species.

Three types of petrified wood are found in the Tertiary strata. *Nondescript silicified wood* has under-

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gone silicification but still appears to be woody structurally. Difficult to identify because of its generic structure, nondescript silicified wood requires expert authentication for accurate labeling. *Petrified palm wood* has rod structures that reinforced the tissue strength before the wood grain became silicified and that look like spots or lines when the wood is cut. Popular among rock collectors, this type of petrified wood is both Arizona's state fossil and state rock. *Massive silicified wood* is difficult to recognize because the tree's grain was destroyed during silicification, thus making identification reliant on awareness of the area in which the tree was located and comparison to other petrified wood in adjacent territory.

Petrified Wood in the United States

Wood in Arizona's Petrified Forest National Park originated from a forest of giant conifer-like trees that grew from Texas to Utah. The park's 93,533 acres are home to one of the world's largest assortments of petrified wood. This desert area is dotted with stone log fragments. Although some visitors expect to see rock trees standing in clumps similar to a natural forest, these petrified trees rest where they fell individually or in groups.

Because the ancient forest lived simultaneously with the dinosaurs, archaeologists look for dinosaur fossils near petrified wood in the Arizona park. Although collection and thefts have greatly reduced the number of petrified logs, authorities believe that some areas of the park may shelter petrified wood buried as much as 100 meters beneath the surface.

By the twentieth century, prospectors and tourists had taken the most beautiful pieces; as a result, local residents sought government protection against further theft. In 1906 the petrified wood site was declared a national monument and was named a national park in 1962. The U.S. National Park Service tries to protect petrified wood by preventing the nearly one million yearly visitors from seizing samples. Rangers patrol sites and ask tourists to report any thefts they witness. Despite these precautions, several tons of petrified wood disappear annually from the park. Privately owned sites adjacent to the park offer collectors opportunities to search for petrified wood without any restrictions. Stores sell small pieces.

Petrified wood has been discovered in many other regions of the United States, especially in western areas where volcanic activity occurred, such as Yellowstone National Park, and in areas where rivers and streams deposited large amounts of sand, such as Louisiana and Texas. Washington State is home to the Ginkgo Petrified Forest State Park, which contains petrified logs that began fossilizing during the Miocene epoch. This petrified wood is unique because it includes petrified ginkgo, an indigenous tree that no longer grows naturally there. An unusual type of petrified wood that resembles pebbles and that originated in the Chehalis Valley is sometimes seen on the state's beaches.

The Calistoga, California, petrified forest is considered one of the best sources of Pliocene fossils similar to existing redwoods. Measuring more than 2 meters in diameter, the fossil logs reveal gray stone veins of quartz. Petrified wood in New Mexico's Bisti Badlands is not as colorful as neighboring Arizona's fossil wood. In Utah, petrified wood has been found near the Escalante River and the Coyote Buttes region near the Paria River. Petrified wood has also been found in Mississippi and Alabama.

Petrified Wood Worldwide

A petrified forest on the Greek island of Lesbos was named a protected site by presidential decree. Scientists have determined that the petrified wood began fossilizing during the Late Oligocene to Lower-Middle Miocene epochs. Unlike other sites of petrified forests, the Lesbos fossil trunks are erect and still have intact roots penetrating into fossilized soil, branches, leaves, cones, and seeds.

These trees were fossilized where they grew, offering insight into the environment and climate of ancient Lesbos. The ancient trees were well preserved during the petrification process, and such details as rings indicating age and growth patterns are visible. Both gymnosperms and angiosperms (flowering plants) grew in the ancient forests, along with pteridophytes such as ferns. Many of these ancient species no longer grow in the Mediterranean. Instead, they are found in Asian and American tropical and subtropical regions, indicating that Lesbos's petrified forest presents information about how life on earth evolved as the continents moved apart.

Other sites of fossilized wood also reveal details about the planet's development. Argentina's Petrified Forest on the Central Steppes was created after the formation of the Andes Mountains. Larger than American wood fossils, Argentinean petrified wood includes pieces 27 meters long and 3 meters in diameter. The petrified forest in Namibia contains giant tree trunks as long as 30 meters. Petrified wood has also been discovered in Australia, India, England, Turkey, and Switzerland.

Petrified Wood's Legacy

Paleobotanists research petrified wood to determine how the earth and the plants that have grown on its surface have changed since ancient times. They study how plants are related and descended from similar ancestors. Throughout history, many more tree species have existed than are documented, and many species, existing and extinct, await discovery. Pieces of fossil wood are often the oldest known specimens of a tree species and might be the predecessors of living trees.

Petrified wood helps researchers comprehend how trees have evolved to adapt to environmental and climatic conditions. For example, researchers have hypothesized that the cell structure of tree xylem has not changed as much as fruit and leaves. Fossil wood sometimes reveals the reason for the demise of extinct trees. The study of petrified wood has altered how scientists perceive both ancient geological ecosystems and modern environments by offering perspective on which plants lived on the earth and survived, adapted, or died according to changes in the atmosphere and crust.

Elizabeth D. Schafer

See also: Fossil plants; Paleobotany; Paleoecology; Plant tissues; Wood.

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PHEROMONES

Categories: Cellular biology; physiology

Pheromones are any chemical or chemical mixture that, when released by one member of a species, affects the physiology or behavior of another member of the same species.

Pheromones are semiochemicals that carry information between members of a single species. To do this, the pheromone must be released into the atmosphere or placed on some structure in the organisms' environment. It is thus made available to other members of the species for interpretation and response. It is also available to members of other species, however, so it is a potential *allelochemic*.

Types of Pheromones

In complex interactions, a pheromone may also be acting as a *kairomone*, passing messages between species to the benefit of the recipient; an *allomone*, passing messages between species to the benefit of the sender; or a *hormone*, passing messages within a single organism. One possible example of a hormone as a pheromone is the plant hormone ethylene, which is produced by an individual plant to stimulate ripening of fruit, loss of leaves, and other physiological changes. Some evidence suggests that ethylene, produced in response to damage caused by insects feeding on the plant, stimulates production of chemicals that are detrimental to the insects, thus acting as a hormone. It also passes through the atmosphere to surrounding plants and stimulates their production of defensive chemicals, thus acting as a pheromone. Not everyone is convinced by the evidence that has been presented for this phenomenon, but the possibility is intriguing.

There are two general types of pheromone: those that elicit an immediate and predictable behavioral response, called *releaser* or *signal pheromones*, and those that bring about a less obvious physiological response, called *primer pheromones* because they prime the system for a possible behavioral response. Pheromones are also categorized according to the messages they carry. There are trail, marker, aggregation, attractant, repellant, arrestant, stimulant, alarm, and other pheromones. Their functions are suggested by the terms used to name them.

The chemical compounds that act as pheromones are numerous and diverse. Most are lipids or chemical relatives of the lipids, including many steroids. Even a single pheromonal message may require a number of different compounds, each present in the proper proportion, so that the active pheromone is actually a mixture of chemical compounds.

Functions and Sources

Different physical and chemical characteristics are required for pheromones with different functions. Attractant pheromones must generally be volatile to permit atmospheric dispersal to their targets. On the other hand, many marking pheromones need not be especially volatile because they are placed at stations which are checked periodically by the target individuals. Some pheromones are exchanged by direct contact, and these need not have any appreciable volatile component.

Pheromones are widespread in nature, occurring in most, if not all, species. Most are poorly understood. The best-known are those found in insects, partly because of their potential use in the control of pest populations and partly because the relative simplicity of insect behavior allowed for rapid progress in the identification of pheromones and their actions. Despite these advantages, much remains to be learned even about insect pheromones.

Pheromones and Pest Control

Pheromones and other semiochemicals are of interest from the standpoint of understanding communication among living things. In addition, they have the potential to provide effective, safe agents for pest control. The possibilities include sex-attractant pheromones to draw insects of a particular species to a trap (or to confuse the males and keep them from finding females) and repellant pheromones to drive a species of insect away from a valuable crop. One reason for the enthusiasm generated by pheromones in this role is their specificity. Whereas insecticides generally kill valuable insects as well as pests, pheromones may target one or a few species.

These chemicals were presented as a panacea for insect and other pest problems in the 1970's, but most actual attempts to control pest populations failed. Lack of understanding of the particular pest and its ecological context was called the most common cause of failure. Some maintain that pest-control applications must be made with extensive knowledge and careful consideration of pest characteristics and the ecological system. In this context, pheromones have become a part of integrated pest management (IPM) strategies, in which they are used along with the pest's parasites and predators, resistant crop varieties, insecticides, and other weapons to control pests. In this role, pheromones have shown great promise.

Carl W. Hoagstrom

See also: Allelopathy; Biopesticides; Hormones; Integrated pest management; Metabolites: primary vs. secondary.

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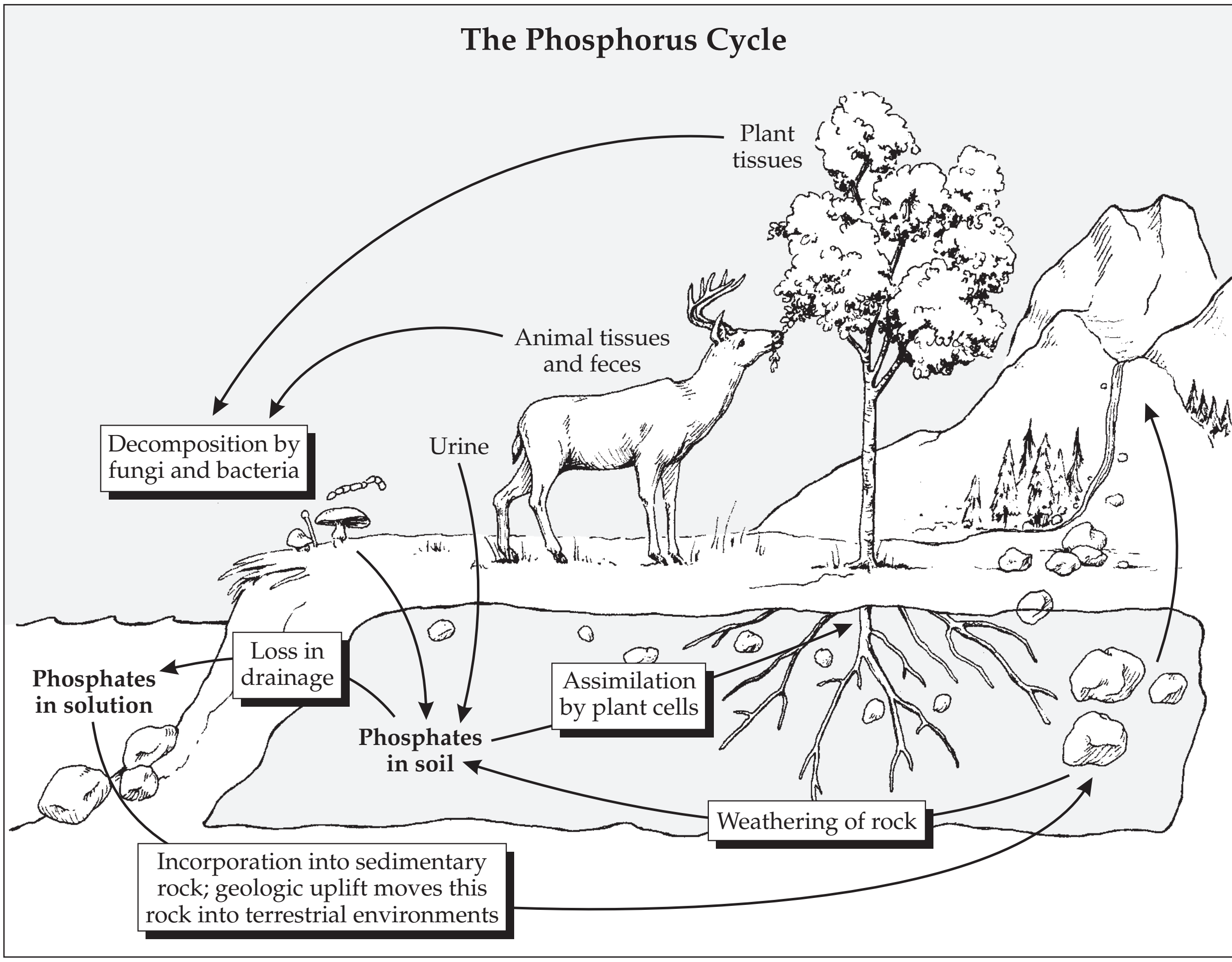
PHOSPHORUS CYCLE

Categories: Biogeochemical cycles; cellular biology; ecology; nutrients and nutrition

The constant exchange of a mineral or elemental nutrient between organisms and the physical environment is called a biogeochemical cycle. Along with the carbon cycle and the oxygen cycle, one of the most important biogeochemical cycles is that of the element phosphorus. The phosphorus cycle involves the movement of the element phosphorus as it circulates through the living and nonliving portions of the biosphere.

Many of the chemical elements found on the earth are vital to the processes and systems of living organisms. Unlike oxygen and carbon, phosphorus follows complex pathways. It circulates



Kimberly L. Dawson Kurnizki

The biogeochemical phosphorus cycle is the movement of the essential element phosphorus through the earth's ecosystems. Released largely from eroding rocks, as well as from dead plant and animal tissues by decomposers such as bacteria and fungi, phosphorus migrates into the soil, where it is picked up by plant cells and is assimilated into plant tissues. The plant tissues are then eaten by animals and released back into the soil via urination, defecation, and decomposition of dead animals. In marine and freshwater aquatic environments, phosphorus is a large component of shells, from which it sediments back into rock and can return to the land environment as a result of seismic uplift.

through the earth's soils, rocks, waters, and atmosphere and through the organisms that inhabit these many ecosystems.

Elements or minerals are stored in discrete parts of the earth's ecosystems called *compartments*. Examples of compartments include all the plants in a forest, a certain species of tree, or even the leaves or needles of a tree. Chemical elements reside within the compartments in certain amounts, or *pools*. A basic description of biogeochemical cycles involves following nutrients in the form of minerals or elements from pool to pool through the multitudes of ecosystem compartments.

Phosphorus and Plants

Phosphorus compounds reside primarily in rocks. Phosphorus does not go through an atmospheric phase, but rather, phosphorus-laden rocks release *phosphate* (PO_4^{-3}) into the ecosystem as the result of weathering and erosion. To plants, phosphorus is a vital nutrient (second only to nitrogen). Plants absorb phosphates through their root hairs. Phosphorus then passes on through the food chain when the plants are consumed by other organisms. Phosphorus is an essential component of many biological molecules, including deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). Adenosine triphosphate (ATP), one of the nucleotides that make up DNA and RNA, is also the main energy transfer molecule in the multitude of chemical reactions taking place within organisms.

Because phosphorus is a major plant nutrient, massive amounts of phosphate-based fertilizers are either derived from natural sources (in the form of bat or bird guano) or chemically manufactured for use by agriculture. As late as the early 1970's, phosphates were a major constituent of household detergents, until it was discovered that large amounts of phosphates were being released into the environment. In aquatic systems such as rivers and lakes, where such runoff eventually appears, an infusion of phosphates can cause *algal blooms* (rapidly forming, dense populations of algae). When the algae die, they are consumed by bacteria. Decomposition by bacteria requires large amounts of oxygen, which soon depletes the available oxygen in the water. If the process is allowed to continue unchecked, fish and other organisms die from lack of oxygen. Both phosphates and nitrates contribute to cultural *eutrophication*.

Phosphates not taken up by plants go into the sedimentary phase, where they are very chemically reactive with other minerals. Some of these reactions produce compounds that effectively remove phosphates from the active nutrient pool. This sedimentary phase is characterized by its long residence time compared to the rapid cycling through the biological phase. Phosphates can remain locked up in rocks for millions of years before being exposed and broken down by weathering, which once again makes them available to plants.

Phosphorus and the Environment

Because the phosphorus cycle is so complex, its interactions with other biogeochemical cycles are not completely understood. The study of these interactions is emerging as a vital field among the environmental sciences. Excessive phosphates in a eutrophic lake disrupt the carbon cycle by reacting with bicarbonates, thus increasing the pH. Many freshwater organisms depend on a neutral pH level for their survival. The presence of phosphorus under these oxygen-depleted conditions can also indirectly affect the sulfur cycle, leading to the conversion of sulfate to sulfide. When sulfide combines with hydrogen to form the gas hydrogen sulfide, it takes on the familiar "rotten egg" smell.

One of the keys to preventing environmental degradation through the altering of global chemical cycles lies in recognizing the effects of such alterations. With the perception of an environmental crisis in the early 1970's, more attention was paid to the role of human activity in these cycles. Test lakes were studied to determine why freshwater fisheries were becoming oxygen-depleted at accelerated rates. Dramatic progress has been made in eliminating the problem of algal blooms and oxygen depletion by limiting the phosphorus-laden effluents being discharged into lakes.

David M. Schlom, updated by Bryan Ness

See also: Eutrophication; Fertilizers; Nutrients.

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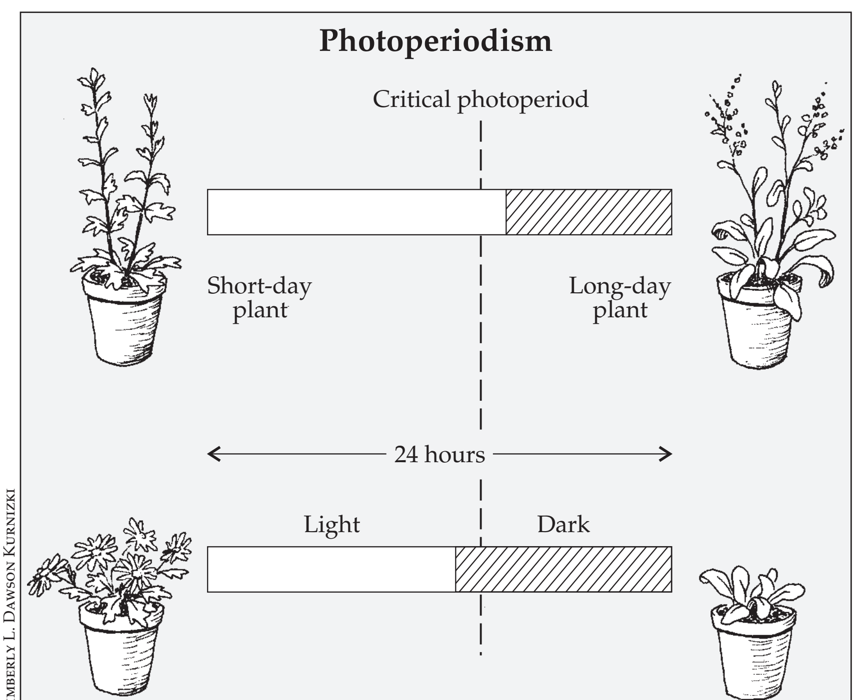
PHOTOPERIODISM

Categories: Physiology; reproduction

The reproductive cycles of many organisms, both plant and animal, are regulated by the length of the light and dark period, called the photoperiod. In flowering plants (angiosperms), flowers are organs for sexual reproduction, and photoperiodism refers to the process by which these plants flower in response to the relative lengths of day and night.

Along the equator, the lengths of day and night remain constant because the sun rises and sets at the same time throughout the year. The lengths of the day and night are also equal (each is six months long) at the exact North and South Poles due to the fact that the sun remains below the horizon for six months each year and above the horizon for the other six months. Anyplace else in the world, the days become longer in the summer and shorter in the winter. The reproductive cycles of many organisms, both plant and animal, are regulated by the length of the light and dark period, called the photoperiod. In flowering plants (angiosperms), flowers are organs for sexual reproduction, and photoperiodism refers to the process by which these plants flower in response to the relative lengths of day and night.



Short-day plants flower when the length of the day is less than the critical photoperiod—that is, when days are relatively short, as in the late fall or early winter. Long-day plants flower when the days are longer than the critical photoperiod—as in late spring and early summer.

The synchronization of reproduction with seasonal time is a very important aspect of plant physiology. Reproduction in many angiosperms is dependent on *cross-pollination*, the process of pollen being transferred from one flower to another. Hence, it is important for all of the plants of the same species in a given region to flower at the same time. Even in nonflowering plants such as mosses, ferns, and some algae, it is usually beneficial for reproductive structures to be formed in a given season. The ability to detect the length of the day or night or both makes it possible to synchronize the reproductive event to a particular time of year. While there have been hundreds of studies which show that many plants respond to changes in the photoperiod, there have been no broad sweeping generalities to provide a better understanding of this phenomenon. Each species, and often each cultivar or variety within a species, appears to have its own photoperiodic response.

Photoperiodic Classification

The photoperiodic classification of plants is usually made on the basis of flowering, but other aspects of their development may also be affected by day length. Based on their flowering response, plants are classified as short-day plants (SDPs), long-day plants (LDPs), intermediate-day plants, ambiphotoperiodic, or day-neutral plants.

Short-day plants flower when the days are relatively short (generally nine hours or less), such as in the late fall or early winter. In some SDP species flowering is *qualitative*, meaning that short days are absolutely required, while in other SDP species flowering is *quantitative*, which means flowering is accelerated under short days, but short days are not an absolute requirement. Some examples of SDPs include rice, cocklebur, and soybean.

Long-day plants flower when the days are relatively long (generally fifteen hours or greater), as would occur in late spring and early summer. As with SDPs, there are qualitative and quantitative species of LDPs.

Intermediate-day plants require quite narrow day lengths (between twelve and fourteen hours) in order to flower, and flowering is inhibited by either short or long days. Sugarcane is an example of an intermediate-day plant.

Ambiphotoperiodic plants are a specialized group of plants that will flower in either short days or long days, but flowering is inhibited by intermediate day lengths.

In *day-neutral plants*, flowering is not regulated by day lengths. In other words, day-neutral plants flower regardless of the day length. There are also many interesting interactions between photoperiod and temperature. A plant may respond to a certain day length at one temperature but exhibit a different response at another temperature. For example, both the poinsettia and morning glory are absolute SDPs at high temperature; however, they are absolute LDPs at low temperature and day-neutral at intermediate temperatures.

Chemical Control

Flowering is regulated by chemicals produced in the plant, and a variety of plant hormones, including *auxins*, *ethylene*, *gibberellins*, *cytokinins*, and *abscisic acid*, have been shown to influence flowering in different species. The critical aspect of photoperiodism, however, is the measurement of seasonal time by detecting the lengths of day and night. The discovery of the *night break phenomenon*, which showed that interruption of the night period with light inhibited flowering in SDPs, established that the length of the dark period is the most critical for initiating a photoperiodic response.

The chemical *phytochrome* is responsible for measuring the dark period. Phytochrome, found in the leaves of plants, exists in two forms, P_r and P_{fr}. P_r absorbs red light during the day and is converted to P_{fr}. P_{fr} absorbs far-red light during the night and is converted to P_r. The prevailing hypothesis is that P_{fr} inhibits flowering, and the length of the dark period has to be sufficient for the P_{fr} to fall below some critical level. When the P_{fr} falls below this level, chemical messages are sent to the floral regions, and flowering is initiated.

While phytochrome definitely has been shown to trigger the flowering response, it is not the only chemical involved. It has been shown that a blue-light photoreceptor may also play a role in photoperiodism. In addition, phytochrome is not translocated in the plant. It remains in the leaves. Hence, other chemicals which have not been positively identified are responsible for signaling the photoperiodic response.

D. R. Gossett

See also: Circadian rhythms; Flower structure; Flowering regulation; Hormones; Pollination; Reproduction in plants.

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PHOTORESPIRATION

Categories: Cellular biology; photosynthesis and respiration; physiology

Photorespiration is a biochemical process in plants in which, especially under conditions of water stress, oxygen inhibits the Calvin cycle, the carbon fixation portion of photosynthesis.

Photorespiration results in the light-dependent uptake of oxygen and release of carbon dioxide and is associated with the synthesis and metabolism of a small molecule called *glycolate*. Photorespiration takes place in green plants at the same time that photosynthesis does. Because in photosynthesis carbon dioxide is taken in, and in photorespiration carbon dioxide is given off, these two processes work against each other. The end result is that photorespiration decreases the net amount of carbon dioxide which is converted into sugars by a photosynthesizing plant. By interfering with photosynthesis in this way, photorespiration may significantly limit the growth rate of some plants.

Photosynthesis

In green plants, photosynthesis takes place in the special energy-storing molecules called *chloroplasts*. Photosynthesis can be divided into two parts: the *light reactions* and the *dark reactions*. In the light reactions, light energy from the sun is captured by the plant and converted into chemical energy in the form of chloroplasts. An additional feature of the light reactions is that a molecule of water is split so that its oxygen is released. In the dark reactions, a series of steps called the *Calvin cycle* converts carbon dioxide from the air into organic molecules such as sugars and starch. The Calvin cycle requires energy in order to operate, and this is provided by the energy-storing molecules (such as adenosine triphosphate) formed in the light reactions. The carbohydrates thus formed can serve as food for the plant or for an animal that eats the plant.

The overall pattern of *gas exchange* in photosynthesis, therefore, is the release of oxygen and the uptake of carbon dioxide. It has been found that, to a lesser extent, light can also cause plants to do just the opposite—that is, to consume oxygen and release carbon dioxide. This phenomenon was discovered in the 1950's and is termed photorespiration. If net photosynthesis is defined as the total amount of carbon dioxide taken in minus the amount given off, it is apparent that increasing the rate of photorespiration will decrease net photosynthesis. In terms of agricultural plants, this translates into a decrease in the productivity of the crop.

Rubisco and Glycolate

Each of the reactions of the Calvin cycle must be catalyzed by an enzyme. The first reaction of the cycle, in which carbon dioxide is taken up, utilizes an enzyme popularly known as *Rubisco*, an abbreviation for ribulose bisphosphate carboxylase/oxygenase. The normal function of Rubisco is to take carbon dioxide from the atmosphere and combine it with another molecule in the chloroplast, ribulose bisphosphate (RuBP). The resulting compound is then acted upon by other enzymes which eventually convert it into the simple sugar glyceraldehydes 3-phosphate, which is used in the synthesis of more complex sugars and other compounds.

Rubisco, however, does not always behave in its normal fashion. It is sometimes unable to distinguish between molecules of carbon dioxide and oxygen. Rubisco will sometimes "mistakenly" incorporate an oxygen molecule into RuBP rather than the carbon dioxide that would normally have been used. The oxygen may come from the atmosphere, or it may originate from the oxygen that is continually being produced by the splitting of water during the light reactions of photosynthesis.

The result of this metabolic error is that, rather than forming compounds that can be converted into sugar, the plant forms a substance known as *glycolate*. Understanding what happens to glycolate is the key to understanding the process of photorespiration. The utilization of oxygen in the formation of glycolate accounts for part of the oxygen uptake that is observed during photorespiration. Instead of being used in sugar synthesis, the glycolate enters a different metabolic pathway, where it is acted upon by a different series of enzymes with different consequences. These sequential reactions, referred to as the *glycolate pathway*, result in the conversion of glycolate into a series of different compounds. This pathway constitutes the remainder of the process of photorespiration.

The Glycolate Pathway

An unusual feature of photorespiration is that it involves three separate cellular organelles: the chloroplast, the *peroxisome*, and the *mitochondrion*. The first stage of photorespiration involves the formation of glycolate in the chloroplast. The glycolate does not undergo further reactions in the chloroplast but instead is transported to the peroxisome.

Once inside the peroxisome, the glycolate enters a series of reactions, one of which causes oxygen to be converted into hydrogen peroxide. This represents a second point in the process at which oxygen is consumed. If hydrogen peroxide were present in large quantities it could have a toxic effect upon the cell, so the peroxisome also contains the enzyme catalase, which destroys most of the hydrogen peroxide thus formed.

In subsequent steps of the glycolate pathway, one of the compounds formed is glycine, which enters the mitochondrion and loses a carbon atom in the form of carbon dioxide. This, then, accounts for the observed release of carbon dioxide during photorespiration. If the carbon dioxide is lost to the atmosphere, it represents a decrease in the net amount of carbon taken up by the plant and, therefore, a decrease in net photosynthesis.

Further reactions of the glycolate pathway occur in the mitochondrion and peroxisome, and eventually a compound is formed which is returned to the chloroplast, where the process began. This compound is capable of reentering the Calvin cycle and can actually be used for the synthesis of sugars. The critical point, however, is that not all the carbon atoms which left the chloroplast in the form of glycolate are returning to it. Part of the carbon was lost in the form of the carbon dioxide that was released in the mitochondrion. Furthermore, certain steps in the glycolate pathway require the expenditure of energy. The process is, therefore, doubly wasteful in that it results in the loss of both carbon dioxide and energy storage molecules.

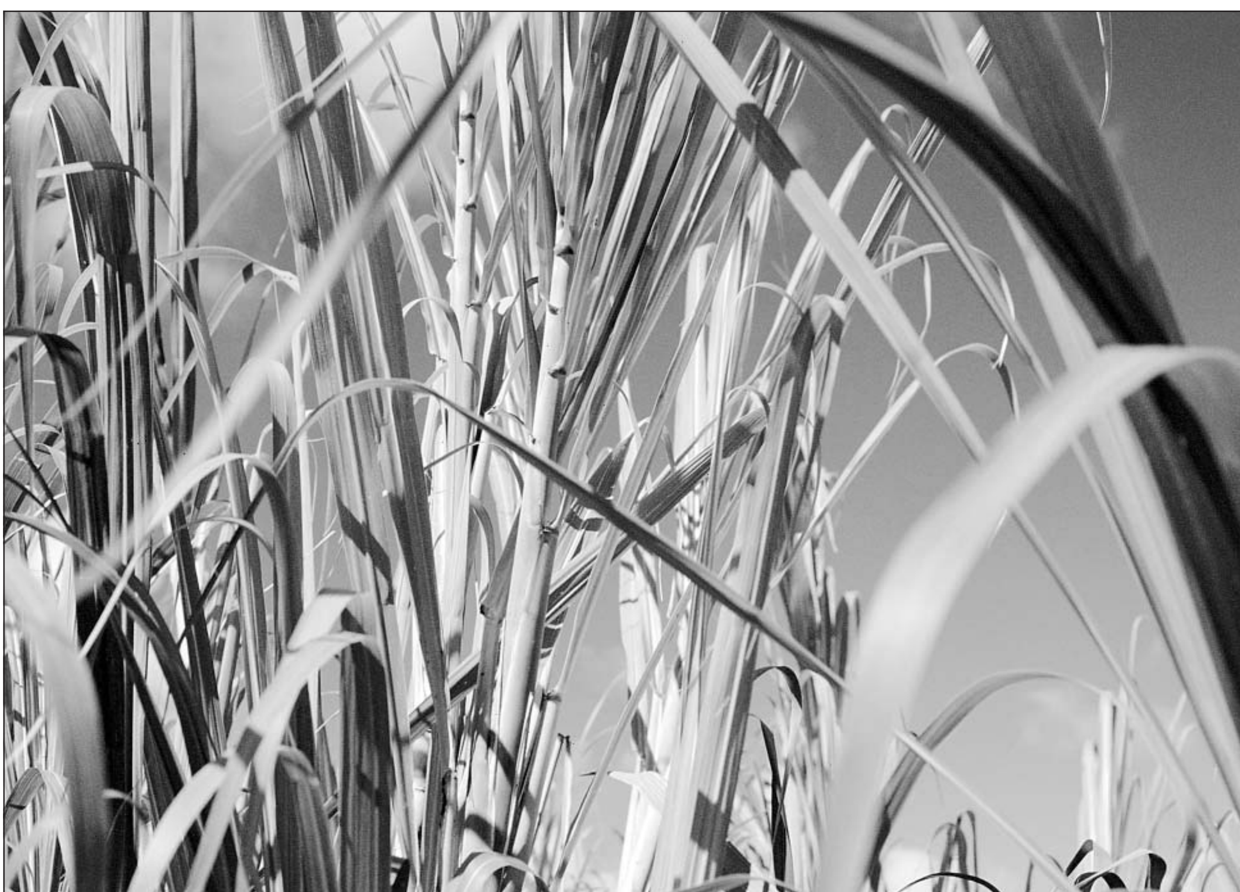
To summarize the process, oxygen is utilized in the chloroplast to form the two-carbon compound glycolate. The glycolate then enters a series of reactions that occur in the peroxisome and mitochondrion and that take up additional oxygen and release a portion of the carbon in the form of carbon dioxide. The remaining carbon is converted into 3-phosphoglycerate, which can be returned to the chloroplast and reenter the Calvin cycle, where it is one of the normal intermediate compounds. This accounts for the light-dependent uptake of oxygen and release of carbon dioxide, which constitute photorespiration.

Factors That Increase Photorespiration

Although some amount of photorespiration occurs in many plants regardless of conditions, photorespiratory rates increase any time that carbon dioxide levels are low and oxygen levels are high. Such conditions occur whenever stomata (specialized pores for gas exchange) remain closed, or partially closed, while photosynthesis is under way. Under most conditions plants are able to keep their stomata open, so photorespiratory rates remain low. When plants become water stressed, they close their stomata to prevent further water loss by transpiration. Water stress is most likely under hot, dry conditions. Under these conditions, the stomata close as far as needed to conserve water, thus restricting normal gas exchange. Carbon dioxide levels slowly rise as water is split during the light reactions. Consequently, photorespiratory rates accelerate, and photosynthetic efficiency drops to as low as 50 percent of normal.

In dry tropical and desert environments water stress, and thus photorespiration, can significantly reduce plant growth potential. Some plants have evolved solutions to this problem by modifying the way they carry out photosynthesis. One common adaptation is called C_4 metabolism. This modification involves a different leaf anatomy, called Kranz anatomy, as well as a different enzyme pathway for initially fixing carbon dioxide that is not prone to problems with oxygen. The Calvin cycle still functions in *C_4 plants*, as they are called, but it is protected from photorespiration by the C_4 adaptations. Many tropical grasses, including corn and sugarcane, use this approach. Unfortunately, many crop plants, including wheat, soybeans, spinach, and tomatoes, do not possess this adaptation.

The other major adaptation is called *CAM metabolism*, which is short for crassulacean acid metabolism. This adaptation is common in succulents (plants that store excess water in their stems and leaves, making them very juicy), such as pineapples, cacti, and stonecrops. Stonecrops are in the



PhotoDisc

In dry tropical and desert environments water stress, and thus photorespiration, can significantly reduce plant growth potential. Some plants have evolved solutions to this problem by modifying the way they carry out photosynthesis. One common adaptation is called C_4 metabolism. The Calvin cycle still functions in C_4 plants, but it is protected from photorespiration by the C_4 adaptations. Many tropical grasses, including sugarcane, use this approach.

family *Crassulaceae*, which is the source of the name for this adaptation. CAM plants, as they are called, only open their stomata at night, when transpiration rates are low and water loss is minimal. Carbon dioxide enters the leaf at night and is attached to organic molecules in a different pathway that does not require light as an energy source. Then during the day, when the stomata are closed, this carbon dioxide is released and enters the Calvin cycle. Photorespiration is prevented because carbon dioxide levels can be maintained at appropriate levels, even though the stomata are closed.

Why Photorespiration?

Several theories have been proposed to explain why plants photorespire. One possibility is that when plants first evolved, conditions on the primitive earth were very different from what they are now. The early atmosphere contained little oxygen, so the inability of Rubisco to distinguish between oxygen and carbon dioxide was not a problem. As the oxygen level in the atmosphere gradually increased, the formation of glycolate during photosynthesis began to occur, and this led to the problem of photorespiration. The glycolate pathway then developed as a mechanism for salvaging some of the material that leaves the Calvin cycle in the form of glycolate, ultimately returning a portion of it to the cycle.

Seen in this context, the real culprit in photorespiration is the formation of glycolate by Rubisco, while the glycolate pathway is an evolutionary adaptation for making the best of a bad situation. Perhaps, millions of years in the future, plants will evolve a form of Rubisco that can more effectively distinguish between these two gases, and photorespiration will diminish or cease.

An alternative theory about why plants photorespire is that the process does, in fact, perform an important function: protecting the plant from the harmful effects of very high internal concentrations of oxygen or energy storage molecules. This high concentration could occur when the plant is exposed to high light intensities, causing photosynthesis to generate these substances very rapidly. Photorespiration would then consume some of the excess oxygen and energetic molecules, depleting them to levels that would not be harmful to the plant. It has not yet been conclusively shown, however, that photorespiration really does play such a protective role. Further research will be required before scientists know whether photorespiration is beneficial to the plant.

Thomas M. Brennan, updated by Bryan Ness

See also: ATP and other energetic molecules; C_4 and CAM photosynthesis; Calvin cycle; Gas exchange in plants; Glycolysis and fermentation; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Respiration.

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PHOTOSYNTHESIS

Category: Cellular biology

Photosynthesis is the process by which organic sugar molecules are synthesized from an inorganic carbon source (carbon dioxide or bicarbonate), using sunlight as the energy source to drive the process. Although most often associated with plants (in which the reactions of photosynthesis occur within compartments called chloroplasts), algae and certain types of bacteria are also capable of photosynthesis.

From an ecological perspective, photosynthesis is significant because the conversion of inorganic carbon to organic carbon represents the entry point of carbon atoms into biological systems. Photosynthesis is also significant because it is the means whereby oxygen is released into the atmosphere. The atmospheric concentration of oxygen is approximately 21 percent, and most of this oxygen originates from photosynthesis. In addition, solar energy absorbed during photosynthesis serves as the ultimate source of energy for almost all nonphotosynthetic organisms.

Nature of Light

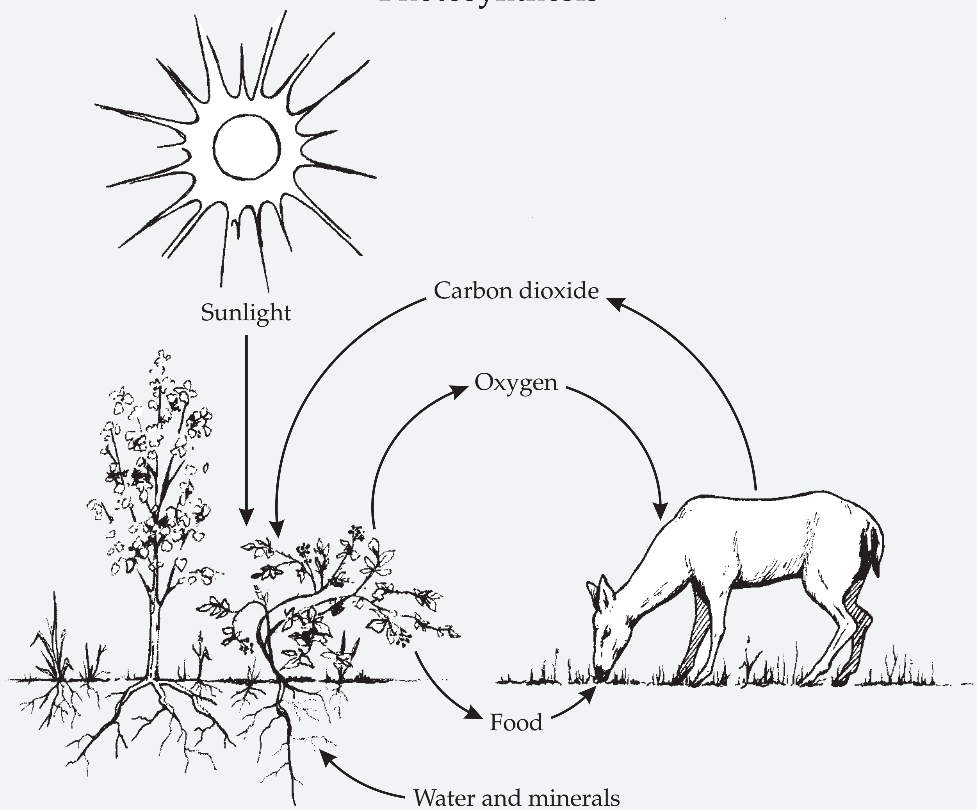
Light from the sun is composed of various types of radiation. Only a portion of this solar radiation can be used by plants for photosynthesis. This *photosynthetically active radiation* (PAR) ranges in wavelength from 400 to 700 nanometers and corresponds approximately to the visible light perceived by the human eye. The energy content of light depends on its wavelength, with shorter wavelengths having a higher energy content than longer wavelengths.

Role of Pigments

For light energy to drive photosynthesis, it first must be absorbed. Several types of photosynthetic pigments are found in plants. When these pigments absorb light, some of the pigments' electrons are elevated to a high energy level. These high-energy electrons are used to drive the reactions of photosynthesis, thus converting light energy into chemical energy. The most common photosynthetic pigment in plants is the green-colored *chlorophyll*. Two types of chlorophyll are found in plants, chlorophyll *a* and chlorophyll *b*, with other types of chlorophyll found in various types of algae and photosynthetic bacteria.

Additional plant accessory pigments, such as *carotenoids*, which are yellow or orange, play a minor role in the absorption of wavelengths of light not absorbed by chlorophyll. Carotenoids also help protect chlorophyll from damage that may occur as a result of absorbing excess light energy. As the most abundant plant pigment, chlorophyll gives plants their green color and usually masks the other colored pigments. In deciduous trees and shrubs, however, chlorophyll is degraded during the au-

Photosynthesis



The processes of photosynthesis and cellular respiration are complementary: Oxygen released into the atmosphere, a by-product of photosynthesis, is breathed in by animals, which in turn breathe out carbon dioxide, essential to photosynthesis. Likewise, photosynthesis is at the beginning of the carbon cycle and the food chain: Algae and plants generate organic (biochemical) energy from nonorganic sunlight, water, and minerals; animals eat plants and one another; decomposers (fungi and bacteria) return the essential elements to the ecosystem; and the cycle begins again.

tumn, revealing a spectacular display of colors from carotenoids and other pigments.

Reactions of Photosynthesis

The process of photosynthesis is complex, involving many biochemical reactions. Historically, the reactions of photosynthesis have been divided into the *light reactions* and the *dark reactions*. The light reactions include the absorption of light and the conversion of light energy to chemical energy. The dark reactions use the chemical energy produced in the light reactions to incorporate (or fix) carbon dioxide molecules into organic molecules (sugars). Within the chloroplast, the light reactions are localized in the internal network of membranes called *thylakoid membranes*.

The dark reactions occur in the aqueous region of the chloroplast called the *stroma*. The term "dark reactions" is somewhat misleading because several photosynthetic enzymes are not active in the dark, so these reactions will not occur without light. Although it is common to separate the light and dark reactions when describing photosynthesis, it should be noted that these reactions are tightly coupled and occur simultaneously in the plant.

Light Reactions

Chlorophyll and other accessory pigments that absorb light energy, along with certain proteins, are organized into structures called *photosystems*. Two types of photosystems occur in plants, photosystem I and photosystem II, and both are embedded in the thylakoid membranes. When light is absorbed by photosystems, the energy is transferred to special chlorophyll molecules, called reaction center chlorophylls, where the energy is transferred to electrons. High-energy electrons are released from the reaction centers and are passed along the thylakoid membranes by a series of electron transport molecules. Energy is extracted from the electrons as they are passed along, and the energy is used to transport protons (H^+) across the thylakoid membrane to the thylakoid interior. This process establishes a proton concentration gradient that is used to make ATP (adenosine triphosphate) from ADP (adenosine diphosphate) and inorganic phosphate (P_i) in a process called *photophosphorylation*. The acceptor molecule $NADP^+$ (nicotinamide adenine dinucleotide phosphate, oxidized form) finally accepts the high-energy electrons and combines them with protons (H^+) to form the high-energy molecule NADPH (nicotinamide adenine dinucleotide phosphate, reduced form). This process is called noncyclic electron flow, and the ATP and NADPH produced are forms of chemical energy that will be utilized by the dark reactions.

Many of the functions of photosytems I and II are similar. However, only photosystem II is able to split apart water molecules in the thylakoid interior into electrons, protons, and oxygen in a process called *photolysis*. The electrons released from water during photolysis replace electrons lost by chlorophyll molecules during the electron transport reactions. The protons released from water accumulate in the thylakoid interior, adding to the concentration gradient established by noncyclic electron flow. Oxygen produced from the photolysis of water is released as a gas to the atmosphere. Therefore, oxygen gas may be considered a by-product of plant photosynthesis. Algae and some bacteria (cyanobacteria) also release oxygen during photosynthesis, but other photosynthetic bacteria do not split water molecules and thus do not release oxygen.

The proton gradient created across the thylakoid membranes represents a source of potential energy used in making ATP. Protons are unable to diffuse across the thylakoid membranes unless permitted to do so by a special enzyme complex called the ATP synthase. The energy required to generate ATP is provided by protons as they move through the ATP synthase from the thylakoid interior, where there is a high concentration of protons to the stroma, where there is a lower concentration of protons. The energy associated with the proton gradient is analogous to a reservoir of water held back by a dam. Water may be allowed to pass through the dam by way of a turbine, thus using water to produce electrical power. The use of a proton gradient across a membrane as the energy source for the synthesis of ATP by ATP synthase is called *chemiosmosis*, and it occurs in both the chloroplast and the mitochondria. In chloroplasts, during photosynthesis, the process is called photophosphorylation. In mitochondria, ATP is synthesized during the process of oxidative phosphorylation, a component of cellular respiration. ATP, like NADPH, is a high-energy molecule produced by the light reactions that is consumed during the dark reactions.

In a process called *cyclic electron flow*, the electrons can travel within the electron transport system as described above but are diverted to an acceptor in the electron transport chain between photosystems I and II. Passing through the chain back to photosystem I, the electrons enable the transport of protons across the thykaloid membrane, thus supplying power for the generation of ATP.

Dark Reactions

Carbon dioxide gas is a normal, but minor, component of the atmosphere and enters leaves when air diffuses through stomata, small pores on the plant surfaces. The first reaction in converting carbon dioxide to sugar molecules occurs when the enzyme *Rubisco* (also known as ribulose bisphosphate carboxylase/oxygenase, and reportedly the most abundant protein on earth) combines ribulose bisphosphate (RuBP) containing five carbon atoms with a carbon dioxide molecule to produce two identical molecules of a simple sugar, each containing three carbon atoms. These three-carbon sugar molecules are then subsequently metabolized through a series of reactions leading to the production of a three-carbon sugar called glyceraldehyde 3-phosphate (G3P). Some of the G3P is used to make glucose and other organic molecules, and the remaining G3P is used to regenerate RuBP so the process can continue. This cyclic pathway is known as the *Calvin cycle* (or the Calvin-Benson cycle).

Sugar products may be stored within the chloroplast as starch, or they may be transported as sucrose to other parts of the plant as needed. ATP and NADPH from the light reactions are required for several of the reactions of the Calvin cycle. Because the first molecule produced by this pathway is a simple sugar with three carbon atoms, the pathway is known as the C_3 pathway. Plants using this pathway are known as *C_3 plants*, and common examples include many trees and the majority of agricultural crops.

The Rubisco enzyme, in addition to catalyzing the uptake of carbon dioxide during the Calvin cycle, can take up oxygen, initiating another metabolic pathway called *photorespiration*. In photorespiration, when oxygen is attached to RuBP instead of carbon dioxide, a product results that cannot be used in the Calvin cycle, and that product must go through a different set of complex reactions. For this reason photorespiration is often described as a wasteful process that competes with photosynthesis. The relative amounts of carbon dioxide and oxygen gases inside the chloroplast determine the relative rates of photosynthesis and photorespiration. Experiments in which the carbon dioxide concentration of air has been altered have demonstrated that the rate of photosynthesis increases and the rate of photorespiration decreases when the concentration of carbon dioxide is increased. In some agricultural and horticultural greenhouse operations, carbon dioxide amounts in the atmosphere are elevated to stimulate photosynthesis, leading to increases in plant production and yield.

Some plants have an adaptation whereby carbon dioxide is initially fixed by a pathway other than the Calvin cycle. This adaptation involves the enzyme phosphoenolpyruvate carboxylase (*PEP carboxylase*), an enzyme that lacks the oxygenase activity of Rubisco. PEP carboxylase actually attaches bicarbonate to phosphoenolpyruvate (PEP) in mesophyll cells that are in contact with air spaces in the leaf. PEP is then converted into a series of organic acids and, in the process, is transported into a specialized set of cells called *bundle sheath cells* that are separated from the air spaces in the leaf. In the bundle sheath cells carbon dioxide is released from the last organic acid in the series, which raises the carbon dioxide level in these cells where the carbon dioxide is used in the C_3 cycle. Raising the carbon dioxide concentration within the chloroplast increases photosynthesis while reducing photorespiration. The initial product of the pathway in the mesophyll cells is an organic acid with four carbon atoms, and thus the pathway is called the C_4 pathway. Plants possessing this pathway are known as C_4 plants. Examples include most grasses and a few crops, including corn and sugarcane.

A second adaptation that circumvents photorespiration is the CAM (crassulacean acid metabolism) pathway, named after the family of plants in it was first observed, *Crassulaceae*, or the stonecrop family. *CAM photosynthesis* is similar to C_4 photosynthesis in that it is another adaptation for raising the concentration of carbon dioxide inside the chloroplast. CAM plants accomplish photosynthesis using a biochemical process essentially the same as that of C_4 plants, but instead of carrying out these reactions in separate cells, they carry out certain reactions at night. CAM plants open their stomata only at night, and the carbon dioxide is transferred to PEP, which is converted into another organic acid that is stored throughout the night. During the day, the stomata remain closed, and the carbon dioxide needed for the C_3 cycle is supplied by releasing carbon dioxide from the last organic acid in the CAM cycle. Examples of CAM plants include cactus and pineapple. Both C_4 and CAM plants typically require less water than do C_3 plants and may be found in warmer and drier environments. C_4 plants tend to have high rates of photosynthesis, whereas CAM plants have low photosynthetic rates because the CAM cycle is less efficient than the C_4 cycle. C_3 plants typically have intermediate photosynthetic rates under optimal conditions.

Photosynthesis and the Environment

Several environmental factors affect the rate of photosynthesis. For example, temperature extremes and water stress inhibit photosynthesis. As light intensity increases, so do photosynthetic rates. However, when photosynthesis becomes light-saturated, further increases in light intensity will not result in greater rates of photosynthesis. Leaves of plants that grow in full-sun conditions are smaller and thicker, with more extensive vascular systems than those found in shade plants. Although so-called sun leaves and shade leaves have similar photosynthetic rates in low light, shade leaves have much lower rates of photosynthesis at high light intensities and can be damaged when exposed to such conditions.

As mentioned above, atmospheric carbon dioxide concentrations can also regulate photosynthesis. At the present time the concentration of carbon dioxide in the atmosphere is less than 0.04 percent, but scientific data show that this concentration is increasing. Higher concentrations of atmospheric carbon dioxide may stimulate plant photosynthesis and plant growth but may have other undesirable climatic effects.

William J. Campbell

See also: Anaerobic photosynthesis; C_4 and CAM photosynthesis; Chemotaxis; Calvin cycle; Chloroplasts and other plastids; Energy flow in plant cells; Eukaryotic cells; Membrane structure; Photosynthetic light absorption; Photosynthetic light reactions; Pigments in plants; Plant cells: molecular level; Respiration.

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PHOTOSYNTHETIC LIGHT ABSORPTION

Categories: Cellular biology; photosynthesis and respiration; physiology

Photosynthetic light absorption involves plants' use of pigments to facilitate the conversion of light energy into chemical energy.

Photosynthesis occurs in green plants, algae, and certain types of bacteria. There is considerable variation among the types of pigments found in these different groups of organisms, but the basic mechanisms by which they absorb light are similar. Photosynthetic pigments are always attached to membranes within a cell. In algae and higher plants, the photosynthetic pigments are located in the *chloroplast*, where photosynthesis takes place. The pigment molecules are not dispersed randomly within the chloroplast but are arrayed on the surface of the *thylakoid membranes*. The chloroplasts become oriented in such a way as to present a large surface area to the sun or other light source, thereby maximizing the ability of the pigments to absorb light energy. In photosynthetic bacteria, the light-absorbing pigments are not organized in chloroplasts but are located on membranes that are dispersed throughout the cell.

Chlorophylls and Carotenoids

The two primary types of pigments utilized by most photosynthetic organisms are the green *chlorophylls* and the yellow to orange *carotenoids*. There are several forms of chlorophyll that differ from one another in small details of their molecular structures. The forms are designated chlorophyll *a*, *b*, *c*, and so on. Chlorophyll *a* is found in all plants and algae, while the other forms are dispersed among various taxonomic groups. The chlorophyll molecule consists of two parts: an elaborate ring structure that actually absorbs the light, and a long tail-like section that anchors the molecule in the membrane. Photosynthetic bacteria contain similar pigments called *bacteriochlorophyll a* and *b*.

Carotenoids, the other major group of photosynthetic pigments, also occur in various forms and are found in all types of photosynthetic plants, algae, and bacteria. The *xanthophylls*, which are oxygenated carotenoids, form another widespread and diverse subgroup of pigments. Carotenoid molecules have elongated structures and, like the chlorophylls, are embedded in the photosynthetic membranes. It is a popular misconception that the change in leaf color that takes place in the fall is the result of the formation of new yellow or orange carotenoid pigments. Actually, the carotenoids are present all the time but are masked by the presence of the green chlorophyll. In fall, the chlorophyll begins to decompose more rapidly than the carotenoids, whose yellow colors are then exposed.

Chlorophyll *a*, or something very similar to it, occurs almost universally in photosynthetic organisms, from bacteria to higher plants, because it is an essential component of photosynthetic reaction centers. All of the other chlorophylls and carotenoids involved in light absorption are referred to as *accessory pigments*. Another kind of accessory pigment found in some groups of algae and photosynthetic bacteria are the *phycobiliproteins*, which may impart a red or blue color to the cells in which they occur. These molecules consist of a light-absorbing portion bound to a protein. In fact, all types of pigment molecules seem to be bound to proteins within the photosynthetic membranes. These pigment-protein associations are sometimes referred to as *light-harvesting complexes*, a term that accurately describes their function.

Properties of Light

To understand the functioning of photosynthetic pigments, it is necessary to consider first the physical nature of light. Visible light is only a small portion of the electromagnetic spectrum, which ranges from very short wavelength radiation, such as X rays, to extremely long wavelength radiation, such as radio waves. The visible portion of the spectrum is intermediate in wavelength and ranges from blue (at the short end) to red (at the long end). Sunlight contains a mixture of all the visible wavelengths, which humans perceive as white light. The energy of light is inversely proportional to its wavelength; blue light has more energy than an equivalent amount of red light. Light may be thought of as consisting of either waves or particles. For purposes of studying light absorption by pigments, it is easier to think of light as particles, referred to as *photons* or *quanta*.

When a photon is absorbed by a pigment molecule, the photon's energy is transferred to one of the electrons of the pigment. The electron is thus said to enter an excited state and contains the energy originally associated with the photon of light. A specific kind of pigment is not capable of absorbing all the photons it encounters. Only photons of certain energy (and therefore wavelength) can be absorbed by each pigment. For example, chlorophyll primarily absorbs light in the blue and red wavelengths but not in the green portion of the spectrum. Consequently, the green light to which chlorophyll is exposed is either transmitted through it or reflected from it, with the result being that the pigment appears green. The color of the pigment results from the wavelengths of light that are not absorbed. Carotenoids do not absorb light in the yellow to orange portion of the spectrum and, therefore, are seen as being that color.

The process of light absorption begins when a photon of appropriate energy strikes a chlorophyll or carotenoid molecule located on a thylakoid or other photosynthetic membrane, thus causing an electron in the pigment to be raised to an excited state. If two pigment molecules are situated adjacent to each other in exactly the right orientation and are separated by a very small distance, it is possible for the energy of excitation to be transferred from one molecule to the next. This transfer process (referred to as *Forster resonance*) enables the excitation energy to migrate throughout the array of pigment molecules that are attached to the photosynthetic membrane.

In addition to pigment molecules, the membranes also contain a smaller number of special structures called *reaction centers*, which consist of special chlorophyll and protein molecules arranged in a very specific fashion. The excitation energy migrating throughout the pigment array will eventually find its way to one of the reaction centers, and there it is utilized to form new energy-containing molecules. All of this occurs with a large number of photons and pigment molecules simultaneously. The array of pigment molecules feeding excitation energy into the reaction centers contains both chlorophylls and carotenoids and is sometimes referred to as an *antenna*, to indicate its role in light absorption. This overall process constitutes the light reactions of photosynthesis. The energy-containing molecules thus formed will then be used in the *Calvin cycle* to convert carbon dioxide into carbohydrates: Light energy has been converted into chemical energy.

Pigment Functions

Chlorophyll *a*, as well as the other chlorophylls, makes up a major portion of the antenna pigments that absorb light energy and transfer it to the reaction centers. The carotenoids, which are also part of the antenna, seem to contribute in two ways to the effectiveness of the light absorption process. First, they increase the range of wavelengths that can be absorbed. Chlorophyll absorbs mainly in the blue and red portions of the spectrum but is not effective at absorbing other wavelengths. Carotenoids are able to absorb some of the green light that would be unusable if chlorophyll were the only pigment present, so having a combination of different pigments makes the organism more effective at using the various wavelengths that occur in sunlight.

A second function of the carotenoids has to do with their ability to protect chlorophyll from damage by intense light. Under conditions of high light intensity, chlorophyll has a tendency to decompose through a process called photooxidation. The presence of carotenoids prevents this decomposition from occurring and enables the chlorophyll to continue to function effectively at light intensities that would otherwise cause damage.

Although virtually all photosynthetic organisms utilize some form of chlorophyll in light absorption, an exception is found in the halobacteria. These bacteria live in conditions of very high salt concentration, such as the Dead Sea or the Great Salt Lake. In these bacteria is found a purple membrane containing molecules of a pigment called *bacteriorhodopsin* which, remarkably, is very similar to rhodopsin, the pigment found in the visual systems of higher animals. When bacteriorhodopsin molecules absorb light, they cause a hydrogen ion (a proton of H^+) to be ejected across the cell membrane, and this leads to the formation of energy-containing molecules that the bacterium can utilize for its various metabolic requirements. Research with these unique photosynthetic organisms may also lead to a better understanding of the molecular basis and evolution of vision in animals.

Thomas M. Brennan

See also: Anaerobic photosynthesis; Calvin cycle; Chloroplasts and other plastids; Photosynthesis; Photosynthetic light reactions; Pigments in plants.

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PHOTOSYNTHETIC LIGHT REACTIONS

Categories: Cellular biology; photosynthesis and respiration; physiology

Photosynthetic light reactions involve the absorption of light energy by plant pigments and the conversion of light energy into adenosine triphosphate (ATP).

Photosynthesis is the process by which plants, algae, and certain types of bacteria use the energy of sunlight to manufacture organic molecules from carbon dioxide and water. The process may be divided into two parts: the *light reactions* and the *dark reactions*. In the light reactions of photosynthesis, light energy coming from the sun or from an artificial light source is absorbed by pigments and used to boost electrons into higher energy levels so they can be used to do cellular work. In the dark reactions (also called the *Calvin cycle*), energy-containing molecules from the light reactions are used to convert carbon dioxide into carbohydrates. All living organisms ultimately depend upon this process as their source of food.

In algae and higher plants, the light reactions of photosynthesis take place on *thylakoid membranes* located within *chloroplasts*. The surfaces of the thylakoids are covered with molecules of the green pigment *chlorophyll* as well as yellow *carotenoid* pigments. Also located on the thylakoids, though fewer in number, are special structures called *reaction centers*. The process begins when a unit of light energy (referred to as a photon or quantum) strikes a pigment molecule and causes one of its electrons to be raised to a higher energy level, or an excited state. Many chlorophyll and carotenoid molecules are located adjacent to one another on the thylakoids, and the energy of the excited electrons may be transferred from one to the next until it reaches a reaction center. Overall, a very large number of pigment molecules are absorbing light, becoming excited, and passing the excitation energy to reaction centers. It is in the reaction centers that the central events of the photosynthetic light reactions take place.

Photosystem I

Higher plants contain two different types of reaction centers, referred to as *photosystem I* and *photosystem II*. (The numbers I and II have no functional significance; they simply reflect the order in which they were discovered.) What the two types of reaction centers actually consist of are groups of special proteins complexed with several chlorophyll molecules and structured in a very specific arrangement within the thylakoid membrane. Also embedded in the thylakoid membrane are a series of proteins and other molecules that are capable of transporting electrons from photosystem II to photosystem I. This process is referred to as the *electron transport system*. The two photosystems and the electron transport system work together to form the energy-containing molecules produced in the photosynthetic light reactions.

The process is best understood by looking first at what happens in photosystem I. As described above, light energy is absorbed by a pigment molecule and transferred to the reaction center, causing two photosystem I electrons to be raised to an excited state. The excited electrons are then passed from the reaction center to a primary electron acceptor. The primary electron acceptor passes the electrons to the first of a series of electron transport proteins in the inner thykaloid membrane, the last of these proteins being ferredoxin, an iron-containing protein. Ferredoxin passes the electrons to a coenzyme called *nicotinamide adenine dinucleotide phosphate* ($NADP^+$), which then becomes reduced and, after joining with a free proton (H^+), becomes NADPH. The important point is that some of the energy of the excited electrons is incorporated into the molecule of NADPH, thereby converting light energy into chemical energy. The NADPH is not attached to the thylakoid membrane but remains in the *stroma* (the region inside both the outer membranes of the chloroplast and surrounding the thykaloids) of the chloroplast, where it will be used in the Calvin cycle.

Photosystem II

However, photosystem I, by itself, could not continue to function in the manner described above without having some way of replacing the electrons which are being removed. This is where photosystem II comes in. The basic operation of photosystem II is similar to photosystem I insofar as light energy is absorbed by pigment molecules and transferred to the reaction center. However, the excited electron is not used to form NADPH; instead it enters the electron transport system and is passed from one molecule to the next until it eventually reaches photosystem I, where it replaces the electron previously lost in the formation of NADPH.

The electron transport system does much more than merely replace electrons in photosystem I. As an electron moves through the electron transport system, its energy is used to transfer protons (hydrogen ions) from the stroma to the thykaloid space (the region inside the thykaloids). The thylakoids are not simply flat sheets of membrane but are folded in such a way as to form numerous saclike compartments within the chloroplast. The result is that a proton gradient is established across the thykaloid membrane.

Many electrons are carried through the electron transport system, resulting in the accumulation of a high concentration of protons within the thylakoid compartments. This high concentration of protons on one side of the membrane and relatively low concentration on the other represents a source of *potential energy*, somewhat analogous to the energy contained in a body of water held back by a dam. The protons are then allowed to move back across the membrane through special proteins called *ATP synthase*. ATP synthase is an enzyme capable of catalyzing the joining of adenosine diphosphate (ADP) with inorganic phosphate (P_i) in the stroma to form adenosine triphosphate (ATP). The passage of protons through ATP synthase results in a change in shape in the protein, which brings about the reaction between ADP and P_i. The formation of ATP by this mechanism is called *photophosphorylation*. Once again, light energy has been transformed into chemical energy.

Electron Replacement

If electrons from photosystem II are used to replace those from photosystem I, then the electrons from photosystem II must be replaced as well. This problem is solved by the use of water as a source of electrons. Photosystem II is capable of splitting apart molecules of water to extract electrons, using the electrons to replace the ones used by the electron transport system. Water is always available in a functioning photosynthetic plant cell, and this represents a virtually limitless source of electrons. Water molecules contain hydrogen and oxygen, and when they are split apart in this manner, the protons left over from hydrogen simply go into solution, but the oxygen forms oxygen gas and is released into the atmosphere. Although the oxygen is really no more than a by-product as far as photosynthesis is concerned, it is of profound significance to all higher organisms.

The overall flow of electrons in the light reactions is from water to photosystem II, through the electron transport system where ATP is formed, to photosystem I and finally to NADPH. This arrangement was hypothesized by Robin Hill and Fay Bendall in 1960. Because of the way in which the process was diagrammed in their paper, it is often referred to as the *Z scheme*. In energy terms, what has been accomplished is the conversion of light energy to chemical energy in the form of ATP and NADPH. These energy-rich molecules are essential to the Calvin cycle as energy for the conversion of carbon dioxide into carbohydrates. The process is known as *noncyclic electron flow*.

Alternatively, in *cyclic electron flow*, the electrons can travel within the electron transport system as described above but are diverted to an acceptor in the electron transport chain between photosystems I and II. Passing through the chain back to photosystem I, the electrons enable the transport of protons across the thykaloid membrane, thus supplying power for the generation of ATP. This process is called *cyclic photophosphorylation*, because it involves a cyclic flow of electrons. In this way, photosystem I can work independently of photosystem II. Apparently, this is the manner in which some bacteria carry out photosynthesis.

Bacterial Photosynthesis

Certain types of bacteria also carry on photosynthesis. These organisms do not contain chloroplasts, so the light-absorbing pigments and reaction centers are located on membranes spread throughout the cell. In one group, the cyanobacteria, the photosynthetic process is similar to that described for algae and higher plants in that there are two photosystems, water serves as the primary electron donor, and oxygen is released.

The other types of photosynthetic bacteria, however, are more primitive. They have only one photosystem and use inorganic compounds such as hydrogen sulfide instead of water as a source of electrons. The cyanobacteria possess chlorophyll, and the other photosynthetic bacteria contain a similar pigment known as *bacteriochlorophyll*. In addition, these organisms contain a variety of accessory pigments that also are involved in the photosynthetic light reactions.

Thomas M. Brennan, updated by Bryan Ness

See also: Active transport; Anaerobic photosynthesis; Calvin cycle; Photosynthesis; Photosynthetic light absorption; Pigments in plants.

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PHYTOPLANKTON

Categories: Algae; microorganisms; water-related life

The term "plankton," from Greek planktos *for "wandering," is applied to any organism that floats or drifts with the movement of the ocean water. Most plankton are microscopic and are usually single-celled, a chain of cells, or a loose group of cells. Algal and cyanobacterial plankton are referred to as phytoplankton. The heterotrophic crustaceans and larvae of animals are referred to as zooplankton.*

The group of organisms known as phytoplankton (literally, "plant" plankton) do not constitute a taxonomic group but rather refer to a collection of diverse, largely algal and cyanobacterial, microorganisms that live in water and are at the base of the food chain. The phytoplankton, including diatoms, unicellular cyanobacteria and coccolithophorids in nutrient-poor waters, and cryptomonads, manufacture organic material from carbon dioxide, usually through photosynthesis. Phytoplankton are responsible for one-half of the world's primary photosynthesis and produce one-half of the oxygen in the atmosphere.

Eighty to ninety percent of the weight of phytoplankton is water, with the rest made up of protein, fat, salt, carbohydrates, and minerals. Some species have compounds of calcium or silica that make up their shells or skeletons. Phytoplankton include many of the algal phyla: *Chrysophyta* (chrysophytes), *Phaeophyta* (golden-brown algae), coccolithophores, silicoflagellates, and diatoms. The most common type of phytoplankton is the *diatom* (phylum *Bacillariophyta*), a single-celled organism that can form complex chains. *Dinoflagellates* (phylum *Dinophyta*) are the most complex of the phytoplankton. They are unicellular and mobile. Green algae (phylum *Chlorophyta*) are usually found in estuaries or lagoons in the late summer and fall. Some species can cause toxic *algal blooms* associated with coastal pollution and eutrophication. Cyanobacteria (often called blue-green algae but not true algae) are prominent near shore waters with limited circulation and brackish waters.

Photosynthesis

Phytoplankton are primary *producers*, responsible for a half the world's primary photosynthesis: the conversion of light energy and inorganic matter into bioenergy and organic matter. Each year, 28 billion tons of carbon and 250 billion to 300 billion tons

Image Not Available

of photosynthetically produced materials are generated in the oceans by phytoplankton. All animal organisms eliminate carbon dioxide into the atmosphere, and plants remove carbon dioxide from the air through photosynthesis. In the oceans' *carbon cycle*, carbon dioxide from the atmosphere dissolves in the ocean. Photosynthesis by marine plants, mainly phytoplankton, converts the carbon dioxide into organic matter. Carbon dioxide is later released by plants and animals during respiration, while carbon is also excreted as waste or in the dead bodies of organisms. Bacteria decompose organic matter and release the carbon dioxide back into the water. Carbon may be deposited as calcium carbonate in biogenous sediments and coral reefs (made of skeletons and shells of marine organisms).

Food Chain

Because they are primary producers of organic matter through photosynthesis, phytoplankton play a key role in the world's food chain: They are its very beginning. Sunlight usually penetrates only 200 to 300 feet deep into ocean waters, a region called the photic zone. Most marine plant and animal life and feeding take place in this zone. Phytoplankton, the first level in the marine food chain, are the primary food source for zooplankton and larger organisms. These microscopic plants use the sun's energy to absorb minerals to make basic nutrients and are eaten by *herbivores*, or plant eaters. Herbivores are a food source for *carnivores*, the meat eaters. In temperate zones, phytoplankton increase greatly in the spring, decline in the summer, and increase again in the fall. Zooplankton (animal plankton) are at their maximum abundance after the spring increase, and their grazing on the phytoplankton causes a decrease in phytoplankton population in the summer. Fish and invertebrates that eat zooplankton become more abundant and so on, up the food chain. Krill, planktonic crustaceans, and larvae commonly eaten by whales, fish, seals, penguins, and seabirds feed on diatom phytoplankton.

Red Tides

The term *red tide* is applied to red, orange, brown, or bright-green phytoplankton blooms, or even to blooms that do not discolor the water. Red tides are poorly understood and unpredictable. No one is certain what causes the rapid growth of a single species of phytoplankton, although they can blossom where sunlight, dissolved nutrient salts, and carbon dioxide are available to trigger photosynthesis. Dense phytoplankton blooms occur in stable water where lots of nutrients from sewage and runoff are available. Natural events, such as storms and hurricanes, may remobilize populations buried in the sediment. These nuisance blooms, usually caused by dinoflagellates, which turn the water a reddish brown, and cyanobacteria, are becoming more frequent in coastal waters, possibly because of increased human populations and sewage. In shallower bodies of water, such as bays and estuaries, nutrients from winter snow runoffs, spring rains, tributaries, and sewage bring about spring and summer blooms.

Some of the poisons produced during red tides are the most powerful toxins known. The release of toxins by dinoflagellates may poison the higher levels of the food chain as well as suppress other phytoplankton species. These toxins cause high mortality in fish and other marine vertebrates. They can kill the whales and seabirds that eat contaminated fish. Dinoflagellates produce a deadly neurotoxin called saxitoxin, which is fifty times more lethal than strychnine or curare. Commercial shellfish, such as mussels, clams, and crabs, can store certain levels of the toxin in their bodies.

People who eat contaminated shellfish may experience minor symptoms, such as nausea, diarrhea, and vomiting, or more severe symptoms such as loss of balance, coordination, and memory, tingling, numbness, slurred speech, shooting pains, and paralysis. In severe cases, death results from cardiac arrest. When the toxins are blown ashore in sea spray, they can cause sore throats or eye and skin irritations.

Toxic blooms costs millions of dollars in economic losses, especially for fisheries which cannot harvest some species of shellfish. Smaller fish farms can be devastated. Additionally, coastal fish deaths foul beaches and shore water with decaying bodies, which can cripple tourism in the coastal regions.

Not all blooms are harmful, but they do affect the marine environment. Even when no toxins are released, massive fish kills can result when the large blooms of phytoplankton die. When the blooming phytoplankton population crashes, bacterial decomposition depletes the oxygen in the water, which in turn reduces water quality and conditions, and fish and other marine animals suffocate.

Virginia L. Hodges

See also: Algae; Aquatic plants; Bacteria; Brown algae; *Chlorophyceae*; Chrysophytes; Diatoms; Dinoflagellates; Eutrophication; Food chain; Green algae; Invasive plants; Marine plants; Photosynthesis; Red algae.

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PIGMENTS IN PLANTS

Categories: Animal-plant interactions; economic botany and plant uses; photosynthesis and respiration; physiology

Photosynthetic pigments color plants and participate in photosynthesis. Other plant pigments are important in flowers and fruits to attract pollinators and seed dispersers. Humans use plant pigments in vitamins and dyes.

Plant pigments can be classified as either *nitrogenous* or *non-nitrogenous*, that is, either nitrogen-containing or non-nitrogen-containing.

Non-nitrogenous pigments

Non-nitrogenous forms are widely distributed and include the *carotenoids* and the *quinones*. Carotenoids are yellow, orange, or red pigments often involved as accessory pigments in photosynthesis. They are insoluble in water but soluble in a variety of nonpolar solvents. They are easily bleached by light or oxygen. Carotenoids occur as hydrocarbon carotenes and oxygenated xanthophylls. They are made by bacteria, fungi, algae, and other plants. Variations of their occurrence and their multiplicity make carotenoids useful in taxonomic differentiation of these organisms.

The quinones include benzoquinones, naphthoquinones, and anthraquinones. Benzoquinones occur in fungi and higher plants as yellow, orange, red, or violet pigments. Yellow coenzyme Q variants (ubiquinones) and plastoquinones are found in most plants. Because of their low tissue levels, they do not affect plant color. Naphthoquinones of bacteria and leaves, seeds, and woody parts of higher plants have yellow, orange, red, or purple pigments, soluble in nonpolar solvents. A familiar example is vitamin K. Brightly colored anthraquinones also occur in many plants.

Many other complex plant quinones are water-soluble *flavonoids*, all containing a common fifteen-carbon skeleton, flavone (2-phenylben-zopyrone). The various flavonoids differ in how many hydroxyl or methoxyl groups they contain. They occur as sugar-containing substances called *glycosides*, which is the basis of their water solubility. The members of one plentiful group of flavonoids are the anthoxanthins, which are yellow pigments. Another important flavonoid group, anthocyanins, are orange, red, crimson, or blue.

Carotenoids are yellow, orange, or red pigments often involved as accessory pigments in photosynthesis. In the fall, destruction of the green pigment chlorophyll is accompanied by increased visibility of the yellow or orange pigments of the carotenoids, which were previously masked by chlorophyll in these maple leaves.

Nitrogenous Pigments

The nitrogenous (nitrogen-containing) pigments are *tetrapyrrole porphyrins* and their derivatives, indigoids and flavins. The porphyrins are water-soluble, cyclic, nitrogen-containing substances. The basic structural unit of all porphyrins is a large tetrapyrrole ring made up of four smaller connected pyrrole rings. Porphyrins combine with metal ions and proteins. In plants they are represented by green *chlorophylls*. The chlorophylls contain magnesium ions and are associated with water-insoluble proteins. Related *bilins* are a group of yellow, green, red, or brown compounds that have linear structures composed of four connected pyrrole rings. The bilins include red bilirubin, green biliverdin, and the phycobilins of red algae or green plants. Examples are blue phycocyanobilin and phytochrome as well as red phycoerythrin. Plant bilins bind water-soluble and water-insoluble proteins.

Indigoids, a group of indole pigments, derive from the amino acid tryptophan. They are red, blue, or purple. The flavins (lyochromes) are pale yellow, water-soluble pigments widely distributed in plants. The most plentiful flavin is riboflavin (vitamin B_2). Flavins are made by bacteria, yeasts, and green plants.

Functions

Non-nitrogenous benzoquinones and ubiquinones are involved in electron transport processes important in respiration. Naphthoquinones have similar functions in photosynthesis and are also represented by K vitamins. Anthroquinones are the brilliantly colored compounds seen in the colors of flowers. Similarly, flavonoid glycosides color many flowers. For example, the anthoxanthins produce the yellow color of buttercups.

Anthocyanins make flower petals orange-red, crimson, and blue. They cause much of the red color seen in some plant buds and shoots, the colors of autumn leaves, fruits (such as berries), or roots (such as beets). A typical anthocyanin is red in acid solution, violet in neutral solution, and blue in alkaline solution. Blue or red cornflowers and violet dahlias contain the same anthocyanin, their color differences simply being the result of pH (acidity or alkalinity) differences of the cell sap.

The function of flavonoids is still unclear. However, it is believed that they are essential in flowers for attracting bees and other pollinators, encouraging cross-pollination. They are also thought to attract larger animals to bright-colored, edible fruits, enhancing seed dissemination, and to protect plants from damage by ultraviolet light.

Nitrogen-containing tetrapyrrole plant porphyrins are best known because of the key role they play in photosynthesis. Chlorophylls enable photosynthetic conversion of sunlight to chemical energy, which is used by plant cells to use carbon dioxide to make organic molecules. Chlorophylls include chlorophylls *a* and *b* of higher plants and green algae and the bacteriochlorophylls in photosynthetic bacteria. The various chlorophylls differ in only minor ways as a result of side chain groups attached to their pyrroles. In higher plants, chlorophylls bind to proteins and lipids in the thylakoid membranes of chloroplasts, where they function in photosynthesis. Some of the phycobilins of blue algae, red algae, and green plants act as accessory photosynthetic pigments. Another function of bilins is as phytochromes, essential to photoperiodic processes.

Economic Uses

Many plant pigments meet human nutritional needs. The carotenes, derived from carotenoids, are used in the biosynthesis of vitamin A, essential to vision and growth. Furthermore, napthoquinone photosynthetic pigments lead to another important vitamin group: K vitamins, essential to blood clotting. Yet another vitamin derived from plant pigments is a nitrogen-containing flavin called riboflavin, better known as vitamin B_2.

Many plant pigments are used as dyes or as model compounds from which other dyes have been synthesized. The naphthoquinones from leaves, seeds, and woody parts of higher plants are isolated as yellow, orange, red, or purple materials soluble in organic solvents and used as fabric dyes. Indigo, a blue indigoid which occurs in many plants of Asia, Africa, and South America, has been used as a blue dye and the model for many industrially synthesized dyes. Similarly, anthraquinones, brightly colored plant pigments, are widely used. Moreover, because their colors change in acidic, basic, and neutral solutions, anthraquinones are used as acid-base indicators. Flavonoid anthocyanins (as was mentioned) are also used as acid-base indicators. A variety of edible plant pigments are also used to add color to foods.

Sanford S. Singer

See also: Algae; *Archaea*; Bacteria; Angiosperm evolution; Angiosperms; Animal-plant interactions; Biochemical coevolution in angiosperms; Chloroplasts and other plastids; Chromatography; Coevolution; Flower types; Flowering regulation; Fruit: structure and types; Leaf abscission; Metabolites: primary vs. secondary; Photoperiodism; Photosynthesis; Photosynthetic light absorption; Photosynthetic light reactions; Vacuoles.

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PLANT BIOTECHNOLOGY

Categories: Biotechnology; economic botany and plant uses; environmental issues; genetics

Plant biotechnology may be defined as the application of knowledge obtained from study of the life sciences to create technological improvements in plant species. By this very broad definition, plant biotechnology has been conducted for more than ten thousand years.

The roots of plant biotechnology can be traced back to the time when humans started collecting seeds from their favorite wild plants and began cultivating them in tended fields. It appears that when the plants were harvested, the seeds of the most desirable plants were retained and replanted the next growing season. While these primitive agriculturists did not have extensive knowledge of the life sciences, they evidently did understand the basic principles of collecting and replanting the seeds of any naturally occurring variant plants with improved qualities, such as those with the largest fruits or the highest yield, in a process that we call *artificial selection*. This domestication and controlled improvement of plant species was the beginning of plant biotechnology. This very simple process of selectively breeding naturally occurring variants with observably improved qualities served as the basis of agriculture for thousands of years and resulted in thousands of domesticated plant cultivars that no longer resembled the wild plants from which they descended.

The second era of plant biotechnology began in the late 1800's as the base of knowledge derived from the study of the life sciences increased dramatically. In the 1860's Gregor Mendel, using data obtained from controlled pea breeding experiments, deduced some basic principles of genetics and presented these in a short monograph modestly titled "Versuche über Pflanzenhybriden" (in *Verhandlungen des naturforschenden Vereins*, 1866; *Experiments with Plant-Hybridisation*, 1910). In this publication, Mendel proposed that heritable genetic factors segregate during sexual reproduction of plants and that factors for different traits assort independently of each other. Mendel's work suggested a mechanism of heritable factors that could be manipulated by controlled breeding of plants through selective fertilization and also suggested that the pattern of inheritance for these factors could be analyzed or, in some cases, predicted by the use of mathematical statistics.

These findings complemented the work of Charles Darwin, who expounded the principles of descent with modification and selection as the chief factor of evolutionary change in his 1859 book *On the Origin of Species by Means of Natural Selection*. The application of these principles to agriculture resulted in deliberately produced hybrid varieties for a large number of cultivated plants via selective fertilization. These artificially selected hybrids soon began to benefit humankind with tremendous increases in both the productivity and the quality of food crops.

Genetic Engineering

The third era of plant biotechnology involves a drastic change in the way crop improvement may be accomplished, by direct manipulation of genetic elements (genes). This process is known as *genetic engineering* and results in plants that are called genetically modified organisms (GMOs), to distinguish them from plants that are produced by conventional plant-breeding methods. Genetically modified plants can contribute desirable genes from outside traditional breeding boundaries.

Even genes from outside the plant kingdom can now be brought into plants. For example, animal genes, including human genes, have been transferred into plants, a feat not replicated in nature.

Public Concern

It is perhaps this lack of natural boundaries for genetic exchange that seems so foreign to conventional scientific thought and that makes plant genetic engineering controversial. The thought of taking genes from animals, bacteria, viruses, or any other organism and putting them into plants, especially plants consumed for food, has raised a host of questions among concerned scientists and public alike. Negative public perception of genetically modified crops has affected the development and commercialization of many plant biotechnology products, especially food plants. While there are dozens of genetically engineered plants ready for field production, public pressure has delayed the release of some of these plants and has caused the withdrawal of others from the marketplace.

This public concern also appears to be driving increased government review of products and decreased government funding for plant biotechnology projects in Europe. Negative public perceptions do not seem to be as strong in Asia, since the pressures of feeding large populations tend to outweigh the perceived risks. The social climate of the United States toward biotechnology, although guarded, appears to be less apprehensive than that of most European countries. Therefore, many agricultural biotechnology projects have moved from European countries to U.S. laboratories.

Economic Goals

To what end are humans genetically engineering plants? This is an essential question for researchers,

Time Line of Plant Biotechnology

Year	*Event*
1838	German scientists Matthias Schleiden and Theodor Schwann presented their cell theory: that all life-forms are made up of cells.
1858	Biologist Rudolf Virchow adds to the cell theory, proposing that, "where a cell exists, there must have been a preexisting cell."
1902	Austrian botanist Gottlieb Haberlandt completes the cell theory with his idea of totipotency: Cells must contain all the genetic information necessary to create an entire, multicellular organism. Therefore, every plant cell is capable of developing into an entire plant.
1939	R. J. Gautheret demonstrates the first successful culture of isolated plant tissues as a continuously dividing callus tissue.
1953	James Watson and Francis Crick make their landmark proposal for the double-helical structure of deoxyribonucleic acid (DNA), the molecule that carries genetic material.
1954	The first whole plant is regenerated, or cloned, from a single adult plant cell by W. H. Muir and colleagues.
1967	DNA ligase, the enzyme that joins DNA molecules, is discovered.
1970	Daniel Nathans, Hamilton Smith, and others discover restriction endonucleases.
1972	Researchers at Stanford University construct the first recombinant DNA molecules, and the following year DNA is inserted into *Escherichia coli* cells.
1980	The U.S. Supreme Court rules that genetically altered life-forms can be patented, allowing Exxon to patent a microorganism that eats oil.
1983	The National Institutes of Health permit scientists at the University of California at Berkeley to release genetically engineered bacteria designed to retard frost formation on crop plants.
1983	The U.S. Patent Office begins to issue a series of patents for genetically modified plants.

executives of biotechnology companies, and consumers at large. Before addressing technical questions about how to apply biotechnology, the desired goals must be clearly defined. The general goals of plant biotechnology appear to be (1) economic improvement of existing products, (2) improvement of human nutrition, and (3) development of novel products from plants.

Economic improvements include increases in yield, quality, pest resistance, nutritional value, harvestability, or any other change that adds value to an established agricultural product. Examples of this category include insect-protected tomatoes, potatoes, cotton, and corn; herbicide-resistant canola, corn, cotton, flax, and soybeans; canola and soybeans with genetically altered oil compositions; virus-resistant squash and papayas; and improved-ripening tomatoes. All these examples were introduced to agriculture in the later half of the 1990's.

Nutritional Goals

Additionally, some products appearing in the scientific literature but awaiting commercialization have the potential to dramatically improve human nutritional deficiencies, which are especially prevalent in developing countries. These products include "golden rice," genetically modified rice that produces carotenoids, a dietary source of vitamin A. Golden rice has the potential to prevent vitamin A deficiency in developing countries, where this vitamin deficiency is a leading cause of blindness.

Researchers are also using genetic engineering to increase the amount of the iron-storing protein ferritin in seed crops such as legumes. Iron deficiency, which affects 30 percent of the human population, can impair cognitive development and cause other other health problems. This proposed enhancement of iron content in consumable plant

Year	*Event*
1984	The Plant Gene Expression Center, a collaborative effort between academia and the U.S. Department of Agriculture, is established to research plant molecular biology, sequence plant genomes, and develop genetically modified plants.
1985	Field testing of plants genetically modified to resist plant pathogens and disease vectors begins.
1986	The first release of a genetically modified crop, genetically engineered tobacco plants, is approved by the Environmental Protection Agency.
1987	Calgene receives a patent for a DNA sequence that extends the shelf life of tomatoes.
1987	Advanced Genetic Sciences, Inc., field-tests a recombinant organism designed to inhibit frost in strawberries.
1990	Calgene conducts field experiments with herbicide-resistant cotton plants.
1990	At the Plant Gene Expression Center, biologist Michael Fromm announces the use of a high-speed "gene gun" to transform corn. Gene guns are used to shoot genetic material directly into cells via DNA-coated microparticles.
1993	Kary Mullis wins the Nobel Prize in Chemistry for development of polymerase chain reaction technology, a technique he invented in 1981 for quickly multiplying DNA sequences in vitro.
1993	The U.S. Food and Drug Administration (FDA) announces its finding that genetically modified foods are not "inherently dangerous" and not in need of regulation. The following year, the FDA approves the first genetically modified whole food crop, Calgene's Flavr Savr tomato.
1996	The genomes of *Saccharomyces cerevisiae* (baker's yeast), with 12 million base pairs, and of ancient archaea cells, which live near thermal vents at the ocean bottom, advance biologists' understanding of the evolution of life.
2000	Researchers complete the full genomic sequence for the model flowering plant *Arabidopsis thaliana.*
2001	Researchers complete the genomic sequence for rice, *Oryza sativa*.

products could help more than a billion people who suffer from chronic iron deficiency.

Novel Products

Novel products include those not traditionally associated with plants and are limited only by imagination and currently available techniques. These include the production of plastics, vaccines, antibodies, human blood proteins, and new pharmaceuticals. One project has involved the production of hepatitis B vaccine in transgenic tomatoes. This project, which underwent clinical trials in the late 1990's, has the potential to provide a simple and inexpensive means of vaccinating people against hepatitis B. By oral administration of tomato juice containing the vaccine protein, humans are thought to develop an immune response that may protect them from infection by the hepatitis B virus. Hepatitis B is epidemic in Asia and increasing at an alarming rate in the rest of the world. The disease ultimately causes liver disease, cancer, and death in millions of infected people.

Plant Tissue Cultures

Central to plant biotechnology is the use of in vitro methods. Researchers use *plant tissue cultures*, for example, to grow plant cells on sterile nutrient media. Countless recipes for these nutrient media exist. The choice of which one to use is based on the plant species and the tissue type to be grown. All such media contain at least some of the important nutitional elements, such as nitrogen, potassium, calcium, magnesium, sulfur, phosphorus, iron, boron, manganese, zinc, iodine, molybdenum, copper, and cobalt, usually in the form of inorganic salts or as metal chelates, and an organic energy source, such as sucrose. The media may also contain vitamins, hormones, and other ingredients, depending on the intended use.

To initiate plant tissue culture, a piece of a living plant is excised and disinfected using a chemical disinfectant. This piece of plant tissue, called an *explant*, is placed on a sterile plant tissue culture medium to grow. Many plant tissues may be used to obtain explants for plant tissue culture, including those from leaves, petioles, shoots, tubers, roots, and meristematic regions. When an explant is placed in the sterile tissue culture medium, cells that are not terminally differentiated will grow and divide. If plant hormones are included in the recipe, the plant cells can be coaxed to develop into different types of tissues or organs. By using a succession of media containing different hormones, it is possible to regenerate whole plants from single cells. The choice of tissue used for the explant and the choice of hormones included in the tissue culture medium depend on the desired result.

Micropropagation

Micropropagation, another biotechnology technique, is the production of many clonal plants using tissue culture methods. By means of micropropagation, it is possible to generate many thousands of plant clones using tissue explants obtained from a single parent plant. The main advantage to micropropagation is the potential of producing thousands of exact copies of a plant with desirable traits. Micropropagation is especially important for rare plants, genetically engineered plants, and plants that have sexual reproductive problems. Many plant species are now routinely propagated by micropropagation methods, including orchids, ferns, many flowering ornamentals, and vegetable plants.

Steps in Genetic Engineering

The first genetically engineered plants, tobacco plants, were reported in the scientific literature in 1984. Since 1984 there have been thousands of genetically engineered plants produced in laboratories worldwide. The process of genetically engineering a plant involves several key steps:

- isolating the genetic sequence (gene) to be placed from its biological source
- placing the gene in an appropriate vehicle to facilitate insertion into plant cells
- inserting the gene into the plant in a process known as *plant transformation*
- selecting the few plant cells that contain the new gene (transformed cells) out of all the plant cells in the explant
- multiplying the transformed cells in sterile tissue culture
- regenerating the transformed cells into a whole plant that can grow outside the tissue culture vessel

The gene or genes to be placed in the plant may be obtained from virtually any biological source:

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animals, bacteria, fungi, viruses, or other plants. Placing genes into an appropriate vehicle for transfer into a plant involves using various molecular biology techniques, such as restriction enzymes and ligation, to essentially "cut and paste" the gene or genes of interest into another DNA molecule, which serves as the transfer vehicle (vector).

Plant Transformation Methods

Currently *plant transformation* with foreign genes may be accomplished by several proven methods, including bacteria-mediated transfer, microparticle bombardment, electroporation, microinjection, sonication, and chemical treatment.

By far, the most often utilized method of plant transformation involves the use of naturally occuring plant pathogenic bacteria from the genus *Agrobacterium*. In nature, this bacterium infects plants and transfers some of its own bacterial DNA into the plant. Through the action of proteins produced by the bacteria, bacterial DNA is made to integrate permanently into the plant's own genomic DNA. Expression of the bacterial DNA in the plant causes the plant to produce unusual quantities of plant hormones and other compounds, called opines, which provide food for the bacteria. The unusual quantities of plant hormones around the infection site cause the plant cells to grow abnormally, producing characteristic tumors. Scientists have harnessed this pathogenic bacterium to insert genes into plants by deleting the bacterial genes that cause tumors in the plant and then inserting desirable genes in their place. When the modified *Agrobacterium* infects a plant, it transfers the desirable genes into the plant genome instead of causing tumors. The desirable genes become a permanent part of the plant genome, and expression of these genes in plant cells produces desirable products.

One major drawback of the *Agrobacterium* method is that insertion of bacterial DNA into the plant genome is essentially random. The gene may not be efficiently transcribed at its location, or the insertion of bacterial DNA may knock out an important plant gene by inserting in the middle of it—or both may occur. Therefore, the fact that a cell is genetically transformed does not guarantee that it will perform as desired.

Microparticle bombardment is the introduction of foreign DNA constructs into plant cells by attaching the DNA to small metal particles and blasting the particles into plant cells using either a compressed air gun or a gun powered by a 0.22 caliber gun cartridge. This is truly a "brute force" method of introducing DNA into a cell that inadvertently causes many lethal casualties among the bombarded plant cells. However, some plant cells blasted with the DNA-containing metal particles will recover and survive. The plant cells may express the DNA for only a short time (transient expression), because the DNA does not readily integrate into the plant genome, but occasionally the foreign DNA may spontaneously recombine into the plant genome and become permanent.

Other ways of introducing foreign DNA into plant cells include electroporation, microinjection, sonication, and chemical treatment. These methods are not used extensively, because they generally require the production of *protoplasts* (plant cells that lack their cell walls) from plant cells before transformation. To create protoplasts, the plant cell wall is removed by digestion with the enzymes cellulase and pectinase. Protoplasts are fragile structures, but the absence of a cell wall is desirable because it leaves only the plasma membrane as a barrier to foreign DNA entering a plant cell.

Electroporation uses very brief pulses of high-voltage electrical energy to create temporary holes in the plasma membrane through which the foreign DNA can pass. *Microinjection* involves physically injecting a small amount of DNA into a plant cell using a microscope and an extremely fine needle. *Sonication* uses ultrasonic waves to punch temporary holes in the plasma membrane; this method is therefore similar to electroporation. *Chemical treatment* involves the use of polyethylene glycol to render the plasma membrane permeable to foreign DNA.

All the transformation procedures produce only a few transformed cells out of the millions of cells in an explant, so selection of transformed cells is essential.

Selection of Transformed Plant Cells

Selecting the few transformed plant cells out of all the plant cells in an explant requires some advance planning. Most foreign DNA constructs introduced into a plant are designed and built to contain additional genes that function as selectable markers or reporter genes. *Selectable markers* include genes for resistance to antibiotics or herbicides. Plant cells containing and expressing these genes will be tolerant of antibiotics or herbicides added to the plant tissue culture media, while the nontransformed plant cells will be killed off. The surviving cells in the tissue culture media are mostly transformed.

Instead of selectable markers, *reporter genes* may be used. Reporter genes induce an easily observable trait to transformed plant cells that facilitates the physical isolation of these cells. Reporter genes include beta-glucuronidase, luciferase, and plant pigment genes. Beta-glucuronidase (commonly known as GUS) allows the plant cells expressing this gene to metabolize colorigenic substrates while nontransformed plant cells cannot. To use this test, researchers treat a small amount of plant tissue with the colorigenic chemical substrate. If the cell turns color (blue) it is known to be transformed and expressing the GUS gene. If the cell does not turn color, it probably is not transformed. Another reporter gene is luciferase, an enzyme isolated from fireflies. Luciferase makes plant cells glow in the presence of certain chemicals if the gene is present; hence, transformed cells glow, whereas nontransformed cells do not glow. Plant pigment genes, such as anthocyanin pigment genes, occur naturally in plants and produce pigments that impart color to flowers. Inclusion of these pigment genes as reporter genes will allow transformed plant cells to be selected by their color. Transformed cells have color, while nontransformed cells remain colorless. Both selectable markers and reporter genes allow selection of cells into which genes have been successfully inserted and are operating properly.

Regenerating Whole Transformed Plants

After successfully getting a gene construct into a plant cell and selecting the transformed cells, it is possible to get the plant cells to multiply in tissue culture. Also, by treating the plant cells with combinations of plant hormones, the cells are made to differentiate into various plant organs or whole plants.

For example, treating transformed plant cells with a high concentration of the plant hormone cytokinin causes shoots to develop. Transferring these shoots to another medium, one that is high in the plant hormone auxin, will cause roots to develop on the shoots. In this way a whole *transgenic plant* may be regenerated from transformed plant cells. Once a transformed plant is regenerated in tissue culture, the plant may be transferred to a climate-controlled greenhouse, where it can grow to maturity.

Future generations of transgenic plants may then be propagated sexually via seeds or asexually via vegetative propagation methods. Often transgenic plants must be grown in containment greenhouses to prevent accidental release into the environment. In such high-tech greenhouses, all factors contributing to optimal plant growth—lighting, temperature, humidity, nutrients, and other environmental conditions—are tightly controlled. Often hydroponic systems, which use a solution of plant nutrients as a growth medium in place of soil, are employed to control all aspects of plant nutrition.

Robert A. Sinnott

See also: Biotechnology; Cloning of plants; DNA: recombinant technology; Environmental biotechnology; Genetically modified bacteria; Genetically modified foods.

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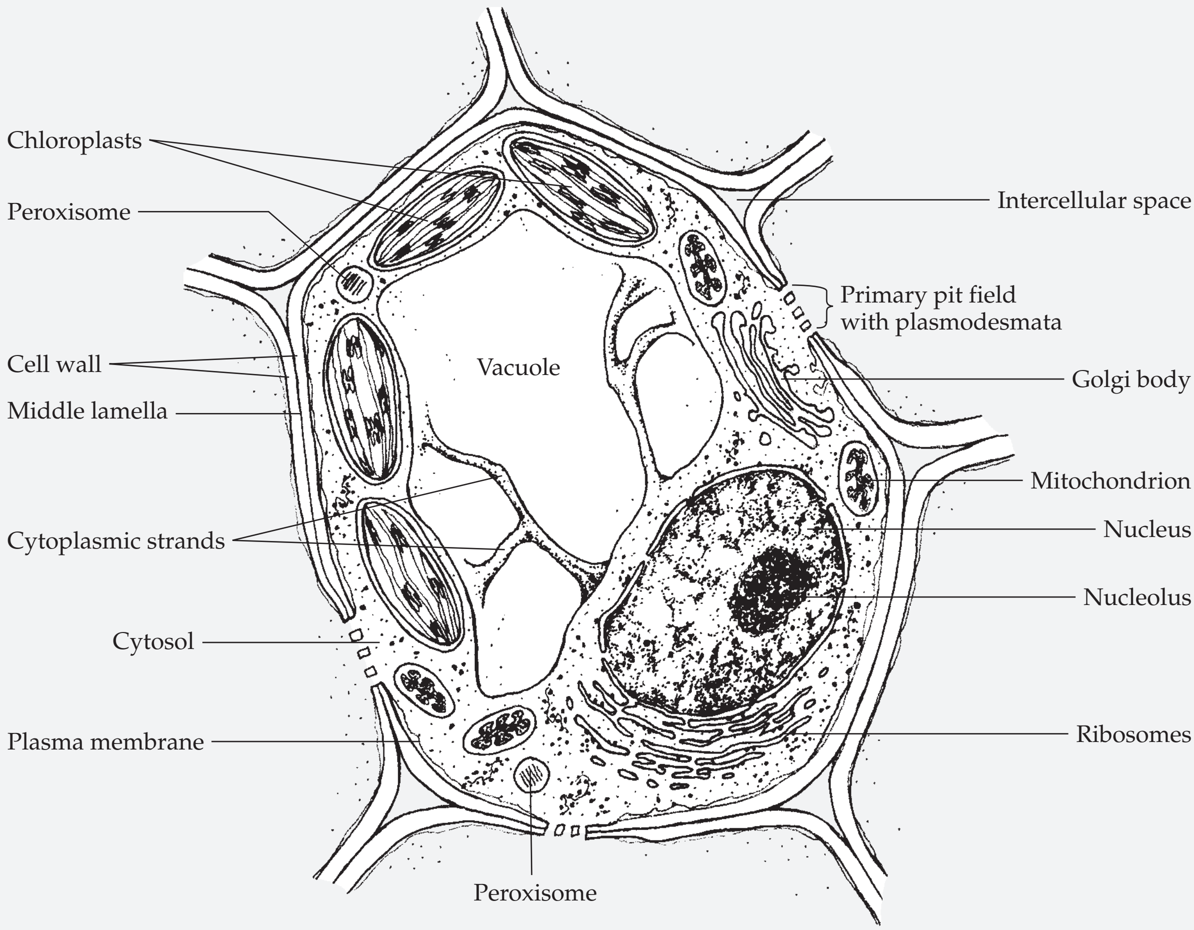
PLANT CELLS: MOLECULAR LEVEL

Categories: Cellular biology; physiology

Water, ions, salts, and gases all are types of inorganic molecules that are essential to cellular function. The chemical properties of water make it an ideal solvent and buffer for the chemistry that occurs inside cells. The capillary action that helps water travel up plant tissues from the roots is a direct consequence of the polarity of the water molecule.

The chemistry of life on earth is carbon and water chemistry. Water is the most abundant compound in living cells and makes up as much as 90 percent of the weight of most plant tissues. Many of the molecules that are part of larger macromolecules in cells are linked together chemically by *dehydration synthesis*, or the loss of water. These macromolecules are broken up into their compo-

Parts of a Plant Cell



nent units by the addition of a water molecule between the units, a process known as *hydrolysis*. The chemical properties of water make it an ideal solvent and buffer for the chemistry that occurs inside cells.

Because the electrons of the covalent bonds within the water molecule are more often orbiting the oxygen atom, the oxygen atom gains a slightly negative charge. The hydrogen atoms are slightly positive. This separation of charge across the water molecule is said to make it polar. Because of its polar nature, water is able to dissolve, or ionize, a variety of molecules. This gives water its buffering capacity.

Water molecules are attracted to one another because of this polarity. This weak attraction, which occurs in the form of hydrogen bonds, has great chemical consequences when many molecules of water are involved. Hydrogen bonding allows water to have surface tension. The capillary action that helps water travel up plant tissues from the roots is a direct consequence of the polarity of the water molecule. Water is also able to absorb heat without vaporizing (changing from a liquid to a gas state) quickly. Therefore, physiological temperatures can be maintained as water molecules absorb the heat from metabolic reactions.

Water, ions, salts, and gases all are types of *inorganic molecules* that are essential to cellular function. Inorganic molecules are chemical molecules that do not contain carbon. The remainder of the molecules within cells are built around the unique properties of the carbon atom and are called organic molecules.

Organic Macromolecules

There are four major classes of organic molecules in cells: *carbohydrates*, *lipids*, *nucleic acids*, and *proteins*. All of these molecules contain carbon backbones, and almost all of them contain oxygen and hydrogen as well as other elements. Some or all of the members of each class of organic molecules occur as very large molecules, called macromolecules, that are polymers of smaller molecules joined together by covalent bonds. For example, starch and cellulose are carbohydrate polymers of simpler carbohydrates called sugars. Likewise, fats and oils are lipid polymers composed of smaller lipids called fatty acids and the sugar alcohol called glycerol.

Carbohydrates

Carbohydrates are molecules that consist of primarily carbon, hydrogen, and oxygen atoms. Carbohydrates are the primary source of stored energy in most living organisms. They can also serve as structural molecules in cell walls and as markers on some cell membranes, identifying different types of cells.

Simple sugars, or *monosaccharides*, are sugars that are small molecules composed of a chain of covalently bonded carbon atoms with associated hydrogen and oxygen atoms. These molecules always have a ratio of one carbon atom to two hydrogen atoms to one oxygen atom (CH_2O). The monosaccharide glucose is the primary sugar produced from simpler sugars made in photosynthesis.

When two simple sugars are covalently linked together, they form a *disaccharide*. In plants, the disaccharide sucrose, which is composed of one fructose molecule and one glucose molecule, is the most common sugar. Sucrose is the same thing as so-called table sugar, which is harvested from sugar cane or sugar beets.

Many sugars can be linked together to form a carbohydrate polymer, or *polysaccharide*. Starch is composed of many glucose molecules linked together and is the major form of carbohydrate storage in plants. When energy is required, the individual sugars of the polysaccharides are hydrolyzed (broken down to simpler molecules), and the glucose that is released is used by the mitochondria to generate energy. Polysaccharides are also important structural molecules in plants. The most abundant polysaccharide in nature is cellulose, another polymer of glucose and a major component of plant cell walls.

Lipids

Lipids are diverse group of unrelated molecules which includes fats, oils, steroids and sterols, waxes, and other water-insoluble molecules. Lipids are characterized by their hydrophobic, or "water-fearing," chemical behavior, which is what makes them insoluble in water. Unlike other molecules that ionize and are dissolved by water, lipid molecules are nonpolar. They are repelled by the polar nature of water and tend to aggregate in aqueous solutions. Lipids also are used to store energy and are especially abundant in seeds because lipids contain more energy by weight than carbohydrates.

Examples of lipids commonly found in biological systems include fats and oils that are storage molecules known as *triglycerides*. A triglyceride consists of glycerol (a three-carbon molecule) and three fatty acid molecules, long-chain hydrocarbon molecules that are attached to each of the three glycerol-carbon atoms by ester linkages.

The long chain of carbon atoms of the fatty acid can be saturated or unsaturated with respect to hydrogen content. *Saturated fatty acids* contain as many hydrogen atoms as allowed bonded to each carbon atom. Saturated fats tend to be solid at room temperature and include substances such as butter and lard. *Unsaturated fatty acids* do not have the maximum number of hydrogen atoms because some of the carbon atoms form double bonds with adjacent carbon atoms in the chain. Unsaturated fats tend to be liquid at room temperature and include substances such as corn oil and olive oil.

Plants have many lipids that are unique to them. For instance, cutin and suberin are two lipid polymers that form structural components of many plant cell walls. These two molecules form a meshwork that secures another type of lipid polymer found in plants, wax. *Waxes* are long-chain lipid compounds that are integrated into the cutin and suberin meshwork and are important in preventing water loss for plants. Waxes give apple peels their characteristic shiny appearance.

Phospholipids are a type of lipid molecule that is found in all living organisms. They are structurally similar to triglycerides, except instead of having three fatty acids attached to glycerol, they have only two. Replacing the third fatty acid is a charged phosphate group. This unique structure results in one end of the molecule being hydrophilic (the phosphate end, often called the head) and the other being hydrophobic (the end with the two fatty acids, often called the tail). Consequently, phospholipids will spontaneously form an oily layer at the water surface, orienting their charged phosphate heads toward the water and their fatty acid tails away from the water and toward the air. This is the basis for the phospholipid bilayer structure that underlies the formation of all cellular membranes. In the case of a lipid bilayer, because there is water on both sides, the two layers are tail to tail, with their heads oriented to the inside and outside of the membrane, where they come into contact with water.

Nucleic Acids

The information that directs all cellular activity is contained within the chemical structure of the *nucleic acids*. Nucleic acids are polymers of smaller molecules called *nucleotides*. Nucleotides, in turn, are composed of three types of covalently linked molecules: a ribose sugar, a phosphate group, and a nitrogen-containing base. The two major nucleotides that are found in cells are *deoxyribonucleic acid* (DNA) and *ribonucleic acid* (RNA).

DNA contains the genetic information that directs the development and activity of the organism. In eukaryotic cells DNA resides in the nucleus in linear molecules of repeating nucleotide units, although there are circular molecules of DNA found in the mitochondria and chloroplasts of eukaryotic cells. DNA nucleotides are composed of a five-carbon deoxyribose sugar, a phosphate group, and one of four possible bases: adenine (A), thymine (T), cytosine (C), and guanine (G). The information of the DNA molecule is found in the sequence of the nitrogenous bases along its length. Any region of DNA that directs a cellular function or encodes another molecule is called a *gene*. Not all DNA regions encode proteins. Some regions encode the instructions for RNA molecules that are used as catalysts and for protein synthesis reactions. Some genes are regulatory, controlling the time and place where certain genes are expressed. In many eukaryotes, genes only account for 10 percent of the DNA. Although some of the remaining 90 percent carries various structural functions, most of it is of uncertain function.

In 1953 Francis Crick and James Watson constructed a molecular structure for the DNA molecule, relying heavily on the experimental data generated by Rosalind Franklin. The structure they proposed, which has since been supported by additional experimental data, was that of a *double helix*. The DNA molecule can be envisioned as a ladder. The sugars and phosphates of the nucleotides alternate with each other to form the backbone, the outside vertical support, and the bases form the individual rungs of the ladder. The ladder is twisted to create a helical structure. DNA can exist as single strands and in other confirmations in the cell, but the "B-form" of the DNA double helix is the most common form in the cell.

RNA molecules are also polymers of nucleotides, but the nucleotides of the RNA molecule differ slightly from those of the DNA molecule. RNA nucleotides contain a five-carbon ribose sugar, a phosphate group, and one of four bases. Three of the four bases are the same as found in DNA: adenine, guanine, and cytosine. Instead of thymine, RNA uses the base uracil. RNA bases can pair in essentially the same way as DNA bases, but most often RNA exists as single-stranded molecules in cells. These long strands of RNA can often pair with other bases in short regions, causing the RNA to fold up into highly complex, three-dimensional structures important for RNA function.

RNA is found throughout cells. Messenger RNA (mRNA) is made by the cell using the DNA sequence in genes as a template for making a complementary strand of RNA in a process called transcription. In After being transcribed and modified in certain complex ways, most mRNA is transported to the cytoplasm where it is used to direct the synthesis of proteins. Ribosomal RNA (rRNA) is a major component of ribosomes, which are responsible for coordinating protein synthesis, along with transfer RNA (tRNA). Some RNA molecules, like protein molecules, can also catalyze chemical reactions. Catalytic RNA molecules are called *ribozymes*, and they play roles in gene expression and protein synthesis.

Single nucleotides and compounds that are made from them are involved in many cellular processes. The universal unit of "energy currency" in the cell is *adenosine triphosphate* (ATP). Guanosine triphosphate (GTP) is a molecule that is involved in relaying signals received at the cell membrane to the nucleus of the cell. Compounds, such as NADH and NADPH, that are involved in metabolic reactions in the mitochondria and in energy capture reactions in the chloroplasts also contain nucleotides.

Proteins

Protein molecules are large, complex molecules with a huge variety of structures and functions within cells. Most chemical reactions in cells are catalyzed by proteins called *enzymes*. Proteins form the basis of the cytoskeleton of cells, providing structure and motility. Proteins are also essential for the communication between cells and within cells. In plants, the largest concentration of proteins can be found in some seeds.

Proteins are polymers of nitrogen-containing molecules called *amino acids*. The amino acids are much simpler molecules than the nitrogenous bases found in nucleic acids. The same twenty amino acids is are used in the manufacture of proteins in the cells of all living organisms. An amino acid is built around a single carbon atom called the *alpha carbon*. Bonded to the alpha carbon are a hydrogen atom (H), a carboxyl group (COOH), and an amino group that contains nitrogen (NH_2). A specialized "R" group is attached at the last site. The R-groups are different for each of the twenty amino acids, and their chemical properties, such as charge, hydrophilic or hydrophobic nature, and size, dictate protein function and shape.

The order and number of amino acids that are linked together to form a protein are determined by the order of the codons in the DNA that encode that protein. The order and number of the amino acids in a protein is called the *primary structure*, and it ultimately determines the shape of the protein. Proteins can have *secondary structures* formed by hydrogen bonding between the peptide bonds that link the amino acids together. The two common secondary structures in proteins are the *alpha helix* and the *beta pleated sheet*. The amino acid chain (also called a peptide chain) can fold up on itself to form globular structures. This is known as *tertiary structure*. Tertiary structure is determined by the number and order of amino acids in the protein and is formed when molecules in the R-groups of the amino acids interact with one another. When two or more peptide chains interact to form a single functional molecule, the protein is said to have *quaternary structure*.

Michele Arduengo

See also: ATP and other energetic molecules; Calvin cycle; Carbohydrates; Cell-to-cell communication; Cell wall; Cells and diffusion; Chloroplast DNA; Chloroplasts and other plastids; Chromatin; Chromosomes; Cytoplasm; Cytoskeleton; Cytosol; DNA: historical overview; DNA in plants; DNA replication; Eukaryotic cells; Fluorescent staining of cytoskeletal elements; Gene regulation; Genetic code; Genetics: mutations; Glycolysis and fermentation; Hormones; Krebs cycle; Lipids; Liquid transport systems; Membrane structure; Metabolites: primary vs. secondary; Microbodies; Mitochondria; Mitochondrial DNA; Mitosis and meiosis; Molecular systematics; Nuclear envelope; Nucleic acids; Nucleolus; Nucleus; Nutrients; Oil bodies; Osmosis, simple diffusion, and facilitated diffusion; Oxidative phosphorylation; Peroxisomes; Pheromones; Plasma membranes; Prokaryotes; Proteins and amino acids; Ribosomes; RNA; Sugars; Vacuoles; Vesicle-mediated transport; Viruses and viroids.

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PLANT DOMESTICATION AND BREEDING

Categories: Agriculture; economic botany and plant uses

Plant domestication and breeding are the processes by which wild plants are intentionally raised to meet human food, fiber, shelter, medicinal, or aesthetic needs.

No one knows exactly when the first crop was cultivated, but most authorities believe that it occurred at some time between eight and ten thousand years ago. For centuries prior to that time, humans had known that some wild plants and plant parts (such as fruits, leaves, and roots) were edible. These plants appeared periodically (usually annually) and randomly throughout a given region. Eventually humans discovered that these wild plants grew from seeds and that the seeds from certain wild plants could be collected, planted, and later gathered for food. This most likely occurred at about the same time in both the Sumerian region between the Tigris and Euphrates Rivers and in Mexico and Central America. While the earliest attempts at domesticating plants were primarily to supplement the food supply provided by hunting and gathering, people soon improved their ability to domesticate and breed plants to the point that they could depend on an annual supply of food. This food supply allowed the development of permanent settlements.

Early Crop Domestication

By six thousand years ago, agriculture was firmly established in Asia, India, Mesopotamia, Egypt, Mexico, Central America, and South America. Before recorded history, these areas had domesticated some of the world's most important food (corn, rice, and wheat) and *fiber* (cotton, flax, and hemp) crops. The place of origin of wheat is unknown, but many authorities believe that it may have grown wild in the Tigris and Euphrates Valleys and spread from there to the rest of the Old World. Wheat was grown by Stone Age Europeans and was reportedly produced in China as far back as 2700 B.C.E. Wheat is now the major staple for about 35 percent of the people of the world. The earliest traces of the human utilization of corn date back to about 5200 B.C.E. It was probably first cultivated in the high plateau region of central or southern Mexico and represented the basic food plant of all pre-Columbian advanced cultures and civilizations, including the Inca of South America and the Maya of Central America.

Botanists believe that rice originated in Southeast Asia. Rice was being cultivated in India as early as 3000 B.C.E. and spread from there throughout Asia and Malaysia. Today rice is one of the world's most important cereal grains and is the principal food crop of almost half of the world's people. Hemp, most likely the first plant cultivated for its fiber, was cultivated for the purpose of making cloth in China as early as the twenty-eighth century B.C.E. It was used as the cordage or rope on almost all ancient sailing vessels. Linen, made from flax, is one of the oldest fabrics. Traces of flax plants have been identified in archaeological sites dating back to the Stone Age, and flax was cultivated in Mesopotamia and Egypt five thousand years ago. Cotton has been known and highly valued by people throughout the world for more than three thousand years. From India, where a vigorous cotton industry began as early as 1500 B.C.E., the cultivation of cotton spread to Egypt and then to Spain and Italy. In the West Indies and South America, a different species of cotton was grown long before the Europeans arrived. Other important plants that have been under domestic cultivation since antiquity include dates, figs, olives, onions, grapes, bananas, lemons, cucumbers, lentils, garlic, lettuce, mint, radishes, and various melons.

Modern Plant Breeding

Genetic variability is prevalent in plants and other organisms that reproduce sexually and thereby produce spontaneous mutants. Throughout most of history, plant domestication and breeding were primarily based on the propagation of mutants. When a grower observed a plant with a potentially desirable *mutation* (such as a change that produced bigger fruit, brighter flowers, or increased insect resistance), the grower would collect seeds or take cuttings and produce additional plants with the desirable characteristic. Advances in the understanding of genetics in the early part of the twentieth century made it possible to breed some of the desirable characteristics resulting from mutation into plants that previously had lacked the characteristic.

The obvious advantages of producing plants with improved characteristics such as higher yield made plant breeding very desirable. As human populations continued to grow, there was a need to select and produce higher-yielding crops. The development and widespread use of new high-yield varieties of crop plants in the 1960's is often referred to as the *Green Revolution*. Basic information supplied by biological scientists allowed plant breeders to fuse a variety of characteristics from different plants to produce new, higher-yielding varieties of numerous crops, particularly seed grains.

When a plant characteristic is identified as desirable, it is studied both morphologically and biochemically to determine the mechanism of inheritance. If it is determined that the mechanism is transferable, attempts are made to incorporate the trait into the target plant. If the plants are closely related, traditional breeding techniques are used to crossbreed the plant with the desirable trait with the plant that lacks the characteristic. Although this process is often tedious, it is based on a fairly simple concept. Basically, pollen from one of the plant types is used to fertilize the other plant type. This

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process often requires specialized handling techniques to ensure that only the pollen from the plant with the desired characteristic is allowed to fertilize the eggs of the recipient plant.

Sometimes this process involves the use of bags or other materials to isolate the recipient flowers, which are then pollinated by hand. Another technique involves the introduction of a gene for male sterility into the recipient plant. In these cases, only pollen from another plant can be used to fertilize the egg. Once plants with the desirable characteristics are developed, the lines are often inbred to maintain large numbers of progeny with the desired traits. In many cases, inbred lines will lose vigor after several generations. When this occurs, two inbred lines may be crossed to produce hybrids. A majority of the hybrid offspring will still contain the desired characteristics but will be more vigorous.

Recombinant Technology

Until recently, the use of traditional breeding techniques between two very closely related species was the only means of transferring heritable characteristics from one to the other. The advent of *recombinant technologies* in the manipulation of deoxyribonucleic acid (DNA), however, made it possible to transfer genetic characteristics from any plant (or from any organism) to any other. The simplest method for accomplishing this transfer involves the use of a vector, usually a piece of circular DNA called a *plasmid*. The plasmid is removed from a microorganism such a bacterium and cut open by an enzyme called a restriction endonuclease, or restriction enzyme. A section of DNA from the plant donor cell that contains the gene for an identified desirable trait is cut from the donor cell DNA by the same restriction endonuclease. The section of plant donor cell DNA with the gene for the characteristic of interest is then combined with the open plasmid DNA, and the plasmid closes with the new gene as part of its structure. The recombinant plasmid (DNA from two sources) is placed back into the bacterium, where it will replicate and code for protein just as it did in the donor cell. The bacterium is then used as a vector to transfer the gene to another plant, where it will also be transcribed and translated.

D. R. Gossett

See also: Agricultural revolution; Agriculture: traditional; Agronomy; DNA: recombinant technology; Genetically modified foods; Green Revolution; High-yield crops; Hybridization; Plant fibers.

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PLANT FIBERS

Categories: Agriculture; economic botany and plant uses

Plants are the natural sources of many raw materials used to produce textiles, ropes, twine, and similar products.

The major fiber crops are cotton, flax, and hemp, although less important plants, such as ramie, jute, and sisal, are grown in small amounts. With a total annual production of more than 13 million tons, cotton is by far the most important fiber crop in the world. Because humans heavily rely on cotton for clothing and other textiles, it enters the daily lives of more people than any other product except salt.

Cotton

Cotton (*Gossypium*) fiber has been known and highly valued by people throughout the world for more than three thousand years. The early history of cotton is obscure. A vigorous cotton industry was present in India as early as 1500 B.C.E. From India, the cultivation of cotton spread to Egypt and then to Spain and Italy. In the New World, a different species of cotton was being grown in the West Indies and South America long before Europeans arrived. In the United States, cotton is grown from the East Coast to the West Coast in the nineteen southernmost states.

Botanically, cotton is in the mallow family, which also includes okra, hollyhock, hibiscus, and althea. Cotton has a taproot and branching stems. Flowers form at the tips of fruiting branches, and the ovary within each flower develops into a *boll*, which contains the *seed*, *fiber*, and *fuzz*. The fiber, most commonly referred to as *lint*, develops from epidermal cells in the seed coat of the cottonseed. The fiber reaches its maximum length in twenty to twenty-five days, and an additional twenty-five days are required for the fiber to thicken. Fiber length from 2.0 to 2.4 centimeters is referred to as short-staple cotton, and fiber length from 2.4 to 3.8 centimeters is called long-staple cotton.

The boll normally opens forty-five to sixty-five days after flowering. Cotton is native to tropical regions but has adapted to the humid, subtropical climate, where there are warm days (30 degrees Celsius), relatively warm nights, and a frost-free season of at least 200 to 210 days. There are eight species of cotton in the genus *Gossypium*, but only three species are of commercial importance. *Gossypium hirsutum*, also known as upland cotton, has a variable staple length and is produced primarily in North and Central America. *Gossypium barbadense*, a long-staple cotton, is primarily produced in South America and Africa. *Gossypium herbaceum* is a shorter-staple cotton native to India and eastern Asia.

Cotton is one of the more labor-intensive and expensive crops to produce. The most opportune time to plant cotton is at least two weeks after the last killing-frost date of the region. Prior to seeding, the field is prepared by plowing to a depth of 2.5 centimeters. Fertilizer, which is applied before seeding or at the same time the seeds are planted, is placed to the side and below the cotton seed. Once the seeds germinate and emerge from the soil, they often have to be thinned, and shortly afterward the producer begins to apply irrigation water as needed. After the plants have developed a stand, weed control becomes crucial. Weeds are controlled both by cultivation and herbicides.

Cotton plants are subject to invasion by a variety of insect pests, such as the boll worm and boll weevil; therefore considerable attention is given to insect control, typically using a number of different insecticides.

When the bolls ripen with mature fiber, the leaves of the plant are removed by the application of a chemical defoliant, and the fiber is harvested. Harvesting was once done almost entirely by hand, but today mechanical pickers harvest almost all the cotton produced in the United States. The picked cotton is ginned to remove the seed and compressed into bales. The bales are transported to a cotton mill, where the cotton is cleaned and spun into yarn, which is then woven into fabric. One pound of fiber is sufficient to produce up to 6 square yards of fabric.

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Flax

Flax (*Linum usitatissimum*) is the fiber used to make linen. While some flax is still grown for the purpose of producing this fabric, much of the flax, particularly that grown in the United States, is used to produce the flaxseed, from which linseed can be extracted. Linen made from flax is one of the oldest fabrics. Flax was cultivated in Mesopotamia and Egypt five thousand years ago, and traces of flax plants have been identified in archaeological sites dating back to the Stone Age. Flax was one of the first crops brought to North America by European settlers. Today, most of the flax produced in the United States is grown in the north-central states.

An annual plant, flax grows to a height of 60 to 100 centimeters and bears five-celled bolls or capsules with ten seeds each at the ends of fertile branches. Because the flax fiber is found in the stems from the ground to the lowest branches, varieties that are long-stemmed with little branching are grown for fiber production. Selection of quality, disease-free seed is essential in flax production. Flax fields are usually prepared in the fall to allow the soil to settle before planting. Flax is usually sown in early spring, two to three weeks prior to the date of the last killing frost of the region. Considerable attention is given to controlling weeds in a flax field. When the crop is harvested for fiber, the plants are pulled from the soil, the seeds are removed, and the flax straw is "retted" to separate the fiber from the woody part of the stem. When the straw is completely retted, it is dried and then broken apart to remove the 50-centimeter fibers which can be woven into fabrics.

Hemp

Hemp (*Cannabis sativa*), a term used to identify both the plant and the fiber it produces, is used to make the strongest and most durable commercial fibers available. Hemp was most likely the first plant cultivated for its fiber. It was cultivated for the purpose of making cloth in China as early as the twenty-eighth century B.C.E. It was also used as a drug by the ancient Persians as early as 1400 B.C.E. and was used as the cordage or rope on almost all ancient sailing vessels. Today hemp is commercially produced for heavy textiles in numerous countries, but less than 1,000 acres is devoted to commercial hemp production in the United States. Hemp production is problematic in the United States because it is illegal to grow *Cannabis sativa*, the source of marijuana.

Hemp is an annual plant in the mulberry family. The plant is dioecious, meaning that it has staminate or "male" flowers and pistillate or "female" flowers. It has a rigid stalk, which can reach a thickness of more than 2.5 centimeters in diameter, and a height of 5 meters. The plant has a hollow stem, and the bark or "bast" located outside the woody shell is used to make the bast fiber, which is then used to make hemp twine, ropes, and other textiles where strength and durability are desired.

Humid climates with moderate temperatures and a period of at least 120 frost-free days are necessary for hemp production. Unlike flax, hemp requires that the soil be plowed and thoroughly disked or harrowed prior to planting. The entire aboveground portion of the plant is harvested when the male plants are in full flower. After two to three days the plants are tied in bundles and set in shocks. Hemp fiber is retted and prepared for the mills in a manner very similar to that of flax except that heavier machines are used to handle the stronger hemp stalks.

Minor Crops

Ramie (*Boehmeria nivea*) is produced primarily in Asia and is used to make strong cloth, such as Chinese linen. Jute (*Corchorus capsularis*) is grown primarily in India and Pakistan and is used to manufacture burlap for bags and sacks. Sisal (*Agave sisalana*) is produced in East Africa and the West Indies and is used to make different types of cordage, such as baler twine.

D. R. Gossett

See also: Plant domestication and breeding; Textiles and fabrics.

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PLANT LIFE SPANS

Category: Reproduction and life cycles

The cycle of a plant's life, from seed germination to death, is referred to as its life span. Some plants have short life spans (less than one year), whereas others have life spans that are measured in centuries.

The longest-lived organisms are plants. For example, one bristlecone pine tree in eastern California is forty-nine hundred years old, and some creosote bushes, also in California, are estimated to be about twelve thousand years old. People have long recognized this variation in plant longevity, but the understanding of plant life spans improved greatly after research during the 1960's.

Types of Life Spans

The life span of an individual plant depends upon two factors. The first is the innate, genetically determined potential for longevity. The second is the effects of the environment, including soil and weather conditions, competing plants, disease-causing microbes, and herbivores.

Historically, people have classified the life spans of plants into three categories: *annuals*, *biennials*, and *perennials*. Annual plants live for up to one year. Biennials live for approximately two years. Perennials live for more than two years, often for several decades, even centuries.

While this categorization is useful in many ways, botanists have come to recognize that it is inaccurate, especially for plants that grow under natural conditions. Plant life histories are now classified mainly according to the number of times that each individual normally reproduces before it dies. Two main categories are recognized using this system: *monocarpic* plants and *polycarpic* plants. Monocarpic plants reproduce once before they die (*mono* means "one"; *carpic* means "fruits"). Polycarpic plants reproduce several or many times before they die (*poly* means "many"). Some botanists have defined a third group, the *paucicarpic* plants, that are intermediate between the two. Paucicarpic plants reproduce up to five times (*pauci* means "few").

Monocarpic Plants

Monocarpic plants have a general life history that involves four separate stages: germination, vegetative growth, reproduction, and death. The period of vegetative growth is very important to the monocarpic plant because during this time the plant manufactures and stores starch, which is rich in energy. When reproduction occurs, all that stored energy is devoted to producing flowers, fruits, and seeds; none is saved for the following year. The plant literally reproduces itself to death. Monocarpic plants vary greatly in their longevity, and it is possible to recognize several subcategories: *ephemerals*, annuals, *obligate biennials*, *facultative biennials*, and *long-lived monocarpic perennials*.

Ephemerals are plants that germinate, grow, reproduce, and die within a few weeks or months. They are typically found in environments in which conditions favor active plant growth for only a short period of time during the year, such as a desert. Desert ephemerals spend most of the year as seeds. When a heavy rainstorm occurs, the seeds germinate, and the new plants grow quickly and reproduce before the soil dries out. One species in the Sahara Desert can complete its life cycle in as little as ten days.

Annuals are plants that progress from germination to true seed within a six- to twelve-month period. Botanists recognize two major subcategories of annual plants. One is the summer annual, which germinates in the spring: The plant grows vegetatively during the summer and reproduces during the autumn. Examples of summer annuals include touch-me-not, common ragweed, and goosefoot. The second subcategory is the winter annual, in which germination occurs in the fall, vegetative growth occurs in the winter, and reproduction occurs in the spring. Daisy fleabane and winter wheat are examples of winter annuals.

Obligate biennials are monocarpic plants that germinate and grow vegetatively over the course of one year and throughout much of a second year. At the end of the second year, the plant always reproduces, sets seed, and dies (hence the designation "obligate"). During the 1960's and 1970's, some botanists doubted that obligate biennials existed in nature. Studies conducted during the 1970's and 1980's demonstrated that some plants, such as the white and yellow sweet clovers, are indeed obligate biennials.

Facultative biennials are monocarpic plants that have the ability to germinate, grow, and reproduce within two years. They can behave as biennials only when they grow under favorable conditions, with adequate moisture, light, and soil nutrients. More commonly, these plants grow under stressful conditions—either infertile soils or high competition. On such sites, they grow vegetatively for three, four, or even five years before they reproduce. Examples of facultative biennials include wild carrot, foxglove, burdock, teasel, and thistle.

Long-lived monocarpic perennials are able to live for many years or a few decades before they reproduce—once—and then die. Well-known examples include bamboo and plants from the arid southwestern United States, such as species of *Yucca* and the century plant *Agave*. These may reproduce only after they attain an age of sixty, eighty, or even one hundred years.

Polycarpic and Paucicarpic Plants

Paucicarpic and polycarpic plants normally reproduce more than once before they die. They are able to survive for at least one year following reproduction and hence are true perennials. Paucicarpic plants are short-lived herbs that may die after reproduction but more commonly live to reproduce two, three, or four times before dying. Paucicarpic plants are therefore intermediate between the true monocarps and the true polycarps. Examples include the common and English plantains, which are weeds found in lawns and fields throughout temperate North America and Europe.

True polycarpic plants survive to reproduce many times during their lifetimes and usually remain alive for at least ten years. Unlike the monocarps, polycarps do not expend all of their energy in reproduction. They save some of their energy and maintain part of the plant for the post-reproductive period. In seasonal climates, some of that energy must be directed to forming structures that allow the plant to survive the unfavorable season—a cold winter or a rainless period. These structures are called *perennating buds*, and they differ from plant to plant in their location relative to the ground surface. In some plants, called *cryptophytes* (the prefix *crypto* means "hidden"), the perennating buds are buried several centimeters under the ground. Examples of cryptophytes include milkweed, iris, and onion. Conversely, *hemicryptophytes* (*hemi* means "partial") have their perennating buds at the soil surface; a good example is the dandelion. Both cryptophytes and hemicryptophytes are herbaceous plants, never producing an aboveground woody structure.

Phanerophytes are polycarpic plants that do produce an aboveground woody structure—the perennating buds are borne above the ground surface. Some phanerophytes are shrubs that have several shoots. Examples of shrubs include lilac, blueberry,

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Extreme examples of seed longevity can be seen in species of lotus which have survived for more than fifteen hundred years.

hawthorn, hydrangea, rhododendron, and many dogwoods and willows. A second category of phanerophytes is the trees, which typically have a single woody stem emerging from the rootstock.

In theory, most species of polycarpic plants can live for decades, if not centuries, under ideal conditions. Many do not appear to have a maximum life span because they rejuvenate their tissues with each reproductive period, as in some polycarpic herbs or because the tissues that they accumulate do not put much of an added strain on the plant, as in many phanerophytes.

In nature, such polycarpic plants are not killed by old age. External factors such as *herbivory* (consumption by animals), fire, severe weather, disease, and competition from other plants contribute heavily to die-off among individuals. Other polycarpic plants form senescent tissue that hastens their death.

Potential and Real Life Spans

There have not been many studies of the longevity of most polycarpic plant species. The logistic problems involved and the consideration of mortality are more closely related to the size of the plant than to its age. Knowledge of the longevity in many species, particularly polycarpic herbs, is very poor.

Many herbs, such as buttercups and clovers, live for five to twenty-five years. Other herbs, such as blazing star, milkweed, and some goldenrods, may live for twenty-five to fifty years. Some shrubs, including blueberries and sumacs, can live for thirty to seventy years. Trees such as gray birch, pin cherry, and trembling aspen live for fifty to one hundred fifty years. Conifers such as hemlock, white pine, and red spruce have longevity in the range of two hundred to three hundred years, with some trees living five hundred to six hundred years. Hardwood trees such as sugar maple, white oak, sycamore, and beech can live for a similar duration. The oldest trees are the redwoods, at thirteen hundred years, and the bristlecone pines, at three thousand to five thousand years.

Most plants do not live to their maximal potential, succumbing to environmental factors. The average age that plants attain is well below the maximum life span. Beginning in the 1960's, ecologists began to examine the length of time that individual plants in a population remain alive. Although the actual patterns differ greatly from one species to another, plants typically suffer heavy mortality shortly after germination. For most species, fewer than 10 percent of newly emergent seedlings survive for two months. After that point, there are additional losses, although the death rate slows.

Some plants produce seeds that can remain dormant for many years. For example, seeds of many weed species, including monocarpic and polycarpic herbs, can remain dormant for seventy years in abandoned farm soil. Under experimental conditions, seeds of some of these species were found to be capable of germinating after one hundred years. Extreme examples of seed longevity can be seen in species of goosefoot and lotus, both of which have survived for more than fifteen hundred years. The variety of plant life cycles appears to be related to the earth's widely divergent habitats.

Kenneth M. Klemow

See also: Angiosperm life cycle; Dendrochronology; Growth and growth control; Hormones; Leaf abscission; Seeds.

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PLANT SCIENCE

Categories: Disciplines; history of plant science

Botany is the study of plants, stationary organisms with chlorophyll that are able to make their own food. Major categories of the plant kingdom include algae, mosses, ferns, and seed plants. Plant science includes many subdisciplines of both botanical (nonapplied science) and applied studies of plants, especially agriculture.

Taxonomy

One of the basic subdisciplines of plant science and life science in general, *taxonomy* (also known as *systematics*) is the study of relationships and organization of plant species. The great diversity within the plant kingdom requires a system by which plant species are named and classified. The modern system is a modification of the system first established in the eighteenth century by the Swedish botanist Carolus Linnaeus. Each species is placed into a hierarchy of groups that indicate its similarity and dissimilarity to other species. These categories (taxa) are from the most to the least inclusive: domain, kingdom, phylum, class, order, family, genus, species.

The species is the most natural and fundamental unit. Similar species are grouped into a genus, similar genera into a family, families into orders, orders into classes, classes into phyla, and phyla into the kingdoms typically studied in plant science courses: true plants, or *Plantae*, *Fungi*, and *Protista* (which include many unicellular organisms and algae). Each species is given a scientific name which includes the genus name followed by the species name. An example is the scientific name of the dwarf crested iris: *Iris cristata*.

Morphology

Morphology includes the study of the general structure of plants. Morphologists study the parts of a plant and how they are arranged and function. For example, when a seed of an angiosperm (flowering plant) germinates, the radicle of the seed embryo develops downward to form a root system. Growth in the length of the root occurs within the meristem (region of cell division). Branch roots form due to the activity of pericycle cells within the root. Some epidermal cells develop root hairs as extensions of the cells. The shoot system, which includes the stem and leaves, develops from the epicotyl of the seed embryo. Stems are often branched, allowing for the attachment of leaves in such a manner as to permit their maximum exposure to sunlight.

Also included in the study of morphology are the reproductive parts of plants. The pollination of flowers causes the ovary of the flower to mature into a fruit. At the same time, the one or more ovules inside the ovary become seeds.

Anatomy

Anatomy is the study of plant tissues. New plant cells are formed within meristems. There, the cells begin the process of becoming specialized (differentiated) for a particular function. As a result, three categories of plant tissues are formed: dermal, vascular, and ground.

Dermal tissues, which form protective coverings, include the epidermis, which covers all parts of a young plant, and others that develop as a plant matures. The periderm commonly replaces the epidermis and includes tissues found in bark.

Vascular tissues, derived from cambium cells within the meristem, conduct water and dissolved compounds within a plant. They include xylem and phloem.

Ground tissues are the less specialized tissues. Among their functions are storage, support, and photosynthesis. A common type is parynchema.

Cytology

Cytology is the study life at the cellular level; another name for this discipline is cell biology. Plant cells share many features with animal cells. Both forms of life are composed of eukaryotic cells, which have a distinct nucleus surrounded by a nuclear envelope which separates it from the cytoplasm. (By contrast, bacteria have nucleus-free cells, called prokaryotic cells.) Inside the nucleus is chromatin, which becomes organized into chromosomes as a cell divides. Chromosomes are composed of functional units called genes, which serve as the control center of the cell. Genes are composed of nucleoprotein. The nucleus also contains a nucleolus.

The cytoplasm is differentiated into numerous organelles, each specializing in a particular activity. Among those which plant cells share with animal cells are mitochondria (which conduct cellular respiration), ribosomes (which conduct protein synthesis), endoplasmic reticulum (for strengthening), Golgi apparatus (for packaging), and a plasma membrane (which functions as the cell's outer boundary). Not found in animal cells are chloroplasts (which conduct photosynthesis). Surrounding each plant cell are several layers of compounds (especially cellulose) that form the cell wall.

Physiology

Physiology is the study of the various functions performed in and by living organisms. Physiological processes of plants include the flow of energy, movement of solutes, and control by hormones. Chemical reactions are mediated (their rate is controlled) by enzymes.

For example, those studying plant physiology are concerned with the way that plants trap light energy as light is absorbed by chlorophyll. As a result of a series of chemical reactions, glucose, a six-carbon carbohydrate, is formed (preceding glucose are molecules of PGAL, a three-carbon sugar, which pair to form glucose). The glucose may be oxidized within the same cell or within another cell of the same plant (or utilized by an animal). This oxidation process produces adenosine triphosphate (ATP). As this compound is converted to adenosine diphosphate (ADP), energy is released, allowing organisms to perform other essential energy-requiring life activities.

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Plant physiologist would also be concerned with the transport of nutrients and water throughout a plant. By means of their roots, plants absorb water and dissolved materials from the soil, after which they are conducted upward, by means of xylem tissue, to all parts of the plant. This upward movement is called transpiration. The glucose formed in leaves is dissolved in water and transported, by means of phloem tissue, to all parts of the plant. This movement, called translocation, is commonly downward, but also may be upward. By these processes, water, minerals, and sugars are transported to all parts of a plant.

Another area of concern for plant physiologists is the function of plant hormones (phytohormones); in fact, those specializing in this area have their own discipline, *endocrinology*. Phytohormones are compounds produced within a plant. They are transported to other parts of plant, where they regulate growth and development. Early in the twentieth century, auxin was the first phytohormone to be discovered. It promotes growth by causing cells to elongate but was found also to inhibit growth of lateral buds. Gibberellins, a second group of hormones, also stimulate growth by causing cell elongation. Among their activities is the promotion of seed germination. Cytokinins are abundant in dividing tissues, where they stimulate cell division. Abscisic acid is a growth-inhibiting hormone that maintains dormancy in buds and fruits and also is associated with the falling of leaves in autumn. Ethylene causes fruits to ripen. Several hormones are used in agriculture for increasing growth rates of crops.

Genetics

Genetics, the study of heredity and the mechanisms that control it, is an outgrowth of the studies of Gregor Mendel. In the 1860's, he performed experiments with garden peas which resulted in a new way of explaining how traits are passed from generation to generation. Mendel's ideas were revived in 1900 as other European investigators confirmed his basic tenets. Heredity is due to discrete hereditary particles which soon came to be called genes, which are located on located on paired chromosomes. The application of the principles of genetics, begun in the first few decades of the twentieth century, has resulted in the development of greatly improved varieties of crop plants.

Molecular Biology

Genetics today is in many ways the concern of another discipline of plant science, *molecular biology*. The basic chemical nature of genes and how they express themselves remained in question until the 1950's, when James Watson and Francis Crick developed the double-helix model of deoxyribonucleic acid (DNA), explaining how genes occur in great variety, replicate (duplicate) themselves, and produce phenotypes (observable traits). Today, genetics is largely concerned with studying the chemical reactions that control DNA replication. Many researchers are also at work mapping the genomes (identifying the genes responsible for expressed characteristics) of various organisms. In 2001, researchers completed a map of the genome of the model plant *Arabidopsis thaliana* as well as the more complex genome of the rice plant, *Oryza sativa*.

Molecular biology has many practical applications. A knowledge of the genetic control of cells has already resulted in new crop plants. The term "genetic engineering" indicates that plants can be designed for specific purposes.

Ecology

The early Greek scientist Theophrastus, in the third century B.C.E., recognized environmental effects on plants. Much later, naturalists documented the geographical distribution of plants as determined by various climatic factors. Such studies were the roots of the scientific discipline *ecology*, which emerged in the late nineteenth century. Plant ecologists of the early twentieth century were concerned largely with describing the nature and distribution of world plant communities and developing a "successional theory" as a means of understanding the dynamics of changing plant communities. Now, ecologists study plants as integral parts of ecosystems that also include animals and microorganisms. They are concerned with countering the threat of loss of species as a result of human activities such as pollution and habitat destruction.

Paleobotany

Fossils have long been recognized as remnants of plants and animals that lived and died many millennia ago. The animal fossil record was an important factor in the development of Charles Darwin's theory of evolution in the 1800's. *Paleobotany* as a subdiscipline can be traced to the efforts of Albert Seward of Cambridge University of England in the late nineteenth and early twentieth centuries. Studies of plant fossils have resulted in a clearer understanding of plant evolution.

Economic Botany

People have always relied on plants to provide basic necessities of life: food, shelter, and clothing.

Economic botany developed as a specialty within botany to acquaint botanists with plant uses. Topics considered in economic botany include plant domestication, food and beverage plants, essential oils, oils and waxes, latexes and resins, medicines, fibers, tannins and dyes, wood products, and ornamental plants.

Related Disciplines

Courses in botany and plant science often address organisms that are not, in the strict sense, plants but that nevertheless are appropriately studied in the same context. Hence, although *bacteria* differ from plants primarily because of their cells, which are prokaryotic (lacking a nucleus and most cytoplasmic organelles), they are often studied in botany courses. Bacteria are early and evolutionarily significant organisms. Some are closely related to the protists known as algae and therefore important in the study of photosynthesis.

Fungi, too, are often studied in the context of plant science. These are mostly multicellular filamentous eukaryotic organisms lacking chlorophyll. Because they do not make their own food but live in or on the food provided by plant and animal tissues, fungi are heterotrophs (rather than autotrophs, like plants, which make their own food through photosynthesis). In some ways, therefore, fungi are more similar to animals than they are to plants. Nevertheless, they are traditionally studied in the context of plant courses because they were once considered to be plants, given their lack of movement and other gross similarities. Their world significance parallels that of bacteria: They, too, are important as *decomposers*, returning nutrients and other elements to the environment. The study of fungi is *mycology*.

Protists are unicellular eukaryotes, forming one of the four kingdoms of *Eukarya*, the others being fungi, plants, and animals. Included among the protists are slime molds and protozoans which, lacking chlorophyll, are said to be heterotrophic protists, obtaining their food from other sources, generally other organisms. Also included are the algae, which are autotrophic eukaryotes—many using photosynthesis, like plants, to generate their own food. For this reason, protists are often studied in the context of plant science, and algae are almost always included in such studies. The study of algae is *phycology*.

Viruses, the study of which is *virology*, are noncellular entities that can reproduce only inside specific host cells. Not generally considered to be living, they are nevertheless important because of the infections they cause. To the extent that they cause infection in plants, they are important in the study of plant science, particularly *plant pathology*.

Thomas E. Hemmerly

See also: Agriculture: history and overview; Agronomy; Algae; Biotechnology; Botany; Cell theory; Cladistics; Dendrochronology; Ecology: history; Environmental biotechnology; Evolution: historical perspective; Fungi; Genetics: Mendelian; Genetics: post-Mendelian; History of plant science; Hormones; Hydroponics; Molecular systematics; Paleobotany; Paleoecology; Plant biotechnology; Population genetics; *Protista*; Systematics and taxonomy; Systematics: overview; Viruses and viroids.

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PLANT TISSUES

Categories: Anatomy; physiology

Plant tissues are the distinctive structural and functional units of a plant that carry out all its basic life functions, including growth, reproduction, support, metabolism, circulation, and protection from the environment.

The body plan of a plant is very different from that of most animals. Terrestrial plant bodies are anchored in a growing medium, which has an enormous influence over the form and behavior of plant tissues.

Growth and Protective Tissue

Meristematic tissues in plant bodies are responsible for the growth that results from an increase in cell number. In the meristems, individual cells divide to produce pairs of daughter cells which have the ability to divide further or to enlarge and differentiate. The meristems are located at the ends of branches and roots (shoot apical meristems and root apical meristems, respectively) and within the *cambia* of woody plants, which grow in girth. The shoot and root apical meristematic tissues produce cells that account for the lengthening of the shoots and roots.

The primary developmental tissues are in a region called the *zone of elongation*. These developmental tissues are distinguished from meristematic tissues by the larger size of their cells and by their locations. Three primary developmental tissues are produced by the shoot and root apical meristems. They are the *protoderm*, the *ground tissues*, and the *procambium*. As these primary developmental tissues mature, they will ultimately differentiate into the metabolically more active portions of the plant.

In a region called the *zone of maturation*, the cells begin to take on the characteristics of mature, functioning tissues. The protoderm differentiates to form the *epidermis*, a mature tissue protecting the surfaces of plant parts which do not have secondary vascular tissues. The epidermis is made of cells which have one side in contact with the environment (air, water, or soil). The other side is in contact with other cells in the plant body.

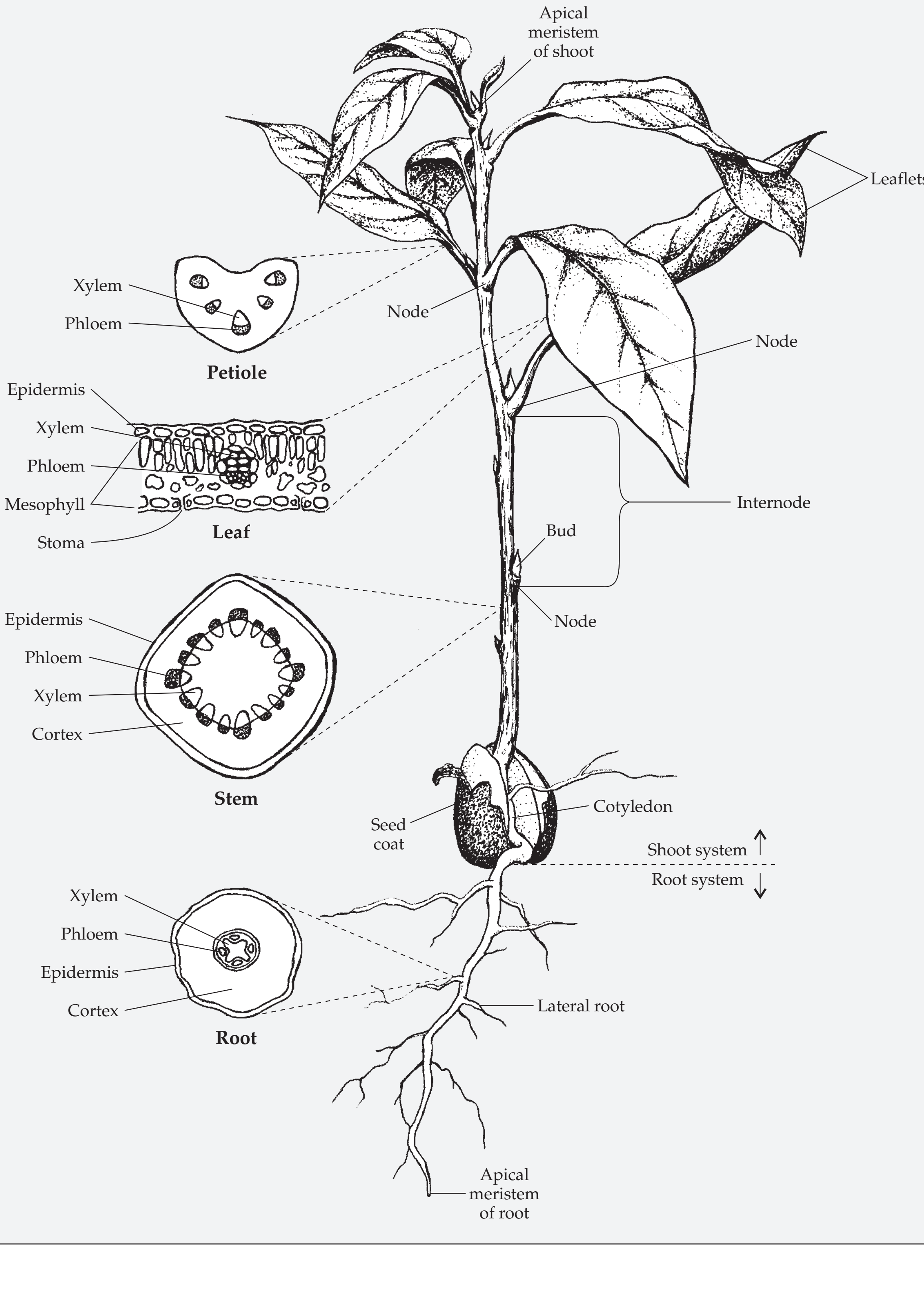
Epidermal tissue in contact with air is usually protected by a layer of wax called the *cuticle*. It may also be covered with hairs, water-filled cells, poison-filled barbs, or even digestive glands. These specialized structures provide protection from particular environmental conditions and may even serve as paths for the absorption of nutrients in the case of carnivorous plants.

The underlying tissues must have access to atmospheric gases for their metabolic activities. To accomplish this, the epidermal tissues are punctuated by pores which open and close (*stomata*) or are permanently open (*lenticels*). Epidermal tissues in contact with the ground require a different kind of protection. These tissues may secrete mucus, which protects growing underground structures. There are epidermal cells that fall off the plant body to provide a lubricating barrier between the rest of the plant and the soil. Finally, the epidermal tissues nearest the root tip may be covered with long subcellular hairs that contribute significantly to the root's ability to absorb water and minerals. Epidermal tissues of plant organs that normally grow in water are less likely to bear the specialized structures of epidermal tissues from aerial or subterranean parts. These cells are often more like parenchyma cells of ground tissues than they are like epidermal cells of subterranean or aerial structures.

Ground Tissues

The ground tissues, the second of the primary developmental tissues, differentiate in the zone of maturation to form tissues called *parenchyma*, *collenchyma*, or *sclerenchyma*. The parenchymous tissues are the primary site of cellular metabolism. The organelles of parenchyma cells in different parts of the plant vary so that they can accommodate differences in metabolic functions. Cells of leaf parenchyma and some stem parenchyma have large numbers of chloroplasts to carry out photosynthesis. Stem and root parenchyma cells have amyloplasts, organelles that store starch. *Chromoplasts* in the pa-

Parts of a Plant



Kimberly L. Dawson Kurnizki

renchyma of flower petals contribute to the color of the flower petals. Parenchyma cells producing large quantities of protein have more ribosomes than those specialized for starch storage. Reproductive parenchyma cells may have unusual nuclear characteristics that prevent these tissues from competing with the developing embryos for nutrients or space.

Parenchyma fill the inner parts of leaves, stems, and roots. These cells have large, water-filled *vacuoles*. The water pressure from these vacuoles provides much of the rigidity of the body of nonwoody plants. When a leaf is limp, its parenchyma cells are usually depleted of water. Many of the chemicals that give plants their unique tastes or pharmaceutical characteristics are produced and stored in parenchyma. For example, the bulk of a carrot root (especially outside the central core), the mass of a potato tuber (which is actually a unique form of stem), and much of a lettuce leaf are all made of parenchyma.

Collenchyma cells are similar to parenchyma cells in many ways. They use water pressure to provide support. However, they are normally found near the surface of stems and leaves. Collenchyma cells have a unique pattern of cell-wall thickening that allows expansion in diameter but not in length. This makes collenchyma especially suited to providing support for soft-bodied plant parts that have completed much of their longitudinal growth. Collenchyma cells rarely provide bulk to plant structures. Instead, they form thin sheets just below the epidermis and outside much of the parenchyma. Because collenchyma is thin, it has a smaller volume than parenchyma and contributes less to the metabolism of the plant organs. It may nevertheless support some of the photosynthesis of the plant, and it provides textures to the organs as well.

Sclerenchyma cells occur throughout the body of the plant and include three types of cells: elongated *fibers*; branched *sclereids*, resembling a three-dimensional jigsaw puzzle piece; and globular *stone cells*. All three cell types have heavy, secondary cell walls and have lost many organelles. Sclerenchyma is a type of differentiated tissue that functions when its cells are dead.

Fibers support plant organs in the same way as does collenchyma, but because the secondary cell walls of sclerenchyma cells resist longitudinal and latitudinal expansion, they are not common in growing tissues. Their rigidity helps to supply support even when tissues are water-stressed, but it also limits the potential for the organs to expand in girth or length. Fibers, sclereids, and stone cells all provide protection against predation. The gritty texture of a ripe pear, the shell of a nut, and the strings of a coconut husk are all composed of sclerenchyma cells and promote the wear and breakage of predators' teeth and other chewing structures.

Procambium

The procambium, the third of the primary developmental tissues, differentiates to form primary *xylem* and primary *phloem* as well as the vascular cambium. The *vascular cambium* produces cells that differentiate into secondary xylem and secondary phloem. It also regenerates the supply of cells in the vascular cambium.

An example of xylem is the woody tissue at the center of most trees. (Palm trees are a notable exception.) Smaller bundles of xylem are found in the roots, stems, and leaves of most plants, even when they are not woody. Xylem tissues are made of four cell types: fibers and parenchyma cells (which also occur in sclerenchyma and parenchyma) and xylem vessel elements and *tracheids* (which are found only in the xylem). These cells work in concert to move water upward through the plant. The xylem vessel elements and tracheids provide the actual channels for the movement, and the fibers serve largely as physical supporting structures.

The parenchyma cells are responsible for some lateral movement in the xylem tissues. These parenchyma cells also have the ability to revert to a meristematic condition, providing a mechanism for the xylem to replace damaged cells. Tracheids and vessels have unusual, patterned secondary cell walls that resist the physical stresses involved in moving xylem sap. The cell organelles are lost before the vessels and tracheids are functional. The sap moves through a channel where the body of the cell had been before it was lost. Xylem is another tissue that contains cell types that function when they are dead.

An example of phloem is the tissue on the inside of the bark of most trees (again, palm trees are an exception). Smaller bundles of phloem are found in the roots, stems, and leaves of most plants, even when they are not woody. Phloem tissues are made of fibers, parenchyma cells, *sieve tube elements*, and *companion cells*. These four cell types work in concert to move sugars, other organic molecules,

Plant Tissues

Tissue Type	*Location in Plant*	*Functions and Characteristics*
Meristems		
Apical meristems	Roots and shoot tips	Site of primary growth; these cells eventually differentiate into the plant's primary tissues: dermal, vascular, and ground.
Lateral meristems	Stems	Secondary growth of vascular and cork cambia, lateral budding and branching limited by apical dominance unless the apical meristem is cut as in pruning.
Dermal tissue (epidermis)	Outer layer	Retention and absorption of water and minerals, protection against herbivores, control of gas exchange. Includes stomata, trichomes, root hairs.
Vascular tissue		
Xylem	Throughout	Conducts water through plant. Contains two kinds of conducting cells: tracheids and vessel elements.
Phloem	Throughout	Transports dissolved organic materials throughout plant. Contains sieve cells, sieve-tube elements, other cells responsible for conducting nutrients and information.
Ground tissue		
Parenchyma cells	Throughout	Food and water storage, sites for metabolism (respiration, photosynthesis), healing.
Chlorenchyma cells	Throughout	Chloroplast-containing parenchyma cells specialized for photosynthesis.
Collenchyma cells	Beneath epidermis	Support growing regions of shoots; common in petioles, elongating stems, expanding leaves.
Sclerenchyma cells	Mature regions	Rigid, producing thick secondary walls; usually dead at maturity. Support and strengthen leaves, stems, roots. Two types: sclereids (short, compact, forming cores, seed coats, other tough, gritty tissue) and fibers (long, slender, occuring in bundles).

and some ions throughout the body of the plant.

The sieve tube elements (or *sieve cells*, in some plants) provide the actual channels for the movement. The fibers serve largely as physical supporting structures. The parenchyma cells are responsible for some lateral movement and also provide a mechanism to replace damaged cells. Sieve tube elements and sieve cells have unusual, perforated cell walls whose appearance indeed resembles a sieve. Many of the cell organelles are lost before the sieve tube elements and sieve cells are functional. The phloem sap moves through living cells, but they resemble no other cells in the plant.

The companion cells (which in some plants are called *albuminous cells*, to indicate a different developmental origin) are similar to parenchyma cells, but they provide substantial metabolic support to the sieve tube elements and sieve cells. These cells function together: The companion cells could live independently, while the sieve tube element could not, but the important function is carried out by the sieve tube element.

Most species that grow in girth are woody, and the wood of woody plants is composed almost entirely of secondary xylem. The bark of woody plants is made of phloem and corky layers. There are two principal cambia, the vascular cambium and the *cork cambium*. Both contribute to the increase in girth. The vascular cambial tissues produce the cells that will differentiate to form the secondary xylem and phloem of woody species. The cork cambium produces the corky cells on the outside of the bark.

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See also: Angiosperm cells and tissues; Flower structure; Growth and growth control; Leaf anatomy; Roots; Shoots; Stems; Wood.

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PLANTAE

Categories: *Plantae*; Taxonomic groups

Life on earth is dependent on the ability of plants to capture the sun's energy. Directly or indirectly, members of the green kingdom, Plantae, *provide food and shelter for nearly all other organisms, including humans. Plants also generate much of the earth's oxygen. The biosphere would not exist without plants.*

Most plants are multicellular, autotrophic organisms, that is, able to produce their own food from inorganic elements by converting water and carbon dioxide to sugar. Plants are sessile, stationed in one spot throughout their lives. Most plants have a complex life cycle called *alternation of generations* between diploid and haploid forms. The diploid generation, in which the plant body is made up of diploid cells, is called the *sporophyte*. The sporophyte produces haploid spores by meiosis.

Phyla of Kingdom *Plantae*

Phylum	*Common Name*	*Living Species*
Bryophytes (nonvascular plants)		
Anthocerotophyta	Hornworts	100
Bryophyta	Mosses	8,000
Hepatophyta	Liverworts	6,000
Seedless vascular plants		
Lycopophyta	Lycopods (Lycophytes)	1,200
Psilotophyta	Whiskferns	2 genera
Pterophyta	Ferns	12,000
Sphenophyta	Horsetails	15
Gymnosperms		
Coniferophyta	Conifers	550
Cycadophyta	Cycads	150-200
Ginkgophyta	Ginkgo	1
Gnetophyta	Gnetophytes	90
Angiosperms		
Anthophyta	Flowering plants	235,000

Source: Data on species are from Peter H. Raven et al., *Biology of Plants*, 6th ed. (New York: W. H. Freeman/Worth, 1999).

These haploid spores then grow mitotically to produce the haploid generation, called the *gametophyte*, which produces haploid gametes. Gametes fuse to form a diploid zygote, a fertilized reproductive cell that marks the beginning of a new sporophyte generation.

Various methods may be used to group members of *Plantae*, which comprises about 300,000 species. Based upon where plants live, they can be divided into terrestrial (land) and aquatic plants. Members of these two groups vary widely in their size, body structure, and level of complexity as a result of their interactions with their environments. Plants that live in water usually lack true roots, stems, and leaves as well as complex reproductive structures, such as flowers. Because they are surrounded by water, aquatic plants also lack the rigid supporting substances required by terrestrial plants. Terrestrial plants are more complex and may be broadly grouped into *vascular* (plants with vessels) and *nonvascular* (plants without vessels). Vascular plants are divided into various phyla, based upon their adaptive features and complexity of structure.

Algae vs. *Plantae*

Those plants known as algae are not members of kingdom *Plantae* but instead are primarily members of another group of eukaryotic life, *Protista*, which also produce their own food by photosynthesis. Algal pigments are red or brown, absorbing the green, violet, and blue lights that most readily penetrate the water. The combination of various pigments with chlorophyll resulted in the distinctive coloration of algae of the three phyla: red algae, brown algae, and green algae.

Within the kingdom *Protista*, three main algal phyla exist. Red algae (phylum *Rhodophyta*) are multicellular with red pigment (phycobilins) masking their green chlorophyll. Brown algae (phylum *Phaeophyta*) are multicellular and include the largest and most complex of the marine algae. Green algae (phylum *Chlorophyta*) are mostly multicellular inhabitants of freshwater environments, with about seven thousand species. The algae are thought to be primitive evolutionary precursors to the species which now make up the kingdom *Plantae*.

Transition from Water to Land

The move from water to land requires adaptations and some new features. The advantages to life on land seem obvious, with plentiful access to carbon dioxide and sunlight, reduced competition, fewer predators, and increased nutrient concentrations. The challenges are also plentiful: The supportive buoyancy of water is missing, and the air tends to dry things out.

Conditions on land favored the evolution of structures that support the plant body, vessels that transport water and nutrients throughout the body, and structures that conserve water. Adaptations to dry land called conducting vessels (collectively known as the vascular system) emerged to transport water and minerals as well as products of photosynthesis. Roots or rootlike structures evolved to help anchor the plant and absorb nutrients and water from the soil. A stiffening substance called lignin, made up of rigid polymer, enables plants to stand in wind, hence exposing maximal surface area to sunlight. Numerous small pores called stomata in the leaves and stems open to allow gas exchange and close to conserve water when necessary. A waxy cuticle covering of the surfaces of leaves and stems also reduces the loss of water.

Based upon their structure, complexity, and distribution over the globe, land plants can be classified into three phyla of *bryophytes* and nine phyla of vascular plants, which include *seedless plants*, *gymnosperms*, and *angiosperms*.

Bryophytes

Three phyla of plants—the liverworts, hornworts, and mosses—have been commonly known as bryophytes. The sixteen thousand species of bryophytes are among the least complex terrestrial plants. They are the plant equivalent of amphibians. Although they have rootlike anchoring structures (rhizoids), they lack true roots, leaves, and stems. They are also nonvascular, lacking well-developed structures for conducting water and nutrients. Because they must rely upon slow diffusion or poorly developed tissues for distribution of water and nutrients, their body size is limited. Most bryophytes are less than 1 inch (2.5 centimeters) tall.

The liverworts, phylum *Hepatophyta*, comprise six thousand species of small, inconspicuous plants forming large colonies in moist, shaded soil or rocks, tree trunks, or branches. Due to the liver-shaped gametophyte in some genera and the fiction that these plants might be useful in treating liver-related diseases, they were named liverworts many centuries ago. Liverworts are the simplest of all living land plants, lacking cuticle, stomata, and vascular tissue.

The hornworts, phylum *Anthocerophyta*, are a small phylum of plants consisting of about one hundred species. By appearance, many species of hornworts have a remarkable resemblance to green algae. Hornworts, however, have stomata, an important structure for land plants. Like liverworts, hornworts lack specialized conducting tissue.

The mosses, phylum *Bryophyta*, constitute a diverse group of some ninety-five hundred species of small plants. Many species have both stomata and specialized conducting tissue, resembling the remaining phyla of land plants. Mosses usually thrive in relatively moist areas, where a variety of species can be found. Some mosses are used to monitor air pollution because of their acute sensitivity to air pollutants such as sulfur dioxide. There are three classes of mosses: *Bryidae* (the "true" mosses), *Sphagnidae* (the peat mosses), and *Andreaeidae* (the granite mosses), each with distinctive features.

Seedless Vascular Plants

The overall pattern of plant diversification may be explained in terms of the successive rise to dominance of each of four major plant groups. Early vascular plants, including *Rhyniophyta*, *Zosterophyllophyta*, and *Trimerophyta*, were primitive in morphology yet dominant during a period from about 420 million to 370 million years ago. Ferns, lycophytes, sphenophytes, and progymnosperms were dominant from about 380 million to 290 million years ago. Seed plants arose about 360 million years ago, with gymnosperms dominating the globe until 100 million years ago. Finally, the angiosperms, or flowering plants (phylum *Anthophyta*) appeared about 127 million years ago and have been the most dominant and diverse group for the past 100 million years.

The seedless vascular plants dominated the landscape during the Carboniferous period. They are the primary source of coal, which was formed through gradual transformation of plant bodies under high pressure and heat. The three dominant phyla—the *Rhyniophyta*, *Zosterophyllophyta*, and *Trimerophyta*—had become extinct by about 360 million years ago. The modern representatives of seedless vascular plants have become reduced in size and importance. The landscape once dominated by seedless plants has largely been replaced by the more versatile seed plants. Five phyla of seedless plants have living representatives: *Psilotophyta*, *Lycophyta*, *Sphenophyta*, *Pterophyta*, and *Progymnospermophyta*.

Psilotophytes

Commonly called the whiskferns, the phylum *Psilotophyta* includes two living genera, *Psilotum* and *Tmesipteris*. Both are very simple plants. *Psilotum* is widely known as a greenhouse weed that prefers tropical and subtropical habitats. In the United States, it is found in Arizona, Florida, Hawaii, Louisiana, Puerto Rico, and Texas. *Tmesipteris* is restricted to South Pacific regions such as Australia, New Caledonia, and New Zealand.

Psilotum is unique among vascular plants in that it lacks both true roots and leaves. The underground portion of *Psilotum* forms a system of rhizomes with many rhizoids that are a result of a symbiotic relationship between fungi and *Psilotum*. *Psilotum* is homosporous, meaning the male and female gametophytes are produced through the germination of the spores of same origin. *Psilotum* sperm require water to swim to and fertilize the egg.

Tmesipteris grows as an epiphyte on tree ferns and other plants and in rock crevices. The leaflike appendages of *Tmesipteris* are larger than those of *Psilotum*. Otherwise, *Tmesipteris* is very similar to *Psilotum*.

Lycophytes

There are about one thousand living species of phylum *Lycophyta* that belong to three orders of ten to fifteen genera. At least three orders of *Lycophyta* have become extinct; these include small and large trees, the dominant plants of the coal-forming forest of the Carboniferous period. The three orders of living *Lycophyta* consist of herbs, each including a single family: *Lycopodiaceae*, *Selaginellaceae*, and *Isoetaceae*.

Lycopodiaceae are commonly known as club mosses. All except two genera of *Lycophyta* belong to this family. Most of the estimated four hundred species of *Lycopodiaceae* are tropical. They rarely form conspicuous elements in any plant community, except in some temperate forests where several species may form distinct mats on the forest floor. Because they are evergreen, they are most noticeable during winter months. *Lycopodiaceae* are homosporous and require water for fertilization. Among the genera that grow in the United States and Canada are *Huperzia* (the fir mosses, seven species), *Lycopodium* (tree club mosses, five species), *Diphasiastrum* (club mosses and ground pines, eleven species), and *Lycopodiella* (six species).

Selaginella is the only living genus of the family *Selaginellaceae*. Among its seven hundred species, most are tropical, growing in moist habitats. A few species occur in deserts, becoming dormant during the driest season. The well-known resurrection plant, *S. lepidophylla*, grows in Mexico, New Mexico, and Texas. *Selaginella* are heterosporous, having separate male and female gametophytes.

The only member of the family *Isoetaceae* is *Isoetes*, commonly known as quillwort. *Isoetes* may be aquatic or grow in pools that have alternate dry and wet seasons. *Isoetes* is also heterosporous. The unique feature of some species of *Isoetes* is their ability to acquire carbon dioxide for photosynthesis from soil where they grow rather than from the atmosphere. Their leaves have thick cuticles and lack stomata.

Horsetails

Only one genus, *Equisetum*, consisting of fifteen living species, makes up the phylum *Sphenophyta*. Members of this phylum are known as the horsetails, believed to be the oldest surviving plants on earth. They are widely distributed in moist or damp places, by streams, and along the edges of woods and roadsides. The leaves are reduced to tiny scales on the branches. The ribs are tough and strengthened with silicon deposits. Due to its abrasive texture, *Equisetum* was used in past times to scour pots, pans, and floors. Hence, they were also called "scouring rushes."

The roots of *Equisetum* are adventitious, emerging at the nodes of the rhizomes. The aerial stems of *Equisetum* arise from branching underground rhizomes. Although the plants may die back during the dry season, the rhizomes are perennial. *Equisetum* is homosporous. Its gametophytes are green and free-living, most being about the size of a pinhead. They become established mainly in mud that has recently been flooded and is rich in nutrients. The gametophytes, which reach sexual maturity in three to five weeks, are either bisexual or male. The sperm require water to swim to the eggs. A fertilized egg develops into an embryo or young sporophyte.

Pterophyta

Members of the phylum *Pterophyta* are commonly called ferns, the largest group of plants other than the flowering plants. About eleven thousand living species of ferns are widely distributed on the earth, among which three-fourths of the species are found in the tropics. There the greatest diversity of fern species exists, and they are abundant in many plant communities. In the small tropical country of Costa Rica, 1,000 species of ferns have been identified, whereas only 380 species of fern occur in the United States and Canada combined. In both form and habitat, ferns exhibit amazing diversity. Some are small and have undivided leaves, while others can reach up to 30 meters in height, with a trunk of more than 30 centimeters in diameter. Most living ferns are homosporous, except for two orders of water ferns.

Two genera of the order *Ophioglossales*, the grape ferns (*Botrychium*), and the adder's-tongues (*Ophioglossum*), are widespread in the north temperate region. A single leaf is usually produced each year from the rhizome. Each leaf consists of two parts:

the blade (the vegetative portion) and a fertile segment that typically bears two rows of eusporangia, hence the name eusporangiate ferns.

The order *Filicales* consists of 35 families and 320 genera, with more than 10,500 species. Most the familiar ferns are members of this order, such as the garden and woodland ferns of temperate regions. They have rhizomes that produce new sets of leaves each year. The root system is primarily adventitious, arising from the rhizomes near the bases of the leaves. They are homosporous. With a high surface-to-volume ratio, their bodies capture sunlight much more effectively than those of the lycophytes.

The water ferns, *Marsileales* and *Salviniales*, are the only living heterosporous ferns. Members of *Marsileales* grow in mud, on damp soil, or often with their four-leaf-clover-like leaves floating on the surface of water. Their unique, drought-resistant, bean-shaped reproductive structures are able to germinate even after one hundred years of dry storage. Members of *Salviniales*, genera *Azolla* and *Salvinia*, are small plants that float on the surface of water. They are harvested and used as feed or fertilizer in some Asian countries.

Gymnosperms

Gymnosperms, literally "naked seeds," are the earliest-evolved plants that produce seeds. Living gymnosperms comprise four phyla: *Cycadophyta*, *Ginkgophyta*, *Coniferophyta*, and *Gnetophyta*. The life cycles of all bear a remarkable resemblance: an alteration of heteromorphic generations, with large, independent sporophytes and greatly reduced gametophytes. The ovules are exposed on the surfaces of the megasporophylls. At maturity the female gametophyte of most gymnosperms is multicellular in structure, with several archegonia. The male gametophytes develop as pollen grains. Except for the ginkgo and cycads, the sperm cells of seed plants are nonmotile.

In seed plants, water is not required for transfer of sperm or fertilization of an egg. Pollen grains that usually contain two sperm nuclei may be transferred to the egg via various means, such as wind,

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The smallest of the modern flowering plants, or angiosperms, is duckweed, a few millimeters in diameter, which floats on ponds.

insects, and animals. A pollen grain then germinates and sends one nucleus to fuse with the egg, which in turn develops into embryo. After fertilization, each ovule develops into a seed.

Among the four phyla, the conifers (*Coniferophyta*) are the largest and most widespread gymnosperms, with about 50 genera and 550 species. They still dominate many of the earth's plant communities, with pines, firs, spruces, and other familiar evergreen trees over wide stretches of the north. Living cycads (*Cycadophyta*) constitute 11 genera, and some 140 species grow primarily in tropical and warm regions. Cycads are palmlike plants, with trunks and sluggish secondary growth. Only one living species of ginkgo (*Ginkgophyta*) exists. The phylum *Gnetophyta* consists of three genera that are close relatives of the angiosperms, with which they share many characteristics.

Angiosperms

As plants adapted to terrestrial environments, more effective means of reproduction and distribution emerged. Flowers, fruits, and seeds resulted in the dominance by *angiosperms*: flowering plants, the most diverse group of plants. Modern flowering plants, or angiosperms, constitute the phylum *Anthophyta*, which are incredibly diverse, with more than 230,000 species. They range in size from a few millimeters in diameter, such as the duckweed that floats on ponds, to more than 320 feet (about 100 meters) tall, such as the eucalyptus. From desert cacti to tropical orchids to grasses to major food crops, angiosperms dominate the plant kingdom.

Anthophyta is divided into two large classes: *Monocotyledons* (65,000 species) and *Eudicotyledones*, or "true" dicots (170,000 species).

In addition to some features shared with gymnosperms, angiosperms have a few unique characteristics. Within seeds, nutrients and food are usually stored in a triploid tissue called an *endosperm*. The presence of *carpels* makes flowers shiny and more attractive for pollinators, enhancing their reproductive success. The nutritious fruit-encasing seeds offer protection and ensure the wide distribution of angiosperms as various animals eat fruits and disperse the seeds throughout the ecosystem. Angiosperms have broad leaves, giving them the advantage of collecting more sunlight for photosynthesis, especially in warm, moist climates. The extra energy gained in spring and summer allows trees to drop their leaves and enter a dormant period, which reduces water evaporation when water is in short supply.

Pollination in angiosperms takes place by the transfer of pollen from anther to stigma. Each pollen grain contains sperm, typically with two or three cells. One cell grows, sending pollen tubes to the ovule, where one sperm nucleus unites with the egg and produces a diploid zygote. The other cell or cells fuse with two polar nuclei, giving rise to primary endosperm nucleus. This phenomenon, called *double fertilization*, is a unique characteristic for angiosperms. The zygote then develops into an embryo (sporophyte). The primary endosperm grows and matures into a nutritive endosperm. Both *self-pollination* and *cross-pollination* occur in flowering plants. The angiosperm domination of earth began about 100 million years ago and has persisted to the present.

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See also: Angiosperms; Angiosperm evolution; Aquatic plants; Bryophytes; Conifers; Cycads and palms; Eudicots; Evolution of plants; Ferns; Ginkgos; Gnetophytes; Gymnosperms; Hornworts; Horsetails; Liverworts; Lycophytes; Monocots vs. dicots; *Monocotyledones*; Mosses; Plant life spans; Psilotophytes; Reproduction in plants; *Rhyniophyta*; Seedless vascular plants; *Spermatophyta*; *Tracheobionta*; *Trimerophytophyta*; *Zosterophyllophyta*.

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PLANTS WITH POTENTIAL

Categories: Agriculture; economic botany and plant uses

One of the primary reasons humans cultivate plants is to satisfy an economic need for natural resources. In order for a plant to realize its full economic potential, it must not only fill an economic need but also do so in a cost-efficient manner.

There are several examples of plants which, because of their unique products, appear to fulfill an economic need. However, these plants may not do so in a cost-effective manner. With development of improved agronomic practices and plant-processing methods, which lower the cost of production, some plants may eventually realize their full economic potential.

Another factor that may affect a plant's economic potential includes the availability and price of competing products on the world market. This factor is beyond the control of domestic agronomists. Drastic changes in world conditions, such as in times of natural disaster, severe economic recession, or wartime, can have a dramatic impact on the economic feasibility of natural resources. Crops with economic potential may move in and out of economically favorable conditions as world markets change and new markets develop.

Guayule

Guayule (*Parthenium argentatum*) is a shrubby member of the *Compositae* family that is native to the desert regions of the southwestern United States and northern Mexico. Other species of this genus are found in all regions of the Americas. Guayule is one of more than two thousand plant species that can potentially be used to produce latex and rubber. Only guayule and its chief competitor, *Hevea brasiliensis*, have been used to produce commercial quantities of rubber.

Although commercial production of guayule-derived rubber dates back to the 1920's, when Continental Rubber Company produced small quantities of latex and rubber from guayule plants grown in Arizona and California, it was not until the Emergency Rubber Project during World War II that large-scale production of guayule rubber commenced. With the U.S. economy on a wartime footing and with supplies of imported Hevea rubber becoming uncertain, U.S. Code Title 7, Section 171, authorized the U.S. Department of Agriculture to acquire the technology of the Continental Rubber Company, plant up to 500,000 acres of guayule, and develop factories for the production of guayule-based rubber. With the end of World War II and reestablishment of the Hevea rubber supply from Asia, guayule-based rubber was no longer economically competitive. The unfavorable price difference between guayule-based rubber and Hevea-based rubber has remained unchanged, even though many agronomic improvements have been made for guayule.

However, new life may be developing for guayule-based rubber in a large niche market: medical products. A method for producing hypoallergenic latex derived from guayule has been developed and patented by the U.S. Department of Agriculture. A private company, Yulex Corporation, has licensed this technology and intends to use it to manufacture medical items, such as surgical gloves. The gloves produced from guayule-based latex do not contain the allergenic proteins that Hevea-based latex contains, so they will not cause allergic reactions in the estimated twenty million Americans who are allergic to Hevea rubber products. In this case, the cost disparity between Hevea rubber and guayule rubber is offset by the technical

Image Not Available

improvement that guayule latex brings to the high-value market for medical devices.

Jojoba

Jojoba (*Simmondsia chinensis*) is a woody, evergreen desert shrub that, despite its misleading species epitaph, *chinensis*, is native to the southwestern United States. In cultivation, jojoba may be irrigated during its two- to three-year establishment period after which, assuming that the roots find groundwater, the plants do not require irrigation. During the plant's initial production period of three to ten years, the female plants may produce 350 kilograms of seeds per hectare. After ten years of growth, the plants may yield 500 to 800 kilograms per hectare for many decades.

Jojoba oil is extracted from jojoba seeds and comprises approximately 40 to 60 percent of the mass of the seeds. Jojoba oil is not really an oil per se, as it is not a triglyceride; jojoba oil is a plant wax similar to plant cuticular waxes, being composed of long-chain alcohols and fatty acids. The value of jojoba oil comes from its desirable stability. Jojoba oil is stable up to 300 degrees Celsius and does not become rancid even after decades of storage. Also, jojoba oil is very similar chemically to the highly prized sperm whale oil, so it is useful in cosmetics.

Jojoba oil was first produced in commercially important quantities during World War II, as a high-temperature lubricant and an extender for petroleum-based lubricants. These jojoba-based products were used for engines, machinery, vehicles, and guns. As seen with guayule, the economics of jojoba oil production did not compare favorably with abundant petroleum products after World War II, so production of jojoba oil decreased sharply after the war.

In recent decades, the economics of jojoba oil production has gone through many fluctuations. In the 1970's the Green Revolution reignited interest in renewable, natural resources, especially products that could replace petrochemicals and animal-derived products. Growers took advantage of tax incentives to start farming jojoba. Then the disappearance of tax incentives and the decade-long production time to achieve commercially useful quantities of jojoba seed proved to be economically disastrous for many growers. Many jojoba farms shut down operations. In the 1990's the price of jojoba oil ranged from $40 per gallon to $200 per gallon, an unacceptable fluctuation in price that discouraged many industries from becoming dependent on jojoba oil. The price of jojoba oil must stabilize before industries can once again explore adding jojoba to their lines. Additionally, some unique, value-added products containing chemically modified jojoba oil are becoming common in many upscale health and beauty products.

Hesperaloe

Hesperaloe (*Hesperaloe funifera*) is a plant in the agave family that produces long, thin fibers that may be processed into exceptionally light and strong paper. Long-term biomass production studies began on hesperaloe in 1988, and since then many agronomic and processing improvements have been made. The fibers of hesperaloe seem suitable for the production of high-value products, such as ultralight coated papers.

Kenaf

Kenaf (*Hibiscus cannabinus*) is another fast-growing fiber crop that is finding utility in niche markets. Kenaf may be used to produce bright white paper, building materials, and absorbent materials. Additionally, the black lignin liquor, a by-product of kenaf processing, may add value to the crop by functioning as a binder for animal feeds, a fertilizer, or a termite-resistant coating.

Lesquerella

Lesquerella (*Lesquerella fendleri*) is an industrial crop under development for its unique seed oils. Initial research indicates that domestically produced lesquerella may eventually replace imported castor oil in many cosmetics, pharmaceuticals, and industrial products. Enhanced agronomic techniques, processing methods, conventional breeding, genetic engineering, and emerging niche markets may one day push lesquerella and other plants with potential into the realm of commercial viability.

Robert A. Sinnott

See also: Agricultural crops: experimental; Culturally significant plants; Green Revolution; Medicinal plants; Rubber.

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PLASMA MEMBRANES

Categories: Anatomy; cellular biology

The plasma membrane is a structure of the plant cell that forms a semipermeable, or selective, barrier between the interior of the cell and the external environment; they also function in transport of molecules into and out of the cell.

In addition to forming the structural barrier between the internal contents of a cell and the external environment, plasma membranes contain proteins involved in the transport of molecules and other substances into and out of the cell, and they contain proteins and other molecules that are essential for receiving signals from the environment and from plant hormones that direct growth and division. Carbohydrates associated with the plasma membrane are markers of cell type. In plants, the plasma membrane is the site of cellulose synthesis.

Lipid molecules provide the structure for the plasma membrane, which is described by the *fluid mosaic model* as a dynamic ocean of lipids in which other molecules float. *Phospholipids* are the most abundant lipid of plasma membranes, and they are organized in a fluid phospholipid bilayer in which

Mechanisms for Transport Across Cell Membranes

Type of Transport	*Mechanisms and Functions*	
Diffusion	Passive movement of substances into and out of the cell.	
	Simple diffusion	Dissolved gases (oxygen, carbon dioxide) and lipid-soluble substances move down the concentration gradient through the lipid portion of the membrane.
	Facilitated diffusion	Specialized membrane proteins allow substances with low lipid-solubility to move down the concentration gradient by binding to carrier (transport) proteins.
	Osmosis	Net movement of water molecules down the concentration gradient across the membrane, driven by the difference in solute concentrations on either side.
Active transport	Movement of substances against the concentration gradient (“uphill”), requiring an expenditure of cellular energy, usually from adenosine triphosphate.	
	Cotransport (symport)	Active transport involving a specialized protein molecule called a symport carrier.
	Countertransport (antiport)	Active transport that uses a specialized protein molecule called an antiport carrier.
Endocytosis (vesicle-mediated)	Movement of materials into the cell: The cell’s plasma membrane engulfs material and packs it into saclike vesicles that detach from the plasma membrane and move into the cell.	
	Phagocytosis	“Cell eating”: cellular intake of large and generally insoluble molecules and macromolecules (and little fluid) that cannot be taken into the cell using other membrane transport mechanisms.
	Pinocytosis	“Cell drinking”: cellular intake of fluids and dissolved solutes by the formation of membrane-bound vesicles at the cell membrane surface, which are then taken into the cell interior and released.
	Receptor-mediated	Cellular intake of nutrients and other essential macromolecules at specific receptor sites. Receptor-ligand complexes combine to form clusters around which a portion of the cell membrane encircles, producing a vesicle that invaginates inward to pinch off as a coated vesicle. Once inside, the vesicle dissolves as a result of changes in the acidity of the cytoplasm.
Exocytosis (vesicle-mediated)	Transport of macromolecules and large particles outside the cell, the reverse of endocytosis. Materials inside the cell are packed in a vesicle, which fuses to the plasma membrane and expels its contents into the extracellular medium.	

sterols, proteins, and other molecules are interspersed. Phospholipids are amphipathic molecules, containing water-loving (hydrophilic) regions and water-fearing (hydrophobic) regions.

Each phospholipid consists of a three-carbon glycerol backbone; two of the carbons are attached to long-chain fatty acid molecules, and the third carbon is attached to a phosphate-containing group. Because the fatty acids are nonpolar and hydrophobic, they tend to aggregate and exclude water. This aggregation allows the phospholipids to form a bilayer structure that has the fatty acids of both layers in the middle and the charged, phosphate-containing groups toward the outside. This bilayer structure allows one surface of the plasma membrane bilayer to interact with the aqueous external environment, while the other interacts with the aqueous internal cellular environment.

Sterols are also found within the plasma membranes of plant cells. The major sterol found in plant cell plasma membranes is stigmasterol (as opposed to cholesterol, which is found in animal cell plasma membranes). Sterols found in plant cells are important economically as the starting material for steroid-based drugs such as birth control pills.

Membrane Proteins and Carbohydrates

Some membrane proteins span the entire length of the phospholipid bilayer and are called *transmembrane proteins*. Transmembrane proteins are sometimes referred to as integral membrane proteins and have varied structures and functions. They may pass through the lipid bilayer only once, or they may be "multiple pass" transmembrane proteins, weaving into and out of the membrane many times.

The portion of a transmembrane protein that passes through the interior of the membrane often consists of amino acids that have nonpolar side chains (R-groups) and is known as the transmembrane domain. The portion of the transmembrane protein that is on the external surface of the membrane and interacts with the aqueous environment often contains charged, or polar, amino acids in its sequence.

Membrane proteins are often important for receiving signals from the external environment as membrane receptors. For instance, protein or peptide hormones interact with transmembrane protein receptors on the plasma membrane. Membrane proteins are also involved in receiving signals such as light photons. Membrane proteins form pores that allow ions (charged particles) to pass through the interior of the membrane. Membrane proteins called carriers are essential for bringing nutrient molecules such as simple sugars into the cell.

Not all proteins within the membrane are transmembrane proteins. Some are only loosely associated with the membrane, attached to other proteins, or anchored in the membrane by a lipid tail. These proteins, which do not span both sides of the membrane, are often called *peripheral membrane proteins*.

In addition to proteins, the plasma membrane contains carbohydrate molecules. Carbohydrate molecules are usually attached to membrane proteins or to lipid molecules within the bilayer. Carbohydrates provide important information about cell type and identity.

Transport Across Membranes

Transport of molecules into and out of the cells is an important function of the plasma membrane. Hydrophobic molecules, such as oxygen, and small, uncharged molecules, such as carbon dioxide, cross the membrane by *simple diffusion*. These molecules use the potential energy of a chemical gradient to drive their movement from an area of higher concentration on one side of the membrane to an area of lower concentration on the other side. Diffusion works best when this concentration gradient is steep. For example, in cells that do not have the ability to carry out photosynthesis, oxygen is used almost as quickly as it enters the cell. This maintains a sharp gradient of oxygen molecules across the membrane, so that molecules continually flow from the area of greater oxygen concentration outside the cell to the area of lower concentration inside the cell.

Molecules that are polar are excluded from the hydrophobic area of the bilayer. Two factors influence the transport of these kinds of molecules: the concentration gradient and the electrical gradient. Lipid bilayers separate differences in electrical charge from one side of the membrane to the other, acting as a kind of biological capacitor. If the inside of the cell is more negative than the outside of the cell, negatively charged ions would have to move from the inside to the outside of the cell to travel with the electrical gradient. The combination of the concentration and electrical gradients is called the *electrochemical gradient*.

Transport of charged or polar molecules requires the assistance of proteins within the membrane, known as transporters. Channel proteins form pores within the membrane and allow small, charged molecules, usually inorganic ions, to flow across the membrane from one side to the other. If the direction of travel of the ion is down its electrochemical gradient, the process does not require additional energy and is called *passive transport*. Carrier proteins change shape to deposit a small molecule, such as a sugar, from one side of a membrane to the other. Pumps are proteins within the membrane that use energy from adenosine triphosphate (ATP) or light to transport molecules across the membrane. When energy is used in transport, the process is called *active transport*.

Cellulose Biosynthesis

In plants, the plasma membrane is the site for the synthesis of cellulose, the most abundant biopolymer on earth. Electron microscope studies suggest that the plant cell membrane contains rosette structures that are complexes of many proteins and are the sites of cellulose synthesis. Studies in bacteria, cotton plants, and the weed *Arabidoposis thaliana* have allowed scientists to isolate the gene that actually carries out the chemical reactions linking glucose molecules together into the long cellulose microfibril structure. This gene encodes a protein called glycosyl transferase. Antibodies against the catalytic, or active, subunit of glycosyl transferase specifically label these rosette structures. Two of these transferase molecules act simultaneously from opposite sides to add two glucoses at a time to the growing microfibril, accounting for the rotation of alternating glucoses in cellulose molecules.

Michele Arduengo

See also: Active transport; ATP and other energetic molecules; Carbohydrates; Cell wall; Cells and diffusion; Endocytosis and exocytosis; Lipids; Liquid transport systems; Membrane structure; Osmosis, simple diffusion, and facilitated diffusion; Plant cells: molecular level; Proteins and amino acids.

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PLASMODIAL SLIME MOLDS

Categories: Molds; *Protista*; taxonomic groups

The plasmodial slime molds, or myxomycetes, phylum Myxomycota, *are a group of funguslike organisms usually present and sometimes abundant in terrestrial ecosystems. However, this group comprises about eight hundred species, related neither to cellular slime molds nor to fungi.*

The plasmodial slime molds have no cell walls and exist as thin masses of protoplasm, which appear to be streaming in a fanlike shape, under favorable conditions. As these masses, called *plasmodia*, travel, they absorb small particles of decaying plant and animal matter as well as bacteria, fungi, and yeasts. When mature, a plasmodium may weigh 20-30 grams and take up an area of 1 meter or more.

Myxomycetes have been known from their *fruit-*

ing bodies (often a sporangium sprouting from a small mound that forms when the plasmodium stops moving) since at least the middle of the seventeenth century. Their life cycle has been understood for more than a century. The reproductive, spore-producing stage in the life cycle can achieve macroscopic dimensions and be collected and preserved for study in much the same way as mushrooms and other fungi or even specimens of bryophytes, lichens, and vascular plants. However, most species of myxomycetes tend to be rather inconspicuous or sporadic in their occurrence and thus not always easy to detect in the field. Moreover, fruiting bodies of most species are relatively ephemeral and do not persist in nature for very long. Myxomycetes also spend a portion of their life cycle as true eukaryotic microorganisms, when their very presence in a given habitat can be exceedingly difficult, if not impossible, to determine.

Life Cycle

The life cycle of a myxomycete involves two very different trophic (or feeding) stages, one consisting of uninucleate (single-nucleus) *amoeboid cells*, with or without flagella, and the other consisting of a distinctive multinucleate structure, the *plasmodium*. Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by some fungi, although they are considerably smaller (usually no more than 1-2 millimeters tall). The spores of myxomycetes are for most species apparently wind-dispersed and complete the life cycle by germinating to produce the uninucleate amoeboid cells. These cells feed and divide by binary fission to build up large populations in the various habitats in which these organisms occur.

The transformation from one trophic stage to the other in the myxomycete life cycle is in most cases the result of fusion between compatible amoeboid cells, which thus function as gametes. The fusion of the two cells produces a diploid zygote that feeds, grows, and undergoes repeated mitotic nuclear divisions to develop into the plasmodium. Bacteria represent the primary food resource for both trophic stages, but plasmodia are also known to feed upon yeasts, cyanobacteria, and fungal spores.

Myxomycete plasmodia usually occur in situations in which they are relatively inconspicuous, but careful examination of the inner surface of dead bark on a fallen log or the lower surface of a piece of coarse woody debris on the ground in a forest, especially after a period of rainy weather, often will turn up an example or two. Most of the plasmodia encountered in nature are relatively small, but some species are capable of producing a plasmodium that can reach a size of more than 1 meter across. Under adverse conditions, such as drying out of the immediate environment or low temperatures, a plasmodium may convert into a hardened, resistant structure called a *sclerotium*, which is capable of reforming the plasmodium upon the return of favorable conditions. Moreover, the amoeboid cells can undergo a reversible transformation to dormant structures called *microcysts*. Both sclerotia and microcysts can remain viable for long periods of time and are probably very important in the continued survival of myxomycetes in some habitats, such as deserts.

Structure of Fruiting Bodies

Identification of myxomycetes is based almost entirely upon features of the fruiting bodies produced by these organisms. Fruiting bodies (also sometimes referred to as "sporophores" or "sporocarps") occur in four generally distinguishable forms or types, although there are a number of species that regularly produce what appears to be a combination of two types. The most common type of fruiting body is the *sporangium*, which may be sessile or stalked, with wide variations in color and shape. The actual spore-containing part of the sporangium (as opposed to the entire structure, which also includes a stalk in those forms characterized by this feature) is referred to as a *sporotheca*. Sporangia usually occur in groups, because they are derived from separate portions of the same plasmodium.

A second type of fruiting body, an *aethalium*, is a cushion-shaped, sessile structure. Aethalia are presumed to be masses of completely fused sporangia and are relatively large, sometimes exceeding several centimeters in extent. A third type is the *pseudoaethalium* (literally, a false aethalium). This type of fruiting body, which is comparatively uncommon, is composed of sporangia closely crowded together. Pseudoaethalia are usually sessile, although a few examples are stalked. The fourth type of fruiting body is called a *plasmodiocarp*. Almost always sessile, plasmodiocarps take the form of the main veins of the plasmodium from which they were derived.

A typical fruiting body consists of as many as six major parts: hypothallus, stalk, columella, peridium, capillitium, and spores. Not all of these parts are present in all types of fruiting bodies. The *hypothallus* is a remnant of the plasmodium sometimes found at the base of a fruiting body. The *stalk* (also called a stipe) is the structure that lifts the sporotheca above the substrate. As already noted, some fruiting bodies are sessile and thus lack a stalk. The *peridium* is a covering over the outside of the sporotheca that encloses the actual mass of spores. It may or may not be evident in a mature fruiting body. The peridium may split open along clearly discernible lines of dehiscence, as a preformed lid, or in an irregular pattern. In an aethalium, the relatively thick covering over the spore mass is referred to as a *cortex* rather than a peridium. The *columella* is an extension of the stalk into the sporotheca, although it may not resemble the stalk.

The *capillitium* consists of threadlike elements within the spore mass of a fruiting body. Many species of myxomycetes have a capillitium, either as a single connected network or as many free elements called *elaters*. The elements of the capillitium may be smooth, sculptured, or spiny, or they may appear to consist of several interwoven strands. Some elements may be elastic, allowing for expansion when the peridium opens, while other types are hygroscopic and capable of dispersing spores by a twisting motion. Spores of myxomycetes are quite small and range in size from slightly less than 5 to occasionally more than 15 micrometers. Nearly all of them appear to be round, and most are ornamented to some degree. Spore size and also color are very important in identification. Spores can be dark or light to brightly colored.

Occurrence in Nature

There are approximately eight hundred recognized species of myxomycetes, and these have been placed in six different taxonomic orders: *Ceratiomyxales*, *Echinosteliales*, *Liceales*, *Physarales*, *Stemonitales*, and *Trichiales*. However, members of the *Ceratiomyxales* are distinctly different from members of the other orders, and many modern biologists have removed these organisms from the myxomycetes and reassigned them to another group of slime molds, the *protostelids*. The majority of species of myxomycetes are probably cosmopolitan, and at least some species apparently occur in any terrestrial ecosystem with plants (and thus plant detritus) present. However, a few species do appear to be confined to the tropics or subtropics, and others have been collected only in temperate regions. Compared to most other organisms, myxomycetes show very little evidence of endemism, with the same species likely to be encountered in any habitat on earth where the environmental conditions suitable for its growth and development apparently exist.

Although the ability of a plasmodium to migrate some distance from the substrate upon or within which it developed has the potential of obscuring myxomycete-substrate relationships, fruiting bodies of particular species of myxomycetes tend to be rather consistently associated with certain types of substrates. For example, some species almost always occur on decaying wood or bark, whereas others are more often found on dead leaves and other plant debris and only rarely occur on wood or bark. In addition to these substrates, myxomycetes also are known to occur on the bark surface of living trees, on the dung of herbivorous animals, in soil, and on aerial portions of dead but still-standing herbaceous plants. The myxomycetes associated with decaying wood are the best known, because the species typically occurring on this substrate tend to be among those characteristically producing fruiting bodies of sufficient size to be detected in the field. Many of the more common and widely known myxomycete taxa, including various species of *Arcyria*, *Lycogala*, *Stemonitis*, and *Trichia*, are predominantly associated with decaying wood.

Steven L. Stephenson

See also: Bacteria; *Protista*.

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POISONOUS AND NOXIOUS PLANTS

Categories: Diseases and conditions; medicine and health; poisonous, toxic, and invasive plants

Poisonous plants have evolved toxic substances that function to defend them against herbivores and thereby better adapt them for survival.

After evolving adaptations that facilitated colonization of terrestrial habitats, plants were confronted with a different type of problem. This was the problem of *herbivory*, or the inclination of many different types of organisms, from bacteria to insects to four-legged herbivores, to eat plants. Pressures from herbivory drove many different types of plants, from many different families, to evolve defenses. Some of these defenses included changes in form, such as the evolution of thorns, spikes, or thicker, tougher leaves. Other plants evolved to produce chemical compounds that make them taste bad, interrupt the growth and life cycles of the herbivores, make the herbivores sick, or kill them outright.

Phytochemicals

One of the most interesting aspects of plants, especially prevalent in the angiosperms (flowering plants), is their evolution of substances called *secondary metabolites*, sometimes referred to as *phytochemicals*. Once considered waste products, these substances include an array of chemical compounds: alkaloids, quinones, essential oils, terpenoids, glycosides (including cyanogenic, cardioactive, anthraquinone, coumarin, and saponin glycosides), flavonoids, raphides (also called oxalates, which contain needle-like crystals of calcium oxalate), resins, and phytotoxins (highly toxic protein molecules). The presence of many of these compounds can characterize whole families, or even genera, of flowering plants.

Effects on Humans

The phytochemicals listed above have a wide range of effects. In humans, some of these compounds will cause mild to severe skin irritation, or contact dermatitis; others cause mild to severe gastric distress. Some cause hallucinations or psychoactive symptoms. The ingestion of many other types of phytochemicals proves fatal. Interestingly, many of these phytochemicals also have important medical uses. The effects of the phytochemicals are dependent on dosage: At low doses, some phytochemicals are therapeutic; at higher doses, some can kill.

Alkaloids

Alkaloids are nitrogenous, bitter-tasting compounds of plant origin. More than three thousand alkaloids have been identified from about four thousand plant species. Their greatest effects are mainly on the nervous system, producing either physiological or psychological results. Plant families producing alkaloids include the *Apocynaceae*, *Berberidaceae*, *Fabaceae*, *Papaveraceae*, *Ranunculaceae*, *Rubiaceae*, and *Solanaceae*. Some well-known alkaloids include caffeine, cocaine, ephedrine, morphine, nicotine, and quinine.

Glycosides

Glycosides are compounds that combine a sugar, usually glucose, with an active component. While there are many types of glycosides, some of the most important groups of potentially poisonous glycosides include the cyanogenic, cardioactive, anthraquinone, coumarin, and saponin glycosides.

Cyanogenic glycosides are found in many members of the *Rosaceae* and are found in the seeds, pits, and bark of almonds, apples, apricots, cherries, peaches, pears, and plums. When cyanogenic glycosides break down, they release a compound called hydrogen cyanide.

Two other types of glycosides, cardioactive glycosides and saponins, feature a steroid molecule as part of their chemical structure. Digitalis, a cardioactive glycoside, in the right amounts can strengthen and slow the heart rate, helping patients who suffer from congestive heart failure. Other cardioactive glycosides from plants such as milkweed and oleander are highly toxic. Saponins can cause severe irritation of the digestive system and hemolytic anemia. Anthraquinone glycosides exhibit purgative activities. Plants containing anthraquinone glycosides include rhubarb (*Rheum* species) and senna (*Cassia senna*).

Household Plants

Many common household plants are poisonous to both humans and animals. One family of popular household plants that can cause problems is the

Common Poisonous Plants and Fungi

Common Name	*Scientific Name*
Aconite	*Aconitum* spp.
Alfalfa	*Medicago sativa*
Amaryllis (bulbs)	*Hippeastrum puniceum*
Anemone	*Anemone tuberosum*
Angel's trumpet	*Datura* spp.
Apple (seeds, leaves)	*Malus sylvestris*
Apricot (seeds, leaves)	*Prunus armeniacea*
Arrowgrass	*Triglochin maritima*
Asparagus (berries)	*Asparagus officinalis*
Azalea	*Rhododendron* spp.
Baneberry	*Actaea* spp.
Belladonna	*Atropa belladonna*
Birdsfoot trefoil	*Lotus corniculatus*
Bitter cherry	*Prunus* spp.
Black cherry	*Prunus* spp.
Black locust	*Robinia pseudoacacia*
Bleeding heart	*Dicentra* spp.
Bloodroot	*Sanquinaria canadensis*
Bouncing bet	*Saponaria* spp.
Bracken fern	*Pteridium aquilinium*
Broad beans	*Vicia* spp.
Buckeye	*Aesculus* spp.
Buckwheat	*Fagoypyrum esculentum*
Buffalo bur	*Solanum* spp.
Buttercups	*Ranunculus* spp.
Caladium	*Caladium bicolor*
Caley pea	*Lathyrus* spp.
Cardinal flower	*Lobelia* spp.
Castor bean	*Ricinus communis*
Celandine	*Chelidonium majus*
Choke cherry	*Prunus* spp.
Christmas rose	*Helleborus niger*
Clovers (alsike, red, white)	*Trifolium* spp.
Cocklebur	*Xanthium strumarium*
Corn cockle	*Agrostemma githago*
Corn lily	*Veratrum californicum*
Cow cockle	*Saponaria* spp.
Creeping charlie	*Glechoma* spp.
Croton	*Croton* spp.
Crowfoot	*Ranunculus* spp.
Crown-of-thorns	*Euphorbia milii*
Crown vetch	*Coronilla varia*
Daffodil (bulbs)	*Narcissus pseudonarcissus*
Daphne	*Daphne* spp.
Datura	*Datura* spp.
Deadly nightshade	*Atropa belladonna*
Death angel mushroom	*Amanita* spp.
Death camas	*Zigadenus* spp.
Death cap mushroom	*Amanita* spp.
Delphiniums and larkspurs	*Delphinium* spp.
Destroying angels	*Amanita verna*
Devil's trumpet	*Datura* spp.
Dock	*Rumex* spp.
Dogbane	*Apocynum* spp.
Dolls eyes	*Actaea* spp.
Downy thornapple	*Datura* spp.
Drooping leucothoe	*Leucothoe axillaris*
Dutchman's breeches	*Dicentra* spp.

Araceae, the philodendron family, including plants such as philodendron and dieffenbachia. All members of this family, including these plants, contain needlelike crystals of calcium oxalate that, when ingested, cause painful burning and swelling of the lips, tongue, mouth, and throat. This burning and swelling can last for several days, making talking and even breathing difficult. *Dieffenbachia* is often referred to by the common name of dumb cane, because eating it makes people unable to talk for a few days.

Landscape Plants

Many landscape plants are also poisonous. For example, the yew (genus *Taxus*), commonly planted as a landscape plant, is deadly poisonous. Children who eat the bright red aril, which contains the seed, are poisoned by the potent alkaloid taxine. Yews are poisonous to livestock as well, causing death to horses and cattle. Death results from cardiac or respiratory failure.

Other poisonous landscape and garden plants include oleander, rhododendrons, azaleas, hyacinths, lily of the valley, daffodils, tulips, and star-of-Bethlehem. Many legumes are also toxic, including rosary pea, lupines, and wisteria. Castor bean plant, a member of the family *Euphorbiaceae*, produces seeds that are so toxic that one seed will kill a child and three seeds are fatal to adults. The toxin produced by the seeds is called ricin, which many scientists consider to be the most potent natural toxin known.

Common Name	*Scientific Name*
Eastern skunk cabbage	*Symplocarpus foetidus*
Eggplant (leaves, stems)	*Solanum melongena*
Elderberry	*Sambucus canadensis*
Ergot	*Claviceps* spp.
Everlasting pea	*Lathyrus* spp.
False hellbore	*Veratrum californicum*
Fiddleneck	*Amsinckia intermedia*
Flax	*Linum usitatissimum*
Fly agaric	*Amanita muscaria*
Foxglove	*Digitalis purpurea*
Gill over the ground	*Glechoma* spp.
Gloriosa lily	*Gloriosa* spp.
Golden chain	*Laburnum anagyroides*
Great lobelia	*Lobelia* spp.
Ground ivy	*Glechoma* spp.
Groundsels	*Senecio* spp.
Halogeton	*Halogeton glomeratus*
Henbane	*Hyoscyanamus niger*
Holly (berries)	*Ilex* spp.
Horse chestnut	*Aesculus* spp.
Horse nettle	*Solanum* spp.
Horsebrush	*Tetradymia* spp.
Horsetail	*Equisetum arvense* & other spp.
Hyacinth (bulbs)	*Hyacinthus orientalis*
Hydrangea	*Hydrangea* spp.
Indian tobacco	*Lobelia* spp.
Irises (leaves, rhizomes)	*Iris* spp.
Ivy (leaves, berries)	*Hedera helix*
Jack in the pulpit	*Arisaema* spp.
Japanese pieris	*Pieris japonica*
Jessamine	*Gelsemium sempervirens*
Jimsonweed	*Datura* spp.
Johnson grass	*Sorghum* spp.
Klamath weed	*Hypericum perforatum*
Laburnum	*Laburnum anagyroides*
Lamb's quarters	*Chenopodium album*
Lantana	*Lantana camara*
Larkspur	*Delphinium* spp.
Lily of the valley	*Convallaria majalis*
Lobelia	*Lobelia cardinalis*
Locoweed	*Astragalus, Oxytropis* spp.
Lucerne	*Medicago sativa*
Lupine	*Lupinus* spp.
Mandrake	*Podophyllum peltatum*
Marijuana	*Cannabis sativa*
Marsh marigold or cowslip	*Caltha palustris*
Mayapple	*Podophyllum peltatum*
Milkweed	*Asclepias* spp.
Mistletoe	*Phoradendron* spp.
Monkey agaric mushroom	*Amanita* spp.
Monkshood	*Aconitum* spp.
Moonseed	*Menispermum canadense*
Morning glory (seeds)	*Ipomoea tricolor*
Mountain fetterbrush	*Pieris* spp.
Mountain laurel	*Kalmia latifolia*
Narcissus (bulbs)	*Narcissus* spp.
Nightshades	*Solanum* spp.
Oak trees	*Quercus* spp.
Oleander	*Nerium oleander*
Panther	*Amanita pantherina*
Panther cap mushroom	*Amanita* spp.

(continued)

Arrow Poisons

Toxic plant and animal products have been used for thousands of years in hunting, executions, and warfare. Usually the poisonous extracts were smeared on arrows or spears. The earliest reliable written evidence for these uses comes from the *Rigveda* from ancient India. Arrow poisons come in many different varieties, and most rain-forest hunters have their own secret blend. South American arrow poisons are generically called *curare*. There are more than seventy different plant species used in making arrow poisons. Two of the main arrow poison plants are woody vines from the Amazon: *Strychnos toxifera* and *Chondodendron tomentosum*. Some types of curare have proven medically useful. They are used as muscle relaxants in surgery, which lessens the amount of general anesthetic needed. A plant called *Strychnos nux-vomica* from Asia yields the poison strychnine, a stimulant of the central nervous system.

In ancient times, toxic plant products were also commonly used in executions. Many people were expert, professional poisoners in the ancient world. They could select a poison that would take days or even months to take effect, thus ensuring, for example, that an unfaithful spouse or lover would not suspect the reason for his or her lingering illness. On occasions when a more rapid result was required, a strong dose or more powerful poison could be prescribed.

Common Poisonous Plants and Fungi *(continued)*

Common Name	*Scientific Name*
Peach (leaves, seeds)	*Prunus persica*
Philodendron	*Philodendron* spp.
Pigweed	*Amaranthus* spp.
Pin cherry	*Prunus* spp.
Poinsettia	*Euphorbia* spp.
Poison hemlock	*Conium maculatum*
Poison ivy	*Toxicodendron radicans*
Poison oak	*Toxicodendron diversiloba*
Poison sumac	*Toxicodendron vernix*
Pokeweed	*Phytolacca americana*
Ponderosa pine	*Pinus ponderosa*
Poppies (inc. opium)	*Papaver* spp.
Potato	*Solanum* spp.
Prickly (Mexican) poppy	*Argemone mexicana*
Privet (leaves, berries)	*Ligustrum japonicum*
Ragworts	*Senecio* spp.
Red sage	*Lantana camara*
Rhodendron	*Rhodendron* spp.
Rhubarb (leaves)	*Rheum rhaponticum*
Rosary pea	*Abrus precatorius*
Senecio	*Senecio* spp.
Sensitive fern	*Onoclea sensibilis*
Sierra laurel	*Leucothoe davisiae*
Singletary pea	*Lathyrus* spp.
Snakeberry	*Actaea* spp.
Snow on the mountain	*Euphorbia* spp.
Sorghum or milo	*Sorghum* spp.
Spurges	*Euphorbia* spp.
Squirrel corn	*Dicentra* spp.
St. John's wort	*Hypericum perforatum*
Star of Bethlehem	*Ornithogalum umbellatum*
Stinging nettle	*Urtica* spp.
Sudan grass	*Sorghum* spp.
Sweet pea	*Lathyrus* spp.
Tall fescue	*Festuca arundinacea*
Tangier pea	*Lathyrus* spp.
Tobacco	*Nicotiana* spp.
Tomato (leaves, stems)	*Lycopersicon lycopersicum*
Tree tobacco	*Nicotiana* spp.
Tung oil tree	*Aleurites fordii*
Vetches	*Vicia* spp.
Virginia creeper (berries)	*Parthenocissus quinquefolia*
Water hemlock/ cowbane	*Cicuta* spp.
West Indian lantana	*Lantana camara*
White cohosh	*Actaea* spp.
White snakeroot	*Eupatorium rugosum*
White sweetclover	*Metilotus alba*
Wild cherries	*Prunus* spp.
Wisteria (pods, seeds)	*Wisteria* spp.
Wolfbane	*Aconitum* spp.
Yellow sage	*Lantana camara*
Yellow star thistle	*Centaurea solstitialis*
Yellow sweetclover	*Metilotus officinalis*
Yew	*Taxus cuspidata*

Note: spp. = species; This is a partial listing only: Parts of some plants that are particularly poisonous are identified in parentheses. However, it should *not* be assumed that other parts are necessarily benign or that plants not listed here are edible.

Source: Data are from Cornell University Poisonous Plants Informational Database, compiled by Dan Brown and staff, http://www.ansci.cornell.edu/plants/comlist.html (accessed April 11, 2002), and from Brian Capon, *Botany for Gardeners: An Introduction and Guide* (Portland, Oreg.: Timber Press, 1990), p. 96.

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Poison Ivy

Toxicodendron radicans, commonly known as poison ivy, is well known for causing contact dermatitis. Poison ivy is a member of the *Anacardiaceae*, or cashew family, and is a widespread weed in the United States and southern Canada. It grows in a variety of habitats: wetlands, disturbed areas, and the edges of forests. It has many forms, appearing as either a shrub or a woody vine which will grow up trees, houses, fences, and fence posts. It has alternate leaves with three leaflets, forming the basis of the old saying "Leaves of three, let it be." After poison ivy flowers, it develops clusters of white or yellowish-white berries. Related species are poison oak, western poison oak, and poison sumac, which some scientists consider to be different types of poison ivy.

Roughly half the world's population is allergic to poison ivy. Very sensitive people develop a severe skin rash; about 10 percent of the people who are allergic require medical attention after exposure. The chemical compound causing the allergic reaction is called *urushiol*, a resin found in all parts of the plant. Urushiol is so potent that in some individuals, just one drop produces a reaction. Inhaling smoke from burning poison ivy can result in eye and lung damage. For some people, mere contact with the smoke from burning poison ivy can trigger a reaction. Urushiol lasts forever; in herbaria, dried plants one hundred years old have given unlucky botanists contact dermatitis.

Carol S. Radford

See also: Allelopathy; Animal-plant interactions; Ascomycetes; Bacterial resistance and super bacteria; *Basidiomycetes*; Basidiosporic fungi; Biochemical evolution in angiosperms; Biological invasions; Biological weapons; Carnivorous plants; Coevolution; Culturally significant plants; Deuteromycetes; Dinoflagellates; Horsetails; Legumes; Medicinal plants; Metabolites: primary vs. secondary; Mushrooms; Parasitic plants.

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POLLINATION

Categories: Physiology; reproduction

Pollination involves the transfer of pollen from anther to stigma in flowering plants, or from male cone to ovules in gymnosperms. There are two different types of pollination: self-pollination and cross-pollination.

Pollination is the process, in sexually reproducing plants (both angiosperms and gymnosperms), whereby the male sperm and female egg are joined via transfer of *pollen* (male microspore). If the anthers and stigmas of the plants involved have the same genetic makeup or they are produced on the same plant, the type of pollination is called *self-pollination*. If anthers and stigmas are from plants with different genetic makeups, the type of pollination is called *cross-pollination*.

Self-pollination is efficient because pollen from the anther of a flower can be transferred easily onto the stigma of the same flower, owing to the proximity of the two parts. On the other hand, cross-pollination is risky because the transfer of pollen involves long distances and precise destinations, both of which depend on animal pollinators. In areas with few animal pollinators, the opportunities for cross-pollination may be greatly reduced (one of the many reasons that preserving biological diversity is an important ecological issue).

In spite of the risk associated with cross-pollination, most flowers have mechanisms that promote this kind of pollination. Cross-pollination increases the likelihood that offspring are vigorous, healthy, fertile, and able to survive even if the environment changes. Self-pollination leads to offspring that are less vigorous, less productive, and more subject to *inbreeding depression* (weakening of the offspring as a result of inbreeding).

When certain consumers forage among plants for food, they often come in contact with flowers. Many insects and other animals become dusted with pollen, and in the course of their travel they unintentionally but effectively bring about pollination. Throughout the evolutionary history of flowering plants, many pollinators have coevolved with plants. *Coevolution* occurs when the floral parts of a plant and the body parts and behavior of the pollinators become mutually adapted to each other, thereby increasing the effectiveness of their interaction. In many instances, the relationship between the plant and pollinator has become highly specialized, resulting in *mutualism*, which is interaction where both organisms benefit from each other.

In the case of pollination by animals, the pollinator receives a reward from the flower in the form of food. When the pollinator moves on, the plant's pollen is transferred to another plant. The adaptations between the flower and its pollinators can be intricate and precise and may even involve force, drugs, deception, or sexual enticement. In flowering plants, pollination is mostly due to insects or wind, but birds, bats, and rodents also act as pollinators for a number of plants.

Insects

Insect pollination occurs in the majority of flowering plants. There is no single set of characteristics for insect-pollinated flowers, because insects are a large and diverse group of animals. Rather, each plant may have a set of reproductive features that attracts mostly a specific species of insect. The principal pollinating insects are bees, although many other kinds of insects act as pollinators, including wasps, flies, moths, butterflies, ants, and beetles.

Bees have body parts suitable for collecting and carrying *nectar* and *pollen*. Their chief source of nourishment is nectar, but they also collect pollen for their larvae. The flowers that bees visit are generally brightly colored and predominantly blue or yellow—rarely pure red, because red appears black to bees. The flowers they visit often have distinctive markings that function as guides that lead them to the nectar. Bees can perceive ultraviolet (UV) light (a part of the spectrum not visible to humans), and some flower markings are visible only in UV light, making patterns perceived by bees sometimes different from those seen by humans. Many bee-pollinated flowers are delicately sweet and fragrant.

Moth- and butterfly-pollinated flowers are similar to bee-pollinated flowers in that they frequently have sweet fragrances. Some butterflies can detect red colors, and so red flowers are sometimes pollinated by them. Many moths forage only at night; the flowers they visit are usually white or cream-colored because these colors stand out against dark backgrounds in starlight or moonlight. With their long mouthparts, moths and butterflies are well adapted for securing nectar from flowers with long, tube-shaped *corollas* (the petals collectively), such as larkspur, nasturtium, tobacco, evening primrose, and amaryllis.

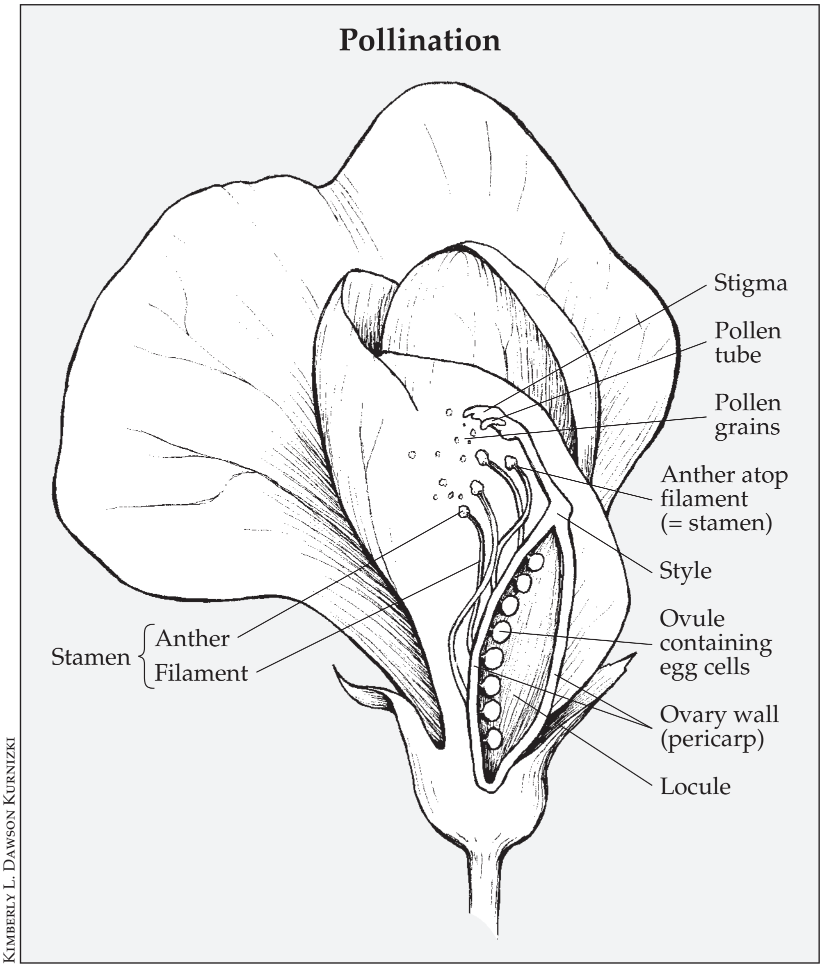
The flowers pollinated by beetles tend to have strong, yeasty, spicy, or fruity odors. They are typically white or dull in color, in keeping with the diminished visual sense of their pollinators. Although some beetle-pollinated flowers do not secrete nectar, they furnish pollen or other foods which are available on the petals in special storage cells.

Birds

Birds and the flowers that they pollinate are also adapted to each other. Birds do not have a highly developed sense of smell, but they have a keen sense of vision. Their flowers are thus frequently bright red or yellow and usually have little, if any, odor. The flowers are typically large or are part of a large inflorescence. Birds are highly active pollinators and tend to use up their energy very rapidly. Therefore, they must feed frequently to sustain themselves. Many of the flowers they visit produce copious quantities of nectar, assuring the birds' continued visitation. The nectar is frequently produced in long floral tubes, which prevent most

PhotoDisc

In a classic example of cross-pollination, this honeybee gathers nectar while inadvertently providing pollen from another plant to the ovule of this sunflower.



Pollination occurs as either self-pollination (shown here) or cross-pollination, in which the pollen from one plant is dispersed via wind, water, or animals to pollinate another plant. In both cases, pollen lands on the stigma and grows a pollen tube down through the style toward the ovule in the ovary, where it deposits the sperm into an egg cell inside the ovule.

insects from gaining access to it. Examples of bird-pollinated flowers are red columbine, fuchsia, scarlet passion flower, eucalyptus, hibiscus, and poinsettia.

Bats and Rodents

Bat-pollinated flowers are found primarily in the tropics, and they open only at night, when the bats are foraging. These flowers are dull in color, and like bird-pollinated flowers, they are large enough for the pollinator to insert part of its head inside. The plants may also consist of ball-like inflorescences containing large numbers of small flowers whose stamens readily dust the visitor with pollen. Bat-pollinated flowers include bananas, mangoes, kapok, and sisal. Like moth-pollinated flowers, flowers that attract bats and small rodents open at night. Mammal-pollinated flowers are usually white and strongly scented, often with a fruity odor. Such flowers are large, to provide the pollinators enough pollen and nectar to fulfill their energy requirements. The flowers are also sturdy, to bear the frequent and vigorous visits of these small mammals.

Orchid Pollinators

The orchid family has pollinators among bees, moths and butterflies, and beetles. Some of the adaptations between orchid flowers and their pollinators are extraordinary. Many orchids produce their pollen in little sacs called *pollinia*, which typically have sticky pads at the bases. When a bee visits such a flower, the pollinia are usually deposited on its head. In some orchids, the pollinia are forcibly "slapped" on the pollinator through a trigger mechanism within the flower. In some orchids, a petal is modified so that it resembles a female wasp or bee. Male wasps or bees emerge from their pupal stage before the females and can mistake the orchids for potential mates. They try to copulate with these flowers, and while they are doing so, pollinia are deposited on their heads. When the wasps or bees visit other flowers, the pollinia are caught in sticky stigma cavities.

When moths and butterflies pollinate orchids, the pollinia become attached to their long tongues by means of sticky clamps instead of pads. The pollinia of certain bog orchids become attached to the eyes of the female mosquitoes that pollinate them. After a few visits, the mosquitoes are blinded and unable to continue their normal activities (a good example of a biological control within an ecosystem).

Among the most bizarre of the orchid pollination mechanisms are those whose effects are to dunk the pollinator in a pool of watery fluid secreted by the orchid itself and then permit the pollinator to escape underwater through a trap door. The route of the insect ensures contact between the pollinia and stigma surfaces. In other orchids with powerful narcotic fragrances, pollinia are slowly attached to the drugged pollinator. When the transfer of pollinia has been completed, the fragrance abruptly fades away, and the insect recovers and flies away.

Wind and Water

Wind pollination is common in those plants with inconspicuous flowers, such as grasses, poplars, walnuts, alders, birches, oaks, and ragweeds. These plants lack odor and nectar and are, hence, unattractive to insects. Furthermore, the petals are either small or absent, and the sex organs are often separate on the same plant. In grasses, the stigmas are feathery and expose a large surface to catch pollen, which is lightweight, dry, and easily blown by the wind. Because wind-pollinated flowers do not depend on animals to transport their pollen, they do not invest in the production of rewards for their visitors. However, they have to produce enormous quantities of pollen. Wind pollination is not efficient because most of the pollen does not end up on the stigmas of appropriate plants but on the ground, bodies of water, and in people's noses (a major cause of allergic reactions). Wind pollination is successful in cases where a large number of individuals of the same species grow fairly close together, as in grasslands and coniferous forests.

Water pollination is rare, simply because fewer plants have flowers that are submerged in water. Such plants include the sea grasses, which release pollen that is carried passively by water currents. In some plants, such as the sea-nymph, pollen is threadlike, thus increasing its chances of coming in contact with stigmas. In eelgrass, the entire male flower floats.

Danilo D. Fernando

See also: Animal-plant interactions; Angiosperm evolution; Angiosperm life cycle; Aquatic plants; Biochemical coevolution in angiosperms; Coevolution; Flower structure; Flower types; Metabolites: primary vs. secondary; Orchids; Population genetics; Reproduction in plants; Reproductive isolating mechanisms.

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POLYPLOIDY AND ANEUPLOIDY

Categories: Genetics; reproduction and life cycles

In aneuploidy, one or more whole chromosomes has been lost or gained from the diploid state. In polyploidy, one or more complete sets of chromosomes has been gained from the usual state (generally diploid), as in triploidy and tetraploidy.

For each species of higher plants and animals, the base number of nuclear chromosomes is called the *haploid* number, denoted as *n*. Individuals of most species are *diploid*, having double the haploid number of chromosomes (2*n*) in each somatic cell. Aneuploid and polyploid organisms have abnormal numbers of whole chromosomes.

Aneuploidy

Strictly speaking, aneuploidy refers to any number of chromosomes in a cell or organism that is not an exact multiple of the haploid number. However, in common practice the term is used to refer specifically to situations in which an organism or cell has only one chromosome or a few chromosomes added or missing. In animals, aneuploidy is usually lethal and so is rarely encountered. In the plant kingdom, on the other hand, the addition or elimination of a small number of individual chromosomes may be better tolerated.

Nullisomy is the aneuploid condition in which two homologous chromosomes are missing, so that the organism has $2n - 2$ chromosomes. *Monosomy* refers to the absence of a single chromosome, giving $2n - 1$ total chromosomes. In *trisomy*, one extra chromosome is present ($2n + 1$). An example of aneuploidy in humans is the case of Down syndrome, trisomy-21, in which the individual has one extra copy of the twenty-first chromosome (thus, three total copies).

Aneuploidy is caused by *nondisjunction*, which occurs when a pair of homologous chromosomes fail to separate during cell division. If nondisjunction occurs in the first stage of meiosis, all four resulting gametes will be abnormal. Two of them will have no copy of the given chromosome, and two, correspondingly, will have one extra copy each. If nondisjunction occurs in the second stage of meiosis, one of the four resulting gametes will have no copy of the given chromosome, another will have an extra copy, and two will be normal.

Polyploidy

Polyploidy is caused by the addition of one or more complete chromosome sets to the normal diploid complement. In the animal kingdom polyploidy is lethal in nearly every case, but it is relatively common in plants. It is estimated that between 30 percent and 70 percent of extant angiosperms are polyploid. The process of sex determination is more sensitive to polyploidy in animals than in plants, and because many plants undergo self-fertilization, those with an even number of chromosome sets (such as those that are tetraploid) may still produce fertile gametes. This fact points to the crucial factor that determines whether a polyploid plant may be fertile: whether it has an even or an odd number of chromosome sets. Plants with an odd number of chromosome sets are almost always sterile. Because they always have an unpaired chromosome of each type, it is extremely unlikely for them to produce viable balanced gametes. On the other hand, there is potential for a polyploid plant with an even number of chromosome sets to produce a balanced gamete if multiple sets of conspecific chromosomes pair during meiosis.

Autopolyploidy and Allopolyploidy

Polyploid plants exist in two categories. *Autopolyploids* have a genome comprising multiple sets of chromosomes that are all from one species. In *allopolyploids*, the multiple sets of chromosomes come from multiple (usually related) species. Autopolyploidy can arise from situations in which a defect in meiosis creates a diploid or triploid gamete. If such a gamete is fused with a typical haploid gamete from the same species, the union leads to a polyploid zygote.

The most common such pairing, of a diploid and a haploid gamete, produces an autotriploid. As the previous section suggests, they are usually sterile. However, some sterile autotriploids that can be cultivated through vegetative propagation (by planting cuttings) are attractive food crops because they lack robust fertile seeds. For example, the cultivated banana is an effectively seedless (and therefore sterile) autotriploid; it cannot reproduce without human intervention.

Allopolyploidy arises through the interbreeding of different species. An allodiploid formed by the union of two haploid gametes from separate species will be sterile because there are no matching chromosomes to pair at meiosis. However, if the two sets of chromosomes become doubled within a cell, the result will be a potentially fertile allotetraploid. An organism in this condition is basically a double-diploid, in which homologous pairs of conspecific chromosomes can join at meiosis to produce a viable gamete. This type of polyploidy has played an important role in the natural history of many plants, including wheat, the most widely cultivated cereal in the world.

Allopolyploidy and Speciation

Contemporary domesticated wheat species can be identified as belonging to one of three groups, based on their number of chromosomes. One group has fourteen chromosomes, another twenty-eight, and a third has forty-two chromosomes. These groups form a series of polyploids based on a haploid number, n, equal to seven chromosomes. It is believed that these groups of domesticated wheat evolved in two major steps. First, members of a diploid genus *Triticum* ($2n$ = fourteen chromosomes) may have hybridized with one of the diploid goat grasses *Aegilops* ($2n$ = fourteen chromosomes) to form allotetraploid species of emmer and durum wheats ($4n$ = twenty-eight chromosomes). Then, it is believed, these species underwent a second round of hybridization with separate goat grass species to form the allohexaploid ($6n$ = forty-two chromosomes) species that is now known as bread wheat, or *Triticum aestivum*. Bread wheat, which probably appeared around eight thousand years ago, combines desirable qualities of all three of its diploid relatives, including nonshattering grains, a high protein content in the endosperm, and good tolerance to various environmental conditions. Allohexaploid wheat can reproduce, thanks to normal meiosis, in which homologous chromosomes pair to form a triploid gamete with twenty-one chromosomes.

The possibility of speciation by allopolyplidy is one danger of introducing plants to new regions. The American species of salt marsh grass *Spartina alterniflora* was introduced to the south coast of England around 1870, probably in ships' ballast water. It crossed with the native salt marsh grass *Spartina maritima* to form an allotetraploid species, *Spartina anglica*, which overran the native grass in the twentieth century and colonized coastal flats so aggressively as to create a floral monoculture that has proved inadequate for wintering populations of wading birds and wildfowl.

Agricultural Applications

Like wheat, many of today's other crops are polyploid. By creating polyploid lines, plant breeders can introduce desirable traits cumulatively. Among major polyploid crops are dietary staples, such as the white potato ($4n$ = forty-eight chromosomes), the domestic oat ($6n$ = forty-two chromosomes), the peanut ($4n$ = forty chromosomes), textile-producing plants such as cotton ($4n$ = fifty-two chromosomes), and the cash crops tobacco ($4n$ = forty-eight chromosomes) and coffee, of which existing species range from diploid to octoploid ($8n$ = eighty-eight chromosomes). As well as the aforementioned domesticated banana, which, as an autotriploid, is sterile and correspondingly seedless, some varieties of cultivated apple are triploid species.

Beyond engineering particular traits, another reason it is desirable to cultivate polyploid species is that polyploid plant cells are usually larger than the corresponding diploid cells. Consequently, the polyploid plants themselves are usually larger. Species of particularly large watermelons, marigolds, and snapdragons have been created through cultivation of polyploid lines.

Plant polyploidy is induced in the laboratory by treating dividing cells with the drug colchicine. It prevents the formation of a spindle during mitosis by disrupting the microtubules, causing the duplicated chromosomes to fail to separate. The most common method of application is to place the roots of a plant in a colchicine solution. Because colchicine inhibits the actual division of cells without affecting the duplication of chromosomes, when full rounds of mitosis commence upon removing the roots from the colchicine, the resulting cells contain an extra set of chromosomes.

Alistair Sponsel

See also: Agriculture: world food supplies; Biotechnology; Chromosomes; DNA in plants; Genetically modified foods; Genetics: Mendelian; Genetics: post-Mendelian; Grains; Green Revolution; High-yield crops; Hybrid zones; Hybridization; Mitosis and meiosis; Plant biotechnology; Population genetics; Species and speciation.

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POPULATION GENETICS

Categories: Evolution; genetics; reproduction and life cycles

Population genetics is concerned with analyzing the frequencies of the alleles, or forms, of genes in a population of individuals within a species. It examines how gene frequencies change across generations in response to external forces, such as mutation, natural selection, migration, or genetic drift.

The natural process that eliminates individuals of low fitness and advances those of high fitness is termed *natural selection*. Natural selection causes changes in allele frequency in a population, which is a process called *evolution*. Thus, population genetics combines Charles Darwin's ideas of natural selection and evolution with the basic principles of genetics set forth by Gregor Mendel.

The study of population genetics has many practical uses: It can help reveal how new diseases arise or why diseases persist in living organisms by examining genetic variation within populations. Population genetics principles also can be useful as guidelines for devising strategies for improving crop plants. Hardy-Weinberg equilibrium provides the framework for population genetics.

Hardy-Weinberg Theorem

The starting point for population genetics is the *Hardy-Weinberg theorem*. Derived from Mendelian principles, it states that in the absence of mutation, selection, migration, or genetic drift, the allele frequencies and genotype frequencies remain constant from generation to generation. This law applies to populations in a state of Hardy-Weinberg equilibrium, meaning large populations that are random-mating. If a population is not in this state, one generation of random mating restores equilibrium.

George H. Hardy, an English mathematician, and Wilhelm Weinberg, a German biologist and physician, independently developed this concept in 1908. In 1903 Harvard University professor William E. Castle also had shown that in the absence of selection, the composition of the randomly bred descendants of a population would remain constant thereafter. Castle did not, however, generalize the concept.

More specifically, Hardy-Weinberg equilibrium is maintained in a population as long as the following assumptions are true. First, there are a large (virtually infinite) number of individuals in the population. Second, there is random mating among individuals. Third, there are no new mutations. Fourth, there is no migration (in or out of the population). Fifth, there are no genotype-dependent differences for survival to reproductive age and transmission of genes to the next generation. This fifth assumption is often stated more succinctly as: There is no natural selection.

The Hardy-Weinberg theorem can also be expressed mathematically in the form of an equation for calculating genotype and phenotype frequencies. If two alleles at a locus, *A* and *a*, occur in a population with frequencies p and q, respectively, then (p + q) = 1. The proportion of individuals resulting from random matings will occur with the following frequencies:

$$AA = p^2,\ Aa = 2pq, \text{ and } aa = q^2$$

Putting these terms together results in the Hardy-Weinberg equation:

$$p^2 + 2pq + q^2 = 1$$

This simple equation can be modified in a variety of ways to mathematically model what happens when one or more of the Hardy Weinberg assumptions are violated. Violation of one or more of these assumptions will result in changes in allele frequencies, and thus, evolution. Changes in allele frequencies across a limited number of generations is often referred to as *microevolution*. Extending such changes across thousands of generations or more results in more extensive change and is often called *macroevolution*.

The Gene Pool

The Hardy-Weinberg equation and its modifications are used by population geneticists to describe changes in allele frequencies in *gene pools*. A gene pool represents all the genes carried and shared by individuals of an interbreeding population, with the assumption that each parent contributes equally to a large pool of gametes (eggs and pollen or sperm). Another assumption is that the parent and offspring generations are distinct, or nonoverlapping.

Species and Speciation

The gene pool of a population, when divided or isolated for a prolonged period of time, may form distinct subgroups. If, through *isolating mechanisms* such as genetic changes or geographical separation, the subpopulations are kept from interbreeding, new species may eventually arise after many generations when the isolated subpopulations evolve in different directions. The entire process of the splitting of a population into two or more reproductively isolated populations is termed *speciation*. Thus, a *species*, according to the commonly accepted *biological species concept*, is a group of interbreeding individuals that are capable of producing fertile offspring but are unable to do so with other such populations. Sometimes hybridization between two species can result in a fertile hybrid, thus exposing one of the weaknesses of the biological species concept. Speciation can be the result of either geographic separation or reproductive isolation at the cellular and molecular levels.

Manjit S. Kang

See also: Genetic drift; Genetics: Mendelian; Genetics: mutations; Genetics: post-Mendelian; Hardy-Weinberg theorem; Hybrid zones; Hybridization; Polyploidy and aneuploidy; Reproductive isolating mechanisms; Species and speciation.

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PROKARYOTES

Categories: Bacteria; cellular biology; microorganisms

Prokaryotes are one of two types of cell that form living organisms. Prokaryotic cells lack a nucleus and other organelles found in eukaryotic cells. Prokaryotes include the unicellular life-forms found in two of the three domains of life, Archaea *and* Bacteria, *whereas all protists, algae, fungi, plants, and animals are eukaryotic organisms, together forming the domain* Eukarya.

There are architecturally two distinct types of cells of living organisms: prokaryotic cells and eukaryotic cells. The defining difference between these two types of cells is that prokaryotic cells lack any of the internal membrane-bound structures (organelles) found in eukaryotic cells, such as a nucleus, mitochondria, chloroplasts, endoplasmic reticulum, and Golgi apparatus. Bacterial and archaeal cells are prokaryotes, while plants, animals, fungi, algae, and protozoa (protists) are composed of eukaryotic cells.

Structure

Although prokaryotic cells do not contain membrane-bound organelles, they do have a highly complex organization and structure. Like all cells, prokaryotes are surrounded by a *cytoplasmic membrane*. This membrane is composed of proteins and lipids and is semipermeable. This semipermeable layer regulates the flow of material into and out of the cell.

For most prokaryotes, the cell membrane is surrounded by a *cell wall*. The cell wall of almost every bacterial cell contains peptidoglycan, a cross-linked structure consisting of chains of sugar molecules, with the chains attached to one another through bridges composed of amino acids. This cell wall protects the bacterial cell from osmotic shock. Some bacterial cells also have an *outer membrane* linked to the peptidoglycan layer by lipoproteins. The outer membrane is a lipid bilayer that contains sugars and lipids and is known as lipopolysaccharide (LPS). LPS is often called endotoxin because this molecule can induce fever, shock, and death in animals. Archaeal cells may have cell walls composed of pseudopeptidoglycan, which is very similar to the peptidoglycan layer found in bacterial cells, or they may have cell walls composed of protein, polysaccharides, or other chemicals. Some bacteria and archaea lack cell walls entirely.

Some prokaryotic cells have structures external to the cell wall. These structures include capsules, slime layers, and S layers. *Capsules* are usually composed of polysaccharides, although some cells have proteinaceous capsules. Capsules are protective layers that are particularly important in allowing disease-causing bacteria to evade attack by mammalian immune systems. *Slime layers* are composed of polysaccharides and resemble less organized capsules. Slime layers help bacteria attach to surfaces, prevent dessication, and assist in trapping nutrients near the cell. *S layers* are crystalline protein layers of unknown function.

Many prokaryotic cells are motile due to the presence of *flagella*. Some bacteria have flagella attached only at one or both ends of the cell. These flagella are known as polar flagella. Other bacteria have flagella all around the cell, an arrangement known as peritrichous. Each flagellum is an inflexible, helical structure composed of molecules of the protein flagellin. Flagella rotate like propellers, causing bacteria to move in a corkscrew fashion.

Some prokaryotes produce *spores*, specialized structures that are extremely resistant to heat, cold, and desiccation. Spores are metabolically inert and can survive for extended periods, possibly for thousands of years. Spores form within prokaryotic cells when environmental conditions become unfavorable for survival. Once the spore is formed, the cell that produced the spore breaks open, releasing the spore. When the spore finds itself in favorable growth conditions, it germinates by swelling, breaking out of the spore coat, and resuming metabolic function.

Reproduction

Prokaryotic cells reproduce by *binary fission*. The cell cycle of prokaryotes has three parts: elongation, DNA synthesis, and cell division. During elongation, the cell synthesizes and secretes cytoplasmic membrane and cell wall material. Prokaryotes usually possess a single, double-stranded, circular DNA chromosome attached to the cytoplasmic membrane at one point. DNA synthesis, which occurs continuously in actively growing cells, results in two complete copies of the chromosome, each attached to the cytoplasmic membrane. As new membrane material is inserted into the cytoplasmic membrane during elongation, the two chromosomes are swept away from one another. During cell division, a septum forms in the center of the cell which eventually divides the cell into two daughter cells.

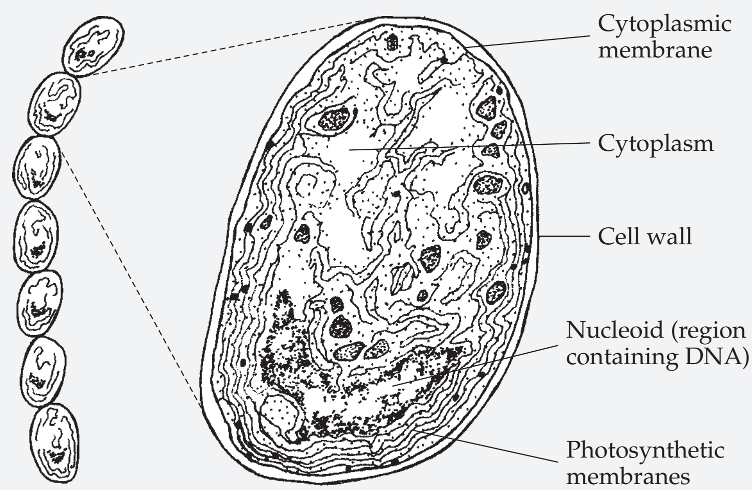
Binary fission is a type of asexual reproduction. Each of the daughter cells is identical to the parent cell, and there is no exchange of genetic material. Some prokaryotes, however, do engage in genetic recombination through a process called *conjugation*. Conjugation requires the presence of extrachromosomal pieces of DNA called *plasmids*. These plasmids are small, circular DNA molecules found in the cytoplasm of many prokaryotic cells. Some of these plasmids contain genes that encode a special structure, the *F-pilus*. The F-pilus is a proteinaceous rod that extends from the surface of cells. Cells that have an F-pilus are donor cells and can attach, via the F-pilus, to recipient cells which lack an F-pilus. Following attachment, the F-pilus contracts, drawing the donor and recipient close together. The donor then transfers DNA to the recipient. Although conjugation results in transfer of genes from one cell to another, it is not itself a method of reproduction.

Metabolism

Prokaryotes are metabolically diverse. Two basic nutritional pathways are found: autotrophy and heterotrophy. Autotrophic prokaryotes are capable of synthesizing their own energy-yielding compounds from simple inorganic compounds such as carbon dioxide and water. Some prokaryotic autotrophs, the cyanobacteria and the green and purple bacteria, utilize the energy from sunlight, in a process known as photosynthesis, to construct food molecules. It has been hypothesized that chloroplasts in plant cells evolved from cyanobacteria that were engulfed by a eukaryotic cell more than one billion years ago. Other autotrophs extract energy from metabolizing inorganic compounds such as hydrogen sulfide, iron sulfide, and ammonia.

Heterotrophic prokaryotes obtain energy from the metabolism of organic compounds. Various prokaryotes are capable of metabolizing a wide variety of organic molecules, including sugars, lipids, proteins, petroleum products, antibiotics, and methanol. Heterotrophs can metabolize food molecules using one of three methods: fermentation, aerobic respiration, and anaerobic respiration. Fermentation and anaerobic respiration do not require

A Prokaryotic Cell



Kimberly L. Dawson Kurnizki

The simplest life-forms, archaea and bacteria, comprise prokaryotic cells. Based on an electron microscope image of one cell in a string forming a cyanobacterium, this depiction shows the basic features of a prokaryote: cell wall, cytoplasmic membrane, cytoplasm, and in this organism photosynthetic membranes and a series of internal membranes housing photosynthetic pigments such as chlorophyll. Prokaryotic cells lack the defined nucleus and organelles found in eukaryotic cells, and instead the genetic material is located in an unbound region called the nucleoid.

the presence of oxygen, while aerobic respiration does require oxygen. Fermentation often results in metabolic end products that include acids, carbon dioxide, alcohol, or a combination of these. The anaerobic respiration process is similar to aerobic respiration, except that molecules such as nitrate, sulfate, and iron are used instead of oxygen. The end products of aerobic respiration are carbon dioxide and water; for anaerobic respiration they are nitrite, hydrogen sulfide, or other reduced compounds.

Roles in the Global Ecosystem

Prokaryotes play important roles in the decay of organic matter as well as in three vital cycles of nature: the carbon, sulfur, and nitrogen cycles. The major categories of biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids) are all carbon-containing compounds. Photosynthetic organisms, including photosynthetic prokaryotes, take carbon dioxide and convert it into carbohydrates. Those carbohydrates can be used for energy and biosynthesis by the photosynthetic organisms as well as by heterotrophs, which consume the photosynthetic organisms. Both heterotrophs and autotrophs also metabolize carbon-containing molecules, releasing carbon dioxide back into the atmosphere.

Sulfur is a component of certain amino acids found in proteins. As *decomposers*, prokaryotes decompose proteins deposited in water and soil by dead organisms and release the sulfur from sulfur-containing amino acids, often in the form of hydrogen sulfide. Some prokaryotes convert hydrogen sulfide to sulfates during their metabolism. The sulfates can then be taken up by plants, where they are reincorporated into sulfur-containing amino acids.

Nitrogen is an essential element in nucleic acids and proteins. Some prokaryotes, particularly soil microbes, digest proteins and release ammonia. Denitrification occurs when groups of symbiotic prokaryotes metabolize ammonia, first to nitrites, then to nitrates, then to atmospheric nitrogen. Nitrogen fixation occurs when nitrogen-fixing prokaryotes in the soil trap atmospheric nitrogen and convert it to ammonia that can be used by plants to synthesize new proteins and amino acids.

Disease

Infectious disease is a disturbance in normal organismal function caused by an infecting agent. Although most prokaryotes do not cause disease, some bacteria are capable of parasitizing a host and disrupting normal function. Prokaryotes capable of producing disease in plants are widely distributed and cause a number of diseases, including wilts, rots, blights, and galls. Some of these diseases are caused by soil-dwelling prokaryotes, while others are seedborne or are caused by obligate parasites, unable to survive outside plant tissue.

Commercial Uses

Prokaryotes are easily manipulated and therefore are useful for many commercial applications. Prokaryotes have been used for centuries in the production of food. Yogurt, sauerkraut, poi, kimchee, dry and semidry sausages, and vinegar are all examples of bacterially produced foods. Genetic engineering is more easily accomplished in prokaryotes than in eukaryotes. Prokaryotes now produce human insulin, antibiotics, plant hormones, and industrial solvents. Prokaryotes have been engineered to protect plants from frost damage, while plants have been genetically engineered, using bacterial vectors, to develop resistance to herbicides and to produce toxins that destroy insect pests.

Lisa M. Sardinia

See also: Anaerobes and heterotrophs; Anaerobic photosynthesis; *Archaea*; Bacteria; Cell wall; Chemotaxis; Chloroplasts and other plastics; Diseases and disorders; Eukaryotic cells; Evolution of cells; Flagella and cilia; Gene regulation; Genetic code; Membrane structure; Microbial nutrition and metabolism; Mitosis and meiosis; Molecular systematics; Paleoecology; Plasma membranes; *Protista*; Respiration; Systematics and taxonomy.

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PROTEINS AND AMINO ACIDS

Category: Cellular biology

Proteins are found in all cells and carry out a variety of important cellular functions. Within any one cell there may be thousands of different proteins having a variety of sizes, structures, and functions. Proteins are also important structural components of the cell wall.

Proteins are the most complex and abundant of the macromolecules. Within cells, many proteins function as enzymes in the catalysis of metabolic reactions, while others serve as transport molecules, storage proteins, electron carriers, and structural components of the cell. They are especially important in seeds, where they make up as much as 40 percent of the seed's weight and serve to store amino acids for the developing embryo. Proteins are also important structural components of the cell wall. Because proteins and their building blocks, amino acids, form such a large component of plant life, plants serve as an important dietary source of the eight to ten essential amino acids for humans and other animals.

Amino Acids

Amino acids are the molecular building blocks of proteins. Amino acids all share a structure, with a central carbon atom, the alpha carbon, covalently bonded to a hydrogen atom, an amino group, a carboxylic acid group, and a group designated as an R group, which varies in structure from amino acid to amino acid. It is the diverse nature of the R group that provides the protein with many of its structural and functional characteristics. Some R groups are either polar or electrically charged at physiological pH, making the R groups hydrophilic (water-loving). Other R groups are nonpolar and hydrophobic (water-avoiding). The twenty standard amino acids the cell uses to synthesize its proteins are alanine, arginine, aspartate (aspartic acid), asparagine, cysteine, glutamate (glutamic acid), glutamine, glycine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, proline, serine, threonine, tryptophan, tyrosine, and valine.

Each of the twenty amino acids differs from the other nineteen in the structure of its R group. Once incorporated into a protein, a standard amino acid may undergo modification to create nonstandard amino acids and an even greater diversity of protein structures. One of the more common nonstandard amino acids found in proteins is hydroxyproline, which is commonly found in plant cell-wall proteins. In addition to the twenty amino acids that build proteins, many nonstandard amino acids occur free in the cell and are not found in proteins. Canavanine, for example, occurs in the seeds of many legumes.

Based on the information in cellular deoxyribonucleic acid (DNA), the cell joins the twenty standard amino acids by peptide bonds in specific sequences, resulting in chains ranging from as few as two amino acids to many thousands. Shorter chains of amino acids are referred to as *peptides* or *oligopeptides*, while longer chains are referred to as *polypeptides*. The term "protein" is usually reserved for those oligopeptides and polypeptides that have biological functions, because single polypeptides often do not have biological functions unless associated with other polypeptides.

Primary Structure

Proteins differ from one another in the sequences of their amino acids. The sequence of amino acids of a protein is called its *primary structure*. Mutations have been shown to result in the change of as few as one amino acid in a protein. Because DNA specifies a protein's primary structure, protein sequence information is often used to study the evolutionary relationships among organisms.

Proteins are often complexed with other compounds in their biologically active state. These proteins are called *conjugated proteins*. Proteins complexed with metals, lipids, sugars, and riboflavin are called *metalloproteins*, *lipoproteins*, *glycoproteins*, and *flavoproteins*, respectively. Glycoproteins (literally, "sugar proteins") are important constituents of the plasma membrane. These sugar molecules can occur singly or in short, simple branched chains.

A protein chain may be folded into a variety of three-dimensional shapes. The three-dimensional shape a protein assumes is called its *conformation* and is determined by its amino acid sequence. In order for a protein to be active, it must assume a certain conformation. Any alteration in its conformation may result in reduced activity. Denaturing agents alter the structure of a protein so that it loses its conformation, biological function, and activity.

Secondary Structure

The *secondary structure* refers to the local folding or conformation of the polypeptide chain over relatively short (fifty amino acids or so) stretches. Two common secondary structures, the alpha helix and the beta sheet, occur regularly in proteins. On average, only about half of the polypeptide chain assumes the alpha or beta conformation, while the remainder exists in turns and random structures. Some proteins show only alpha structure, others only the beta structure, while still others show either a mixture of the two structures or neither secondary structure. Both the alpha and the beta structures increase the structural stability of the protein. The amino acid sequence determines whether a particular sequence of amino acids in a protein will assume the alpha or beta structure.

Tertiary Structure

The overall spatial orientation of the entire polypeptide chain in space is referred to as its *tertiary structure*. Generally, two tertiary structures are recognized. Fibrous or filamentous proteins are arranged as fibers or sheets, while globular proteins are arranged roughly as spherical or globular structures. The amino acid sequence determines the overall folding of the protein tertiary structure. Fibrous proteins are primarily involved with structural functions, whereas globular proteins function as enzymes, transport molecules, electron carriers, and regulatory proteins.

Quaternary Structure

Some proteins are composed of more than one polypeptide chain. A protein composed of only one polypeptide is called a *monomer*, while proteins composed of two, three, four, and so on are referred to as *dimers*, *trimers*, and *tetramers*, and so on, respectively.

Charles L. Vigue

See also: Carbohydrates; Cell wall; Chromosomes; Cytoskeleton; Cytoplasm; Cytosol; DNA in plants; DNA replication; Endomembrane system and Golgi complex; Endoplasmic reticulum; Energy flow in plant cells; Evolution of cells; Lipids; Membrane structure; Nuclear envelope; Nucleic acids; Nucleolus; Nucleoplasm; Nucleus; Oil bodies; Plasma membranes; RNA.

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PROTISTA

Categories: Microorganisms; *Protista*; taxonomic groups; water-related life

The Protista *form one of the four kingdoms of eukaryotic organisms and include the algae, protozoans, slime molds, and oomycota.*

Included among the diverse organisms called protistans (kingdom *Protista*) are algae, protozoans, slime molds, and the oomycota. Algae were long considered to be simple plants and were assigned to kingdom *Plantae* but lack the more highly differentiated tissues and organs characteristic of "higher plants" such as mosses, ferns, and seed plants. Protozoa, all of which are unicellular, were assigned to the kingdom *Animalia*; considered more animal-like than plant-like, they are not considered here in detail.

The two remaining groups of protists, the slime molds and oomycota, were traditionally considered fungi, as indicated by their names (*mycoto* means "fungus"), and accordingly were assigned to the kingdom *Fungi*, largely due to their being heterotrophs (nonphotosynthetic). As information about the true nature of these life-forms has accumulated, however, they were grouped together with the protists. Nevertheless, *Protista* is a heterogeneous kingdom, composed of both the heterotrophic slime molds and oomycetes and the autotrophic (photosynthetic) algae. Thus, the kingdom *Protista* is a "catch-all" group, containing various organisms that seem not to fit into any of the other kingdoms.

Biology of the *Protista*

Most protistans are unicellular, but some, notably the large species of marine algae called kelps and seaweed, are multicellular. All are eukaryotic (with cells that have nuclei, making them members of the domain *Eukarya*, along with fungi, plants, and animals), in contrast to prokaryotic bacteria (which are divided between the domains *Archaea* and *Bacteria*).

In addition to having a distinct nucleus surrounded by a nuclear membrane (envelope), the cytoplasm of a eukaryotic cell contains various types of organelles, each specialized for performing a particular task (or related ones). Examples are mitochondria (cellular respiration), chloroplasts (photosynthesis), Golgi bodies (packaging of molecules), and the endoplasmic reticulum (to lend rigidity). As a result of this specialization, eukaryotic cells are able to function more efficiently than do prokaryotic cells, which must perform the same functions but within the cell as a whole. In this way, protistans are similar to plants, animals, and fungi. Furthermore, the evolution of eukaryotic cells from prokaryotic ones was a pivotal event in the evolution of life, leading not only to protistans but also from them to the more highly evolved kingdoms.

As previously stated, protists exist in great variety. Included are some that, due to the absence of a rigid cell wall, are able to change shape rapidly. Other protists have cell walls surrounding their cell membranes, resulting in a more permanent shape. Some possess fringelike cilia or whiplike flagella which they use to swim; others move by other means; many are nonmotile. Some protists live solitary lives, while others aggregate to form colonies. Some are parasitic, whereas most are free-living (nonparasitic).

In size there is also great variation: Many are unicellular and microscopic, while some algae, such as the kelps and seaweeds, grow to many meters in length. Furthermore, many protists have complex life cycles, with the various stages possessing different combinations of these characteristics.

Biologists generally agree that fungi, plants, and

Phyla of *Protista*

Phylum	*Common Name*	*Approx. Species*
Slime molds		
Dictyosteliomycota	Cellular slime molds	50
Myxomycota	Plasmodial slime molds	700
Water molds		
Oomycota	Oomycetes	700
Algae		
Bacillariophyta	Diatoms	100,000+
Chlorophyta	Green algae	17,000
Chrysophyta	Chrysophytes	1,000
Cryptophyta	Cryptomonads	200
Dinophyta	Dinoflagellates	4,000
Euglenophyta	Euglenoids	1,000
Haptophyta	Haptophytes	300
Phaeophyta	Brown algae	1,500
Rhodophyta	Red algae	6,000

Source: Data on numbers of species adapted from Peter H. Raven et al., *Biology of Plants*, 6th ed. (New York: W. H. Freeman/Worth, 1999).

animals are derived from ancient protists. Thus, the study of protists, which continue to inhabit the earth, sheds light on the origin of these groups of more highly evolved organisms. Also, each of these modern protists plays an ecological role together with the other organisms that occupy its ecosystem. Some protists affect humans more directly as agents of disease; some serve as a source (or potential source) of medicines that can be used to combat various diseases.

Algae: Classification

The term "algae" (singular "alga"), when unqualified, refers generally to an organism, usually inhabiting water or a wet habitat, that is somewhat plantlike (photosynthetic) but that lacks the more specialized tissues characteristic of plants. Furthermore, nearly all algae produce reproductive cells, spores or gametes, which lack surrounding specialized enclosures such as are typical of plants.

The blue-green "algae," historically considered to be algae, are now recognized as a separate group of organisms. As they are prokaryotic, they are now considered to be a special type of bacteria, the *cyanobacteria*. They differ from other bacteria primarily because they possess chlorophyll and therefore have the ability to photosynthesize.

Within the kingdom *Protista*, algae are currently divided by phycologists (scientists who study algae) among anywhere from four to thirteen phyla. Here, a system is used in which nine phyla of the kingdom *Protista* include algae. The nine phyla include the following.

Euglenophyta (euglenoids). This small group of protists (about nine hundred species) is a good starting point for studying algae, as euglenoids combine traits characteristic of plants, fungi, and animals. All are unicellular, and nearly all are mobile by means of two flagella that emerge from a groove at the end of the cell. By means of an eyespot near the base of the flagella, euglenoids can detect light and swim toward it. Most members of the phylum lack chlorophyll and therefore must absorb food from external sources. Others, though, such as *Euglena*, have chloroplasts with chlorophylls *a* and *b*, along with carotenoids and accessory pigments. They reproduce by fission (cell division). Most are freshwater organisms, but a few occur in brackish or marine environments.

Cryptophyta (cryptomonads). These algae are single-celled flagellates that are commonly brownish, blue-green, or red. Their name (Greek *kryptos* means "hidden") refers to their small size (3-50 micrometers), which makes them inconspicuous. Like euglenoids, they include both colorless (unpigmented) and pigmented photosynthetic members. Pigments includes chlorophylls *a* and *c* and carotenoids. Evidence exists to indicate that cryptomonads arose from the fusion of two different kinds of eukaryotic cells. Of the two hundred known species, some are marine; others live in fresh water.

Rhodophyta (red algae). Red algae are primarily multicellular marine organisms and are commonly referred to as *seaweeds*. However, about one hundred of the five hundred species are unicellular and live in fresh water. The chloroplasts of red algae contain chlorophyll *a*, but the presence of phycobilins (red pigments) usually masks the chlorophyll, giving them a red or reddish appearance. The red pigment aids in light absorption in deep water, where many red algae are found. As chloroplasts of red algae resemble those of cyanobacteria, there is reason to believe that they probably evolved from these prokaryotic organisms.

One group of red algae, the *coralline algae*, deposit calcium carbonate in their cell walls, resulting in stony formations in the ocean. They are often associated with coral reefs, which they help to stabilize.

Many red algae have complicated life histories. The simplest type is that in which a haploid gametophyte alternates with a diploid sporophyte. This pattern, known also throughout the plant kingdom, is known as alternation of generations. In most red algae, there are three generations: a haploid gametophyte, a carposporophyte, and a tetrasporophyte (both diploid). It has now been recognized that some red algae previously considered to be different species are actually different stages of the same species.

Dinophyta (dinoflagellates). Most dinoflagellates are unicellular marine algae, each with two flagella. Of the two, one is within an equatorial groove around the cell; the other passes down a longitudinal groove before extending outward. In addition to chlorophyll, they have accessory pigments that give them a golden-brown color. Many dinoflagellates are associated symbiotically with various invertebrates; for example, many corals benefit from the food they derive from these algae. Other dinoflagellates are nonphotosynthetic and live as parasites within other marine organisms.

Many dinoflagellates are bioluminescent; they emit a faint light that can be seen in darkness from a passing ship. Others are responsible for fish kills when they become superabundant in warm stagnant water. The death of the fish within these "red tides" is often due to toxins produced by the dinoflagellates.

Haptophyta (haptophytes). This group, consisting of only about three hundred known species, includes a diversity of primarily marine species, but some freshwater and even terrestial species are known. Included are both unicellular and colonial flagellates, along with others that are nonmotile. The distinctive feature of haptophytes is the haptonema, a threadlike structure that bends and coils as it apparently helps the cell to catch food particles. It differs from a flagellum by lacking the 9 + 2 arrangement of microtubules, which is characteristic of flagella of eukaryotic cells. Most haptophytes are photosynthetic and possess chlorophylls *a* and *c* together with an accessory pigment such as fucoxanthin. Although the phenomenon is not as well documented as for dinoflagellates, haptophytes also cause marine fish kills by releasing toxins.

Chrysophyta (chrysophytes). Some one thousand species of chrysophytes exist, including both unicellular and colonial organisms that are often abundant in both fresh and marine habitats. Some lack chlorophylls *a* and *c*. However, the golden color of fucoxanthin, which they possess, usually masks the green pigments, giving them their characteristic golden hue and accounting for their name (*chrysos* means "gold"). Some chrysophytes feed on bacteria. Some are responsible for "brown tides" that causes damage to shellfish and salmon fisheries.

Bacillariophyta (diatoms). The name "diatom" comes from the two overlapping shells that fit together like the two parts of a candy box. Composed of silica (silicon dioxide), the shells persist long after the living cell inside has died. Most species are photosynthetic, possessing chlorophylls *a* and *c* as well as fucoxanthin. The life cycles of diatoms include both asexual (cell division) and sexual phases.

It would be difficult to overestimate the importance of diatoms. There are more than 100,000 known species, and they are abundant in practically all aquatic and marine habitats. Due to the persistence of their shells, it is known that there aremany extinct species also. Diatoms are responsible for as much as 25 percent of total world food production (photosynthesis). Especially in polar waters, they are the primary food source for aquatic animals. Large accumulations of diatom shells, known as "diatomaceous earth," are mined, cleaned, and used in filters, in gas masks, in toothpaste, and for a variety of other purposes.

Phaeophyta (brown algae). Found only in salt water, this group includes large, conspicuous, multicellular forms generally called *kelps* or seaweeds. Often seen on rocky shores, various of the fifteen hundred species inhabit the ocean, especially in temperate and cooler waters. *Laminaria* are called kelps and often form "kelp forests" along the gently sloping shores off the coast of California.

Although lacking true roots, stems, and leaves, kelps have the most highly differentiated bodies of any of the algae. Some of their cells resemble the phloem (food-conducting cells) of vascular plants. The brown pigment fucoxanthin is present in addition to chlorophylls *a* and *c*.

Chlorophyta (green algae). The seventeen thousand or more species of green algae are perhaps the most diverse group of the algae. Most live in fresh water, but some live in the ocean, and others live in soil or on tree trunks. Many form symbiotic associations with sponges, protozoa, and other invertebrates; others are associated with fungi within lichens. As green algae resemble plants more than do any other group of algae, plants are believed to have evolved from green algae. They, like plants, possess chlorophyll *a* and *b*; food is stored in specialized cytoplasmic organelles called plastids.

The phylum is divided into three classes. In the class *Chlorophyceae* are included a diversity of forms, nearly all of which are freshwater species. *Chlamydomonas* is a motile unicellular species which, nevertheless, exhibits a complex life cycle. *Volvox* and several other large spherical colonial forms are composed of cells, each of which strongly resembles *Chlamydomonas*. Other members of this class are filamentous.

The class *Ulvophyceae* includes primarily marine species. A common example is the *Ulva* species (sea lettuce), composed of flat sheets of cells; it is found in shallow seas around the world.

Included in the class *Charophyceae* is the familiar *Spirogyra*, a freshwater filamentous species with spiral chloroplasts.

Human Uses of Algae

References have already been made to ways that algae are involved in the overall "economy of nature." Because algae are autotrophs (producers) and photosynthesize, they generate food that is made available to the heterotrophic animals (consumers). At the same time, oxygen, which results as a by-product, is made available to these same animals. As algae perform functions in marine and freshwater environments that are similar to those performed by grasses (and other plants) on land, algae have been called "the grasses of many waters."

Algae are often involved also in human affairs in more direct ways. In Asian countries especially, kelps and other multicellular algae have been used for food for centuries. Nori, a red alga of the genus *Porphyra* has been collected and eaten as a vegetable in Japan and China. It is now cultivated on a large scale, thus increasing its availability and popularity. Unfortunately, most seaweeds are not high in food value, although they do provide some needed minerals and vitamins. Another problem is their taste, which is not acceptable to many Westerners.

Of more commercial value in Europe and North America are a number of products derived from kelps and various seaweeds: alginates, carrageenans, and agar. *Alginates* are hydrophobic (water-attracting) compounds derived from various brown algae such as *Laminaria*. After they are harvested mechanically from the ocean, the algae are processed. The resulting products are salts of sodium and potassium alginate. These alginates are used in the paper industry as a sizing and polishing agent and in the manufacture of paints, cosmetics, and a wide variety of foods. In each case, the role of the alginate is to improve the consistency of the product and to prevent the separation of its ingredients.

Carrageenans are obtained primarily from Irish moss (*Chondrus crispus*), a red alga found off the coast of New England. After processing, the resulting carrageenans are used for some of the same purposes as alginates. However, because of their higher melting point, they have been found superior for uses in many kinds of foods, especially desserts.

The pioneer German bacteriologist Robert Koch popularized the use of *agar* for the culture of bacteria. Agar is obtained from certain red algae. After processing and cleaning, agar is added in small quantities (1-2 percent) to water along with nutrients required by the bacteria. The result is a solid medium on which bacteria can be isolated from a mixed culture.

Although Asians have long used certain algae for folk medicinal purposes, their use in Western medicine has until recently been limited largely to serving as a binder in medicinal tablets or as a laxative. Their potential as a source of therapeutic drugs is being pursued by an increasing number of researchers. Included are those from which antibiotics and anticancer drugs may be extracted.

Slime Molds

As the name indicates, these organisms resemble molds (kingdom *Fungi*) and thus have historically been considered to be fungi. Like fungi, they are heterotrophic and are found growing on decaying organic matter. However, the accumulation of more data, including molecular information, indicates that they are a group distinct from fungi. Slime molds are typically divided between two phyla.

Plasmodial slime molds (phylum *Myxomycota*) often exist as a conspicuous fan-shaped mass of protoplasm that creeps along a surface somewhat as do amoebas. From this stage, known as a plasmodium, are formed sporangia with spores inside. From the spores are formed the single-celled amoebalike stage; they converge to form the plasmodium.

Cellular slime molds (phylum *Dictyosteliomycota*) are amoeba-like organisms that combine at one stage to form "slugs," or pseudoplasmodia. Like that in plasmodial slime molds, reproduction in cellular slime molds is both sexual and asexual, but, unlike plasmodial slime molds, no flagellated cells are known. In both types of slime molds, particulate food such as bacteria can be ingested (fungi absorb only digested food).

Oomycetes

Also previously considered to be fungi, oomycetes (phylum *Oomycota*) are probably more nearly related to certain algae than to fungi. Like algae, their cell walls are of cellulose. Some species are unicellular, whereas others are filamentous or highly branched. Some of the filamentous forms are coenocytic (no cell walls separate adjacent cells). The name of the group reflects the large female gamete or egg; this type of sexual reproduction is called oogamy.

Some terrestial oomycetes are plant pathogens of considerable importance. Downy mildew of grapes, caused by *Plasmopara viticola*, has often threatened the wine industry of France. Species of the genus *Phytophthora* cause diseases of many fruit crops and other plants of economic importance. Among these is *P. infestans*, which causes the potato late blight. One particular outbreak of this parasite caused the infamous Irish Potato Famine of the mid-1840's, during which more than a million people (some estimates say four million) were affected.

Saprolegnia is a prominent member of a group of aquatic oomycetes called "water molds." Most are saprophytic on dead plants and animals, but a few are parasitic.

Thomas E. Hemmerly

See also: Algae; Brown algae; Cellular slime molds; *Charophyceae*; *Chlorophyceae*; Chrysophytes; Cryptomonads; Diatoms; Dinoflagellates; Euglenoids; Eukaryotic cells; Evolution of cells; Green algae; Haptophytes; Oomycetes; Phytoplankton; Plasmodial slime molds; Red algae; *Ulvophyceae*.

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PSILOTOPHYTES

Categories: Evolution; paleobotany; *Plantae*; seedless vascular plants; taxonomic groups

Psilotophyte is the common name for members of the phylum Psilotophyta *(from the Greek word* psilos, *meaning "bare"). Molecular evidence points to the likelihood of psilotophytes as being highly reduced (and therefore derived) ferns. If psilotophytes are indeed reduced ferns, they probably diverged from the fern lineage early, after ferns arose some 400 million years ago during the Devonian period.*

The family *Psilotaceae* is the only family of psilotophytes. There are two living genera: *Psilotum* and *Tmesipteris*. *Psilotum*, the whiskfern, is widespread throughout tropical and subtropical regions. Lacking leaves and roots, *Psilotum* species grow in a variety of soil conditions, including very warm soils near active volcanoes, or they may be epiphytic, growing on the trunks of host trees. *Psilotum nudum*, the best-known species of psilotophyte, has an upright growth habit and is easily maintained in greenhouse culture. One epiphytic species of *Psilotum* has a pendulous, or hanging, growth habit.

Tmesipteris is found only in the South Pacific region, including Australia, New Zealand, and some South Pacific islands. Terrestrial species of *Tmesipteris* may be upright in growth habit, while some species are epiphytes growing on the stems of ferns and trees or in mounds of moist humus. Epiphytic *Tmesipteris* species express a pendulous growth habit.

Although psilotophytes have a rather restricted range and do not appear to be a highly diverse group, they are important members of the ecosystems in which they are found. *Psilotum* has been cultivated as a horticultural specimen for many years in Asia. One particular variety, called *Bunryu-zan*, has been selected to express no prophylls and to produce synangia (fused sporangia, the sites of spore production) at the tips of the aerial branches, which makes this *Psilotum* variety appear even more similar to plants known only from the fossil record.

Life Cycle

Psilotophytes exhibit a life cycle pattern called alternation of generations. Haploid spores produced in the sporangia of the diploid sporophytes (the diploid, spore-producing, generation) are released when the sporangium splits open. The spores fall to the ground or into rock or bark crevices, where they germinate in complete darkness.

Haploid gametophytes (the haploid, gamete-producing generation) develop from the spores. The nonphotosynthetic underground gametophytes are completely dependent on their endophytic fungal partners for energy. Male and female sex organs develop on a single gametophyte. Usually, the male antheridia and the female archegonia develop at slightly different times to reduce the likelihood of self-fertilization. When gametes (egg and sperm) are mature and when liquid water is present, multiflagellated sperm are released from the antheridia and swim to a nearby archegonium. The sperm swim through the neck of the archegonium, where fertilization takes place in the venter. The resulting zygote develops into an embryo, which in turn develops into a young sporophyte. The young sporophyte stage is dependent on the gametophyte for support until it grows through the soil and begins photosynthesis.

Image Not Available

Sporophyte Anatomy

As is the pattern in vascular plants, the diploid sporophyte generation is the dominant phase of the life cycle. Psilotophytes have many features that are similar to primitive vascular plants. Like fossil vascular plants, psilotophytes have a horizontal stem called a rhizome. Aerial branches grow from the rhizome. The lower portions of the aerial stems in *Psilotum* are often five-sided, while the upper aerial stems are usually three-sided. Both the rhizome and the aerial stem branch dichotomously, which means they tend to produce two equal branches at each node. *Psilotum* usually produces several dichotomies, or branching series, while *Tmesipteris* may have only one dichotomy on a particular aerial stem. Dichotomous branching is considered a primitive characteristic.

The outermost layer of the stem is composed of epidermal tissue. A waxy cuticle covers the epidermis of the aerial branches. Stomata are present in spaces between the ribs, which run lengthwise along the branch. Interior to the epidermis is a wide cortex region. The cortex is composed of parenchyma cells. The cortex parenchyma is important for storage, as is evident from the presence of the many starch granules in each cell. Lying inward from the cortex in *Psilotum* is a layer of cells called the endodermis. Endodermal cells have a layer of suberin (fatty material) called a Casparian strip embedded in part of their cell walls to restrict water movement into and out of the vascular cylinder. The endodermis is well developed throughout the aerial part of the *Psilotum* plant body as well as the underground parts. In *Tmesipteris*, the endodermis is present only in the rhizome. A layer of cells containing tannins and phenolic compounds lies between the phloem cylinder and the cortex in Tmesipteris stems. This layer may be the physiologically active equivalent of an endodermis.

Although psilotophytes lack true roots, they do possess rootlike epidermal extensions called rhizoids. The rhizoids aid in absorption of water and mineral nutrients and also act as the points of entry for symbiotic fungi, whose presence may be essential for the survival of the organism. The association of mutualistic fungi with plant roots or rhizoids is called a mycorrhiza. Because the fungi invade the body of the plant, they are sometimes referred to as endophytic fungi.

The xylem tissue of psilotophytes is composed of tracheids. Phloem tissue is made up of sieve cells, along with some parenchyma helper cells called albuminous cells. The stele, or vascular cylinder, of the psilotophyte rhizome is usually interpreted as a type of protostele. Protosteles have no pith; they have a solid core of vascular tissue. In the protostelic actinostele of *Psilotum*, the solid core of xylem has armlike extensions that reach into the surrounding tissues. Phloem surrounds the xylem. In the lower portions of the aerial branches of *Psilotum*, the stele is considered to be a type of siphonostele. In this case, the center of the stele is interpreted as a pith made up of sclerotic (hard, thick-walled) cells. This is similar to the aerial stem pattern in *Tmesipteris*. The tips of the aerial branches in *Psilotum* are strictly actinosteles.

Psilotum lacks true leaves. The leaflike appendages of the *Psilotum* shoot are called enations, or prophylls. The prophylls are composed of small flaps of photosynthetic tissue. Small traces of vascular tissue end at the base of the prophyll and do not actually enter the structure. In contrast, the foliar appendages of *Tmesipteris* are larger and are considered to be a type of true leaf called a microphyll. Microphylls have a single vein extending into the blade of the leaf.

Spores are produced in sporangia located on very short shoots on the sides of aerial branches. The lateral placement of sporangia in psilotophytes contrasts with the terminal placement of sporangia in primitive vascular plants such as *Rhynia*. Because each sporangium appears to represent a fusion of two sporangia (as in *Tmesipteris*) or three sporangia (as in *Psilotum*), they are generally called synangia. Cells within the synangium undergo meiosis to produce haploid spores. The spores are described as monolete, meaning that they have a single ridge. The monolete character is considered a derived trait, which is different from the *trilete*, or three-ridged, spores of primitive vascular plants.

Gametophyte Anatomy

The haploid psilotophyte gametophytes are very small and grow underground. In general, they are cylindrical, brown in color, covered with rhizoids, and are often branched. The branching may be dichotomous, as in the sporophyte, or irregular in response to the wounding of the gametophyte's apical meristems.

Gametophytes rely on endophytic fungi to obtain energy. Fungi invade nearly all of the cells of the gametophyte body except the apical meristems and the gametangia, or gamete-producing organs.

Both male and female sex organs are found scattered throughout a single plant. The antheridia (male organs) are small, multicellular, hemispherical structures that protrude from the surface of the gametophyte. Cells inside the antheridia undergo mitosis to produce multiflagellated sperm cells. The archegonia (female organ) has a swollen base called the venter. The venter is sunken below the surface of the gametophyte.

A cell within the venter undergoes mitotic cell division to produce an egg. Four rows of cells form the neck of the archegonium, which surrounds a neck canal. Two cells initially fill the neck canal. These neck canal cells break down when the archegonium is ready for fertilization.

Darrell L. Ray

See also: Evolution of plants; Ferns; Horsetails; Lycophytes; Seedless vascular plants.

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RAIN-FOREST BIOMES

Categories: Biomes; ecosystems; forests and forestry

Tropical forests exist in frost-free areas between the Tropic of Cancer and the Tropic of Capricorn. Temperatures range from warm to hot year-round. These forests are found in northern Australia, the East Indies, Southeast Asia, equatorial Africa, and parts of Central America and northern South America.

Rain forests are complicated tropical ecosystems with extremely high levels of *biodiversity*. Occupying only 6 percent of the earth's surface, they contain at least 50 percent of the world's known plant and animal species. The rain forests are being destroyed at such an unprecedented rate, however, that if the trend continues, no sustainable tropical rain forests will remain by the middle of the twenty-first century.

Tropical rain forests are the most complex ecosystems on earth, consisting of interacting systems of vegetation and animal species, all interdependent and coexisting in a concentrated cacophony of life. Because species found in one area may differ radically from those in another region only miles away, rain forests are individualistic and highly diversified.

The rain forests surrounding the Amazon basin in South America represent the last great contiguous expanse of tropical rain forest remaining in the world. Containing at least 20 percent of the earth's higher plant species and an equal percentage of the world's birds, Amazonia is being systematically devastated by human actions. About 20 percent has already been destroyed, and the rate has accelerated. In the mid-1990's about 14,000 acres were being cleared every day.

The environmental, economic, and social consequences of large-scale tropical deforestation are numerous and severe for the entire earth. The implications of losing the rain forests' biodiversity are dire. Moreover, rain forests act as giant solar-powered engines that pump water, nutrients, and carbon dioxide through the *biosphere*. Water captured by vegetation is returned to the atmosphere by evaporation and then to the forest as rain. The forest also stores large quantities of water in the vines and roots of the plants, water that is slowly released to streams and rivers. When large tracts of rain forest are cleared, the system's ability to store water decreases, disrupting the local climate and causing alternating periods of drought and floods.

Rain forests consist of lush, abundant growth, but the soil is deficient in nutrients and only marginally fertile. Although organic materials decompose rapidly in warm, humid climates, heavy rains leach nutrients from the soil. Plant life has adapted by rapidly ingesting nutrients as they become available; thus most nutrients are stored in the vegetation itself, not in the soil. When the land is cleared for agriculture or livestock grazing, the necessary crop-sustaining nutrients are depleted within a few growing seasons. Rain-forest destruction also adversely impacts the environment and human life by reducing the conversion of atmospheric carbon dioxide into oxygen.

Food Resources

Tropical rain forests are important sources of genetic material for improving crop plants or breeding new varieties. As the population size of a species shrinks, genetic diversity shrinks in direct proportion because as a species diminishes in number, genes disappear even if the species survives. A reduction of the gene pool renders a species less adaptable to changing environments and more susceptible to extinction. Future generations will be unable to benefit from currently unidentified but potentially useful properties of these species if their genetic diversity is extinguished.

Without periodic infusions of new germ plasm, crops bred specifically for humans, such as coffee, bananas, and cocoa, cannot continue to produce high yields at low cost. As the products of generations of selective breeding, these crops continually require the amalgamation of new genetic material to maintain productivity and flavor, to counteract new diseases and insect strains, and to endure environmental stresses such as unusual cold or drought.

In recent decades, a number of important crops, including cocoa, coffee, bananas, and sugarcane, have been saved from viruses and other pathogens by being crossbred with wild species having naturally acquired resistance. Although crop diseases can be contained or eliminated by applying pesticides, the cost is more than many farmers can afford. It is much less expensive, and more environmentally benign, to find a resistant strain of the same species in the wild.

Future contributions from wild germ plasm, in addition to breeding new disease-resistant varieties of crops, might include the creation of hybrid perennial varieties of annual crops, eliminating the need for yearly plowing and sowing. Another possibility may be new varieties of conventional crops which could survive in conditions or environments that are currently unsuitable, extending the plants' cultivation range.

Rain forests also provide opportunities for humans to develop and cultivate entirely new crops. Many staples, such as rice, peanuts, yams, and pineapples, originated in ancient tropical forests. These staples are not necessarily the best possible sources of nutrition and protein; they were merely the crops most easily cultivated by Neolithic humans.

While temperate forests produce fewer than two dozen edible fruits, more than twenty-five hundred palatable fruits grow in the tropics. Only about 10 percent of these are typically consumed, and only about one dozen are exported. The variety of fruits that Americans purchase from grocery stores is but a small fraction of those potentially available.

Because Americans consume an enormous quantity of sugar annually, there is a need for a sweetening agent lacking the potentially undesirable side effects of synthetic sweeteners. Natural sweeteners found in common fruits are problematic because Americans already consume more of these than is healthy. However, a new class of nonfattening natural sweeteners made of protein compounds has been identified. At least one thousand times sweeter than sucrose, and with no known detrimental side effects, these tropical sweeteners may prove a viable replacement for the sucrose commonly added to food items ranging from salad dressing to fish products.

African Rain Forests

Although the rain forests of central Africa are at lower risk of deforestation than are tropical forests in some other parts of the world, they are still in great danger. First, they contain many valuable timber trees that are being exploited actively. Second, these forested areas are in demand for other uses. In some areas, excessive timber harvesting and clearing to make way for oil palm and rubber plantations leaves little untouched forest. Some of the worst damage has occurred in Liberia and the Ivory Coast, where populations are on the rise. Much research is being done to develop sustainable and regenerative ways to harvest trees. In many areas, certain parts of the forest are considered sacred by local tribes and are jealously guarded from all encroachment. Medicinal plants are obtained from these areas, and they also are used as burial grounds that shelter the tribes' ancestral spirits.

Medicinal Plants

Rain-forest plants contain a plethora of yet uninvestigated biodynamic compounds with undiscovered potential for use in modern medicine. Future generations may benefit from these substances only if the species containing them are preserved and studied. Although the medicinal properties of plants have been known for at least thirty-five thousand years, modern science has reduced human dependence on medicinal plants. Nevertheless, approximately 50 percent of all U.S. prescription drugs contain substances of natural origin, and at least half of these contain active ingredients derived from plants.

Medicinal plants from the tropics aid modern pharmacologists in four ways. Plants may be used as a direct source of therapeutic drugs that cannot effectively be synthesized in the laboratory. Plant extracts may become the starting point for more complex compounds. Derived substances can serve as "blueprints" for new synthetic compounds. Finally, plants may assist as taxonomic markers for uncovering new healing compounds. Of the hundreds of thousands of plant species inhabiting the rain forests, only a small fraction have been identified and studied, and the potentially beneficial pharmacological properties of many of these are yet to be ascertained.

Endangered Biome

Although extinction is a natural process, tropical rain forests are disappearing at a rate four hundred times faster than during the recent geological past. One prominent and direct cause of the destruction of the rain forest in Amazonia is the production and transportation of oil. The fragile rain forest environment is easily contaminated by leaks, spills, and the ejection of effluents during pumping operations. Of even greater environmental impact is the oil companies' practice of building roads from inhabited areas to the well sites. Pipelines are built along the roads to carry the oil out of the jungle, but unemployed urban residents often follow the roads into the jungle and become squatters on adjoining land. They clear a small section of rain forest, using the *slash-and-burn* method, to eke out a living as subsistence farmers.

Unfortunately, when the rain forest is gone, so are most of the nutrients needed for local agriculture; the land cannot sustain crops for long. Then the farmers and their families must move on and claim more of the forest, regardless of the effects on the jungle or its native species. The tens of thousands of squatters engaging in this practice contribute to the rapid rate of rain-forest destruction.

Although aware of the problem, the governments of most South American oil-exporting countries have a strong incentive to underplay or ignore the negative impact of oil production in their rain forests: Their economies depend on oil, which is one of South America's largest exports. Ultimately the demand for oil, driven by high consumption rates in the industrialized nations of the Northern Hemisphere, particularly the United States, is one of the primary factors causing rain-forest destruction.

George R. Plitnik

See also: African flora; African agriculture; Asian flora; Asian agriculture; Australian flora; Australian agriculture; Biomes: types; Endangered species; Plant domestication and breeding; Rain forests and the atmosphere; Slash-and-burn agriculture; South American flora; South American agriculture.

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RAIN FORESTS AND THE ATMOSPHERE

Categories: Biomes; ecosystems; environmental issues; forests and forestry; pollution

Because photosynthesis releases large amounts of oxygen into the air, a curtailment of the process by rain-forest deforestation may have negative effects on the global atmosphere.

Rain forests are ecosystems noted for their high *biodiversity* and high rate of *photosynthesis*. The rapid *deforestation* of such areas is of great concern to environmentalists both because it may lead to the extinction of numerous species and because it may reduce the amount of photosynthesis occurring on the earth.

All living things on the earth—plants, animals, and microorganisms—depend on the "sea" of air surrounding them. The atmosphere includes abundant, permanent gases such as nitrogen (78 percent) and oxygen (21 percent) as well as smaller, variable amounts of other gases such as water vapor and carbon dioxide. Organisms absorb and use this air as a source of raw materials and release into it byproducts of their life activities.

Cellular Respiration

Cellular respiration is the most universal of the life processes. A series of chemical reactions beginning with glucose and occurring in cytoplasmic organelles called mitochondria, cellular respiration produces a chemical compound called adenosine triphosphate (ATP). This essential substance furnishes the energy cells need to move, to divide, and to synthesize chemical compounds—in essence, to perform all the activities necessary to sustain life. Cellular respiration occurs in plants as well as animals, and it occurs during both the day and the night. In order for the last of the series of chemical reactions in the process to be completed, oxygen from the surrounding air (or water, in the case of aquatic plants) must be absorbed. The carbon dioxide that forms is released into the air.

For cellular respiration to occur, a supply of glucose (a simple carbohydrate compound) is required. Photosynthesis, an elaborate series of chemical reactions occurring in chloroplasts, produces glucose, an organic carbon compound with six carbon atoms. Energy present in light must be trapped by the chlorophyll within the chloroplasts to drive photosynthesis. Therefore, photosynthesis occurs only in plants and related organisms, such as algae, and only during the daytime. Carbon dioxide, required as a raw material, is absorbed from the air, while the resulting oxygen is released into the atmosphere. The exchange of gases typically involves tiny openings in leaves, called stomata.

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Oxygen Cycle

Oxygen is required for the survival of the majority of microorganisms and all plants and animals. From the surrounding air, organisms obtain the oxygen used in cell respiration. Plants absorb oxygen through the epidermal coverings of their roots and stems and through the stomatal openings of their leaves.

The huge amounts of oxygen removed from the air during respiration must be replaced in order to maintain a constant reservoir of oxygen in the atmosphere. There are two significant sources of oxygen. One involves water molecules of the atmosphere that undergo a process called *photodissociation*: Oxygen remains after the lighter hydrogen atoms are released from the molecule and escape into outer space.

The other source is *photosynthesis*. Chlorophyll-containing organisms release oxygen as they use light as the energy source to split water molecules in a process called photolysis. The hydrogen is transported to the terminal phase of photosynthesis called the *Calvin cycle*, where it is used as the hydrogen source necessary to produce and release molecules of the carbohydrate glucose. In the meantime, the oxygen from the split water is released into the surrounding air.

Early in the history of the earth, before certain organisms evolved the cellular machinery necessary for photosynthesis, the amount of atmospheric oxygen was very low. As the number and sizes of photosynthetic organisms gradually increased, so did the levels of oxygen in the air. A plateau was reached several million years ago as the rate of oxygen release and absorption reached an equilibrium.

Ozone

Another form of oxygen is ozone. Unlike ordinary atmospheric oxygen, in which each molecule contains two atoms, ozone molecules have three oxygen atoms each. Most ozone is found in the stratosphere at elevations between 10 and 50 kilometers (6 and 31 miles). This layer of ozone helps to protect life on earth from the harmful effects of ultraviolet radiation. Scientists, especially ecologists, are concerned as the amount of ozone has been reduced drastically over the last few decades. Already, an increase in the incidence of skin cancer in humans and a decrease in the efficiency of photosynthesis has been documented. Another concern related to ozone is that of an increase in ozone levels nearer to the ground, where living things are harmed as a result. The formation of ozone from ordinary oxygen within the atmosphere is greatly accelerated by the presence of gaseous pollutants released from industrial processes.

Carbon Cycle

All forms of life are composed of organic (carbon-containing) molecules. Carbohydrates include glucose as well as lipids (fats, oils, steroids, and waxes), proteins, and nucleic acids. The ability of carbon to serve as the backbone of these molecules results from the ability of carbon atoms to form chemical bonds with other carbon atoms and also with oxygen, hydrogen, and nitrogen atoms.

Like oxygen, carbon cycles in a predictable manner between living things and the atmosphere. In photosynthesis, carbon is "fixed" as carbon dioxide in the air (or dissolved in water) is absorbed and converted into carbohydrates. Carbon cycles to animals as they feed on plants and algae. As both green and nongreen organisms respire, some of their carbohydrates are oxidized, releasing carbon dioxide into the air. Each organism must eventually die, after which decay processes return the remainder of the carbon to the atmosphere.

Greenhouse Effect

Levels of atmospheric carbon dioxide have fluctuated gradually during past millennia, as revealed by the analysis of the gas trapped in air bubbles of ice from deep within the earth. In general, levels were lower during glacial periods and higher during warmer ones. After the nineteenth century, levels rose slowly until about 1950 and then much more rapidly afterward. The apparent cause has been the burning of increased amounts of fossil fuels associated with the Industrial Revolution and growing energy demands in its wake. The global warming that is now being experienced is believed by most scientists to be the cause of increased carbon dioxide levels. The *greenhouse effect* is the term given to the insulating effects of the atmosphere with increased amounts of carbon dioxide. The earth's heat is lost to outer space less rapidly, thus increasing the earth's average temperature.

Forest Ecosystems

The *biotic* (living) portions of all ecosystems include three ecological or functional categories: *pro-*

ducers (plants and algae), *consumers* (animals), and *decomposers* (bacteria and fungi). The everyday activities of all organisms involve the constant exchange of oxygen and carbon dioxide between the organisms of all categories and the surrounding atmosphere.

Because they release huge quantities of oxygen during the day, producers deserve special attention. In both fresh and salt water, algae are the principal producers. On land, this role is played by a variety of grasses, other small plants, and trees. Forest ecosystems, dominated by trees but also harboring many other plants, are major systems that produce a disproportionate amount of the oxygen released into the atmosphere by terrestrial ecosystems.

Forests occupy all continents except for Antarctica. A common classification of forests recognizes these principal categories: coniferous (northern evergreen), temperate deciduous, and tropical evergreen, with many subcategories for each. The designation "rain forest" refers to the subcategories of these types that receive an amount of rainfall well above the average. Included are tropical rain forests (the more widespread type) and temperate rain forests. Because of the ample moisture they receive, both types contain lush vegetation that produces and releases oxygen into the atmosphere on a larger scale than do other forests.

Tropical and Temperate Rain Forests

Tropical rain forests exist at relatively low elevations in a band about the equator. The Amazon basin of South America contains the largest continuous tropical rain forest. Other large expanses are located in western and central Africa and the region from Southeast Asia to Australia. Smaller areas of tropical rain forests occur in Central America and on certain islands of the Caribbean Sea, the Pacific Ocean, and the Indian Ocean. Seasonal changes within tropical rain forests are minimal. Temperatures, with a mean near 25 degrees Celsius, seldom vary more than 4 degrees Celsius. Rainfall each year measures at least 400 centimeters.

Tropical rain forests have the highest biodiversity of any terrestrial ecosystem. Included is a large number of species of flowering plants, insects, and animals. The plants are arranged into layers, or strata. In fact, all forests are stratified but not to the same degree as tropical rain forests. A mature tropical rain forest typically has five layers. Beginning with the uppermost, they are an *emergent* layer (the tallest trees that project above the next layer); a *canopy* of tall trees; *understory* trees; shrubs, tall herbs, and ferns; and low plants on the forest floor.

Several special life-forms are characteristic of the plants of tropical rain forests. *Epiphytes* are plants such as orchids that are perched high in the branches of trees. Vines called *lianas* wrap themselves around trees. Most tall trees have trunks that are flared at their bases to form buttresses that help support them in the thin soil.

This brief description of tropical rain forests helps to explain their role in world photosynthesis and the related release of oxygen into the atmosphere. As a result of the many layers of forest vegetation, the energy from sunlight as it passes downward is efficiently utilized. Furthermore, the huge amounts of oxygen released are available for use not only by the forests themselves but also, because of global air movement, by other ecosystems throughout the world. Because of this, tropical rain forests are often referred to as "the earth's lungs."

Temperate rain forests are much less extensive than tropical rain forests. Temperate rain forests occur primarily along the Pacific Coast in a narrow band from southern Alaska to central California. Growing in this region is a coniferous forest but one with higher temperatures and greater rainfall than those to the north and inland. This rainfall of 65 to 400 centimeters per year is much less than that of a tropical rain forest but is supplemented in the summer by frequent heavy fogs. As a result, evaporation rates are greatly reduced. Because of generally favorable climatic conditions, temperate rain forests, like tropical ones, support a lush vegetation. The rate of photosynthesis and release of oxygen is higher than in most other world ecosystems.

Ecologists and conservationists are greatly concerned about the massive destruction of rain forests. Rain forests are being cut and burned at a rapid rate to plant crops, to graze animals, and to provide timber. The ultimate effect of deforestation of these special ecosystems is yet to be seen.

Thomas E. Hemmerly

See also: Acid rain; Air pollution; Biosphere concept; Calvin cycle; Carbon cycle; Deforestation; Ecosystems: overview; Ecosystems: studies; Greenhouse effect; Hydrologic cycle; Ozone layer and ozone hole debate; Photorespiration; Photosynthesis; Rain-forest biomes; Respiration; Savannas and deciduous tropical forests.

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RANGELAND

Categories: Animal-plant interactions; economic botany and plant uses; ecosystems.

Open land of a wide variety of types, including grasslands, shrublands, marshes, and meadows as well as some desert and alpine land, is known as rangeland.

Rangeland is a valuable and resilient *ecosystem* resource that supports considerable plant and animal life. Rangeland generally refers to a kind of land rather than a use of that land. The Society for Range Management defines rangelands as "land on which the native vegetation (climax or natural potential) is predominantly grasses, grass-like plants, forbs, or shrubs." Rangeland "includes lands revegetated naturally or artificially" as well as "natural grasslands, savannas, shrublands, most deserts, tundra, alpine communities, coastal marshes and wet meadows."

Rangelands usually have some limitation for intensive agriculture, such as low and erratic precipitation, lack of soil fertility, shallow or rocky soil, or steep slopes. In addition to livestock *grazing*, rangelands serve multiple-use functions such as providing recreational opportunities, *watersheds*, mining locations, and habitat for many animal species. Renewable natural resources associated with rangelands are plants and animals (and, in some senses, water). Nonrenewable resources include minerals and other extractable materials.

Location and Characteristics

Rangelands are extensive and extremely variable. As defined by the Society for Range Management, they occupy more than 50 percent of the world's total land surface and about 1 billion acres in the United States alone. Rangelands are home to nomadic herders on nearly every continent. They vary from high-elevation alpine tundra and high-latitude Arctic tundra to tropical grasslands. The *tall-grass prairies* in the United States (now mostly plowed for intensive agriculture) and the rich grasslands of eastern Africa are among the most productive.

Rangelands grade into woodlands and forests as woody species and trees become more abundant. Some forests are grazed by wild and domestic animals, and the distinction between rangeland and forest is often not clear. The other difficult distinction is between rangeland and pastureland. Pastureland is generally improved by seeding, fertilization, or irrigation, whereas rangelands support native plants and have little intensive improvement.

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In the United States, rangeland improvements during the twenty years following World War II often included brush control, grazing management, and seeding, but rangelands were not irrigated. After the 1970's, when fuel costs increased and environmental concerns about pesticide use increased, brush control practices were reduced considerably. Today environmental concerns include rangeland degradation from *overgrazing*, especially on riparian vegetation along streams, and concern for endangered animal and plant species. These issues have become controversial in the United States.

Rangelands as Ecosystems

Rangelands constitute natural ecosystems with nonliving environmental factors such as soil and climatic factors. Life-forms are *primary producers* (grasses, forbs, and shrubs), *herbivores* (livestock; big game animals such as deer and bison; and many rodents and insects), *carnivores* (such as coyotes, bears, and eagles), and *decomposers* (fungi and bacteria) that break down organic matter into elements that can be utilized by plants. Plants convert carbon dioxide and water into complex carbohydrates, fats, and proteins that nourish animals feeding on the plants.

Individual chemical elements are circulated throughout the various components. Many of these elements are present in the soil, including phosphorus, magnesium, potassium, and sulfur. Nitrogen, on the other hand, is present in large amounts in the atmosphere but must be converted (fixed) into forms that can be utilized by plants before it can be cycled. Energy is fixed through the process of photosynthesis and transformed to forms useful for the plants, then the animals that feed on plants.

When chemicals are taken up by plant roots from the soil, they become available to a wide group of herbivores, from small microbes to large ungulates. Eventually nutrients are passed on to organisms at higher *trophic levels* (omnivores and carnivores). Both plant and animal litter is eventually broken down by decomposers—bacteria, fungi, and other soil organisms—and returned to the soil or, in the case of carbon or nitrogen, given off to the atmosphere.

However, energy is degraded at each step along the way; energy is transferred but not cycled. Grazing animals on rangelands influence plants by removing living tissue, by trampling, and by altering competitive relations with other plants. Large grazing animals tend to compact the soil, reducing infiltration and increasing surface runoff.

Rangeland Dynamics

Rangelands vary considerably with time. Scientists are gaining a better understanding of some factors related to rangeland change. Pollen records and, in the southwestern United States, packrat middens have been used to reconstruct past climate and vegetational conditions. Some areas have become drier and others more mesic. The formation and retreat of glaciers influenced climatic patterns and soil development. A recent general trend in many rangelands is an increase in woody plants at the expense of grasses. Many factors are probably responsible for these shifts, but fire control, overgrazing, climatic shifts, introduction of exotic species, and influence of native animals are likely causal agents.

Rangelands are being threatened by encroachment from crop agriculture as worldwide development increases. Nomadic herders traditionally met periodic drought conditions by having the flexibility to move to areas not impacted by drought. Now, with area lost to livestock grazing and other political restrictions, herders are often forced to maintain higher livestock numbers to support those directly dependent on livestock. Despite various kinds of disturbances and stresses on rangelands, these areas have supported many large grazing animals and people for centuries.

Rex D. Pieper

See also: Agriculture: history and overview; Agriculture: modern problems; Forest and range policy; Forests; Grasses and bamboos; Grasslands; Grazing and overgrazing; Trophic levels and ecological niches; Tundra and high-altitude biomes.

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RED ALGAE

Categories: Algae; economic botany and plant use; food; taxonomic groups; water-related life

Red algae, from the phylum Rhodophyta *(from the Greek* rhodos, *meaning "red"), are named for their reddish color because of their pigment phycoerythrin. Despite their name, not all rhodophytes are red. Some of them have very little phycoerythrin and appear green or bluish. Most are multicellular and vary greatly in shape; platelike, coral-like, crustlike, leathery, and featherlike forms are known.*

The bodies of some rhodophytes are relatively complex, characterized by a great deal of branching of their leaflike structures as well as the presence of a *holdfast* that resembles plant roots. These rhodophytes are commonly known as seaweeds. Red algae are distinctive from other eukaryotic algae in that they lack flagella (or motile cells of any kind) in their vegetative cells, spores, and gametes.

There are four thousand to six thousand species of red algae, and although some rhodophytes do inhabit fresh water (about fifty species), red algae are most common in tropical marine environments. Many are found at great depths, living 210-260 meters below the surface of the ocean. The pigment *phycoerythrin* allows red algae to live and photosynthesize at these depths. Phycoerythrin absorbs blue light, which penetrates water to a greater depth than light of longer wavelengths normally used in photosynthesis. Reds are the deepest-growing photosynthetic eukaryotes.

Habitats

Rhodophytes are important members of many *periphyton* communities (which typically grow attached to substrata) from tropical to polar seas. Epiphytism is common among red algae. Epiphytic rhodophytes grow on the surface of larger, typically brown, algae. Although their holdfasts penetrate the tissue of their hosts, they do not obtain any nutrients from host algae.

Nearly 15 percent of red algae are parasites, often living on closely related species. Parasitic reds transfer nuclei into host cells and transform them. Host reproductive cells may then carry the parasite's genes. Other *Rhodophyta* are extremophiles. For example, the red alga *Cyanidium* lives in acidic (pH 2-4) hot springs at 55 degrees Celsius. Some calcified rhodophytes are major contributors to the formation of tropical reefs. Reef-building red algae are called coralline algae.

Structure and Properties

A red algal cell is surrounded by a cell wall. In many species, the main wall component is cellulose (similar to cell walls of various other algae and plants), but other reds have mannans (polymers of mannose) and xylans (polymers of xylose). Other polymers associated with the cell walls include *agar* and *carrageenan*. The majority of coralline red algae contain calcium carbonate, which forms limestone in the cell walls. Because of their ability to secrete calcium carbonate, red algae do not decay and have a better preserved fossil record than many other algae. Fossils of red algae have been found in rocks 500 million years old. Production of calcium carbonate is linked to photosynthetic carbon fixation. Apparently, carbon dioxide fixation results in a pH increase (an increase in alkalinity), which facilitates calcium carbonate precipitation.

An unusual feature of red algae compared to other algae is the occurrence of protein plugs (pit connections) in cell walls between the cells, although some red algae lack them. All plugs consist of protein, and in some species protein polysaccharides are an additional component. Cells of the *Rhodophyta* may contain several nuclei as a result of either the fusion of nongamete cells or mitosis without cytokinesis. Cell fusion is a very important feature of parasitic reds. Red algae lack centrioles, but the mitotic spindle radiates from the "nuclear-associated organelle," which often appears as a pair of short, hollow cylinders. Some red algae have large vacuoles in the centers of their cells. Cells of the *Rhodophyta* may produce mucilage, which plays an important role in the attachment of their reproductive cells. Mucilages are polymers of D-xylose, D-glucose, D-glucuronic acid, and galactose and are produced within Golgi apparatuses.

Pigments of red algae include chlorophyll *a* and two classes of accessory pigments: phycobilins and carotenoids. Phycoerythrin, phycocyanin, and allophycocyanin are phycobilins. They attach to proteins known as phycobiliproteins, which occur in highly organized structures called *phycobilisomes*. Phycoerythrin occurs in at least five forms in the *Rhodophyta* (B-phycoerythrin I and II, R-phycoerythrin I, II, and II). Carotenoids are also found in plants, and those in red algae are similar in structure and function.

Some parasitic forms of red algae lack photosynthetic pigments. In red algae that have pigments, all pigments are located in the chloroplasts. Red algae chloroplasts have a highly distinctive ultrastructure. Two membranes surround each chloroplast. Chloroplasts of red algae probably originated from cyanobacteria that formed an ancient symbiotic relationship with the reds. Both red algal chloroplasts and cyanobacteria share same phycobilin pigments. Inside the chloroplast are thylakoids, which are not stacked. This is the same arrangement found in cyanobacteria, but it is different from that of other algae and from plants. On the thylakoid surface there are many phycobilisomes. Some red algae have chloroplasts that contain pyrenoids, which have no known function.

Photoautotrophy is the principal mode of nutrition in red algae; in other words, they are "self-feeders," using light energy and photosynthetic apparatuses to produce their own food (organic carbon) from carbon dioxide and water. A few *Rhodophyta* are heterotrophic, and these organisms are generally obligate parasites (parasites that must live off a host) of other algae. Carbon and nitrogen metabolism in red algae is similar to that in other algae. Various rhodophytes produce unusual carbohydrates, such as digeneaside, which is used to regulate osmotic status of cells in response to drought stress in shoreline environments. Some red algae are covered by surface-protein *cuticle*, which is different from that found in higher plants. The food storage of red algae is a unique polysaccharide floridean starch. This starch differs from that synthesized by green algae and plants. Floridean starch grains are formed in the cytoplasm. Red algae store inorganic nitrogen in the form of phycobilin pigments.

Reproduction

Red algae reproduce both asexually and sexually. Methods of asexual reproduction include discharging spores and fragmentation of the algal bodies. Sexual reproduction, as well as alteration of generations, is widespread among the *Rhodophyta*, but two classes of red algae (floridean and bangean) have particular variations.

In contrast to the two phases in an alteration of generations of other algae and plants (gametophyte and sporophyte, haploid and diploid stages, correspondingly), most species of red floridean algae have three phases: free-living, haploid gametophytes, diploid carposporophytes, and diploid tetrasporophytes. Male and female gametophytes are often separate. The male gametophytes produce male nonflagellated gametes called spermatia. Female gamethophytes produce a special branch, the carpogonial branch, that produces a terminal carpogonium (oogonium, an egg-bearing structure).

Contact between spermatia and carpogonia is facilitated by water movements. The carposporophyte is a diploid stage that develops from the zygote (fertilized carpogonium) and produces carpospores. Diploid tetrasporophytes develop from carpospores. Tetrasporophytes form tetrasporangia, which produce four haploid tetraspores. When released, tetraspores develop into new gametophytes. The gametophyte and tetrasporophyte may appear nearly identical, and therefore can be said to be isomorphic, as in the *Polysiphonia*. Alternatively, the tetrasporophyte and gametophyte may be very different in size and appearance (heteromorphic), as in *Phyllophora*.

Diversity of Red Algae

Red algae are divided into two subclasses or classes: *Florideophyceae* (florideophyceans or floridean) and *Bangiophyceae* (bangiophyceans or bangean). Floridean algae have numerous small chloroplasts and a complex life cycle. Bangean algae have life cycles without carpogonia and carposporophyte development and have a single central chloroplast. Representative species of *Florideophyceae* are *Batrachospermum*, *Chondrus*, *Corallina*, *Gelidium*, and *Polysiphonia*. Representatives of *Bangiophyceae* include *Porphyra*, *Bangia*, and *Cyanidium*.

Uses

People have used red algae for thousands of years. Most are collected along seashores for use in human food or for the extraction of gelling compounds. A few red algae, such as *Porphyra*, *Eucheuma*, and *Gracilaria*, are cultivated. More than 60,000 hectares of sea along Japanese coasts are occupied by "red algal culture." Thousands of people worldwide are engaged in cultivating red seaweeds.

The most valuable of all algae is *Porphyra*. The annual *Porphyra* harvest worldwide has been estimated to be worth 2.5 billion dollars. *Porphyra* (in Japanese, *Nori*; in Chinese, *Zicai*) is used as a wrapper for sushi or may be eaten mixed with rice and fish and in salads. It is very rich in vitamins B and C as well as minerals, including iodine. There are about seventy species of *Porphyra*, but the most widely used species is *Porphyra yezoensis*. Two important compounds derived from red algae are agar and carrageenan, both of which are polymers of galactose. Agar is used as a medium for culturing microorganisms, including algae; as a food gel (for jams and jelly); and in pharmaceutical capsules. In the United States, agar is used in the canning industry as a protective agent against the unwanted effects of metals. In addition, agar is the source of agarose, which is widely used in recombinant DNA (deoxyribonucleic acid) technology for gel electrophoresis. The first agar was produced in 1670 in Japan, and Japan is still the largest producer of agar.

The red algae *Gelidium*, *Gracelaria*, and *Pterocladia* are harvested for extraction of agar. Carrageenan is used in toothpaste, cosmetics, and food, such as ice cream and chocolate milk. *Eucheuma*, *Kappaphycus*, and *Chondus* (the so-called Irish moss) are the sources of carrageenan. The most important producer of carrageenan is Europe, followed by the Philippines and Indonesia.

Sergei A. Markov

See also: Agriculture: marine; Algae; Brown algae; Cell wall; *Charophyceae*; *Chlorophyceae*; Chrysophytes; Cryptomonads; Diatoms; Dinoflagellates; Electrophoresis; Euglenoids; Eutrophication; Green algae; Haptophytes; Marine plants; Photosynthesis; Phytoplankton; Pigments in plants; *Protista*; *Ulvophyceae*.

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REFORESTATION

Categories: Forests and forestry; environmental issues

Reforestation is the growth of new trees in an area that has been cleared for human activities. It can occur naturally or be initiated by people.

Many areas of the eastern United States, such as the New England region, reforested naturally in the nineteenth and early twentieth centuries after farmland that had been abandoned was allowed to lie fallow for decades. After an area has been logged, environmentalists, as well as the commercial logging industry, advocate planting trees rather than waiting for natural regrowth because the process of natural regeneration can be both slow and unpredictable. In natural regeneration, the mixture of trees in an area may differ significantly from the forest that preceded it. For example, when nineteenth century loggers *clear-cut* the white pine forests of the Great Lakes region, many logged-over tracts grew back primarily in mixed hardwoods.

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Land that has been damaged by industrial pollution or inefficient agricultural practices sometimes loses the ability to reforest naturally. In some regions of Africa, soils exposed by *slash-and-burn agriculture* contain high levels of iron or aluminum oxide. Without a protective cover of vegetation, even under cultivation, soil may undergo a process known as *laterization*. Laterite is a residual product of rock decay that makes soil rock-hard. Such abandoned farmland is likely to remain barren of plant life for many years. In polluted areas such as former mining districts, native trees may not be able to tolerate the toxins in the soil; in these cases, more tolerant species must be introduced.

Safeguarding Timber Resources

Reforestation differs from *tree farming* in that the goal of reforestation is not always to provide woodlands for future harvest. Although tree farming is a type of reforestation (trees are planted to replace those that have been removed), generally only one species of tree is planted, with explicit plans for its future harvest. The trees are seen first as a crop and only incidentally as wildlife habitat or a means of erosion control.

As foresters have become knowledgeable about the complex interactions within forest ecosystems, however, tree farming methods have begun to change. Rather than *monocropping* (planting only one variety of tree), the commercial forest industry has begun planting mixed stands. Trees that possessed no commercial value, once considered undesirable weed trees, are now recognized as nitrogen fixers necessary for the healthy growth of other species. In addition to providing woodlands for possible use in commercial forestry, goals of reforestation include wildlife habitat restoration and the reversal of environmental degradation.

Early Efforts

Reforestation to replace trees removed for commercial purposes has been practiced in Western

Europe since the late Middle Ages. English monarchs, including Queen Elizabeth I, realized that forests were a vanishing resource and established plantations of oaks and other hardwoods to ensure a supply of ship timbers. Similarly, Sweden created a corps of royal foresters to plant trees and watch over existing woodlands. These early efforts at reforestation were inspired by the reduction of a valuable natural resource. By the mid-nineteenth century it was widely understood that the removal of forest cover contributes to soil erosion, water pollution, and the disappearance of many species of wildlife.

Ecological and Environmental Aspects

Water falling on hillsides made barren by clear-cutting timber washes away *topsoil* and causes rivers to choke with sediment, killing aquatic life. Without trees to slow the flow of water, rain can also run off slopes too quickly, causing rivers to flood. For many years, soil conservationists advocated reforestation as a way to counteract the ecological damage caused by erosion.

In the mid-twentieth century, scientists established the vital role that trees, particularly those in tropical rain forests, play in removing carbon dioxide from the earth's atmosphere through the process of photosynthesis. Carbon dioxide is a greenhouse gas: It helps trap heat in the atmosphere. As forests disappear, the risk of global warming—caused in part by an increase in the amount of carbon dioxide in the atmosphere—becomes greater. Since the 1980's, scientists and environmental activists concerned about global warming have joined foresters and soil conservationists in urging that for every tree removed anywhere, whether to clear land for development or to harvest timber, replacement trees be planted. As the area covered by tropical rain forests shrinks in size, the threat of irreversible damage to the global environment becomes greater.

Reforestation Programs

In 1988 American Forests, an industry group, established the Global ReLeaf program to encourage reforestation efforts in an attempt to combat global warming. In addition to supporting reforestation efforts by government agencies, corporations, and environmental organizations, Global ReLeaf and similar programs encourage people to practice reforestation in their own neighborhoods. Trees serve as a natural climate control, helping to moderate extremes in temperature and wind. Trees in a well-landscaped yard can reduce a homeowner's energy costs by providing shade in the summer and serving as a windbreak during the winter. Global ReLeaf is one of many programs that support reforestation efforts.

Arbor Day, an annual day devoted to planting trees for the beautification of towns or the forestation of empty tracts of land, was established in the United States in 1872. The holiday originated in Nebraska, a prairie state that seemed unnaturally barren to homesteaders used to eastern woodlands. Initially emphasizing planting trees where none had existed before, Arbor Day is observed in U.S. public schools to educate young people about the importance of forest preservation. Organizations such as the National Arbor Day Foundation provide *saplings* (young trees) to schools and other organizations for planting in their own neighborhoods.

Nancy Farm Männikkö

See also: Deforestation; Erosion and erosion control; Forest management; Logging and clear-cutting; Rain-forest biomes; Rain forests and the atmosphere; Slash-and-burn agriculture; Soil management; Sustainable forestry; Timber industry.

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REPRODUCTION IN PLANTS

Categories: Genetics; physiology; reproduction and life cycles

Plants have evolved a remarkable number of ways to increase their numbers. These include not only a variety of forms of sexual reproduction, in which two individuals produce specialized cells that fuse to become a new offspring, but also many ways of achieving asexual reproduction, in which a single plant produces offspring.

In unicellular organisms three steps result in *cellular reproduction*. Among prokaryotic organisms (made of cells that have no nuclei), the single loop of DNA (deoxyribonucleic acid, the molecule that carries genetic information) replicates; then one copy is carried to each daughter cell as the original cell elongates and then "pinches" in two, a process called *fission*.

In eukaryotic organisms (whose cells have nuclei), the DNA is located within a nucleus in discrete *chromosomes* that must be precisely divided between the two daughter cells. Nuclear division to produce two identical daughter cells (asexual reproduction) is called *mitosis*. A chromosome during cell division consists of two halves, *sister chromatids*, each of which is identical to the other. During mitosis, every chromosome in the nucleus splits in half so that one chromatid will migrate to the first daughter cell, and the second chromatid migrates to the other. When cell division is complete, the result is two genetically identical daughter cells.

In *sexual reproduction*, a nucleus must divide by *meiosis*. In sexually reproducing organisms, at least some cells will have pairs of every type of chromosome. Such cells are *diploid*, or $2n$, where n is the number of different types of chromosomes. During meiosis, the pairs separate so that each daughter cell has only one of each type of chromosomes and is *haploid*, or n. If two different haploid cells fuse, the resulting cell will have pairs of every type of chromosome but with one of each pair contributed by each of the two parents. The offspring will thus be different from either parent.

Sexual Reproduction: Alternation of Generations

Sexual reproduction provides an opportunity for an organism to have different kinds of cells at different stages of its life cycle. The most familiar example is what is known from animals, including humans. The body cells of the adult are diploid, but in the reproductive organs, meiosis occurs to form haploid cells, either *eggs* or *sperm*. If these haploid reproductive cells (*gametes*) fuse, a new diploid cell is formed, the *zygote*. The zygote divides mitotically to form an *embryo* and eventually a new adult consisting of diploid body cells similar to those of both parents. This is a *gametic life cycle*, in which the gametes are the only haploid cells, and they are formed directly by *meiosis*. Fertilization occurs immediately after meiosis.

Some algae, particularly diatoms and some of the green algae, also have a gametic life cycle. In many plant species the gametes are large, immotile eggs and small, motile sperm, just as in animals. This condition is *oogamy*. However, many other plants are not oogamous. In some cases the two gametes appear to be identical (*isogamous*), while in others there may be two distinctive sizes of gametes, but their shape and motility are the same (*anisogamous*).

Some of the green algae have a life cycle exactly the opposite of the gametic cycle described above. In these plants, the diploid zygote divides by meiosis to produce haploid daughter cells, which multiply to form either a population of haploid unicellular plants or a multicellular plant with a haploid body. Eventually some of these haploid cells will differentiate into gametes, and two gametes will fuse to form a new zygote. In this type of *zygotic life cycle*, the zygote is the only diploid cell in the plant's life cycle, and fertilization is delayed after meiosis occurs.

Even more interesting is the *sporic life cycle*, in which a plant will have both a haploid *gametophyte* and diploid *sporophyte* body at different stages of its life. This type of life cycle is often called *alternation of generations*. These bodies may look the same (*isomorphic*), or they may look completely different (*heteromorphic*). In some cases two different species have been described and later discovered to be simply the haploid and diploid forms of the same species. Most plants, including most algae and fungi, have some form of a sporic life cycle. In a sporic life cycle, the diploid adult sporophyte plant forms reproductive organs in which meiosis occurs to form *spores*. These spores germinate and undergo mitosis to form a multicellular haploid gametophyte body. The gametophyte forms reproductive organs in which gametes are produced. Following fertilization, the resulting zygote undergoes mitosis to form the new sporophyte.

Many red algae and some of the green and brown algae are isomorphic; that is, the gametophyte and sporophyte bodies look identical. Bryophytes, some green algae, some brown algae, and most fungi are heteromorphic, with the gametophyte being the dominant, more conspicuous body. For instance, in mosses the green leafy plant is the gametophyte. When it is mature, the gametophyte will produce two types of *gametangia*, archegonia and antherida. *Archegonia* are flask-shaped structures that produce an egg, and *antheridia* are saclike structures that produce multiple sperm. After a sperm cell fertilizes the egg, the zygote grows into a sporophyte plant, still attached to and growing out of the gametophyte. The tip of the sporophyte swells to become a *capsule*, or *sporangium*, where meiosis occurs to form haploid spores. Each spore that falls onto a suitable place will germinate and grow into a new, leafy gametophyte plant.

Vascular plants and many brown algae are heteromorphic, with the sporophyte dominant. For instance, leafy ferns are the leaves of a sporophyte plant with an underground stem and roots. Sporangia typically develop on the underside of the fern, and meiosis occurs inside the sporangia to produce haploid spores. If a spore falls onto a suitable habitat it will germinate to form a small, inconspicuous gametophyte plant. The gametophyte typically produces archegonia and antheridia. Following fertilization, a new sporophyte plant grows out of the archegonium, but it is usually not seen until the first leaves enlarge enough to be visible above the soil surface.

Asexual Reproduction

In theory, any cell from a plant body should be capable of generating an entire new plant, because the nucleus of each cell has identical genetic information to every other cell in that body. In fact, since the mid-1950's it has been possible to *clone* many plants—produce entire new plants from single cells of a parent plant. The techniques of plant cell and tissue culture are used to propagate many commercially important species of ornamental plants. These techniques are also valuable tools in plant research. The basis for these tools is found in nature—the variety of methods of asexual reproduction found in plants.

In nonvascular plants, particularly fungi and filamentous algae, fragmentation can be an effective way of increasing the number of individuals of a plant. If the plant body is physically broken into pieces, each piece may continue to grow and develop as an independent plant. Most algae also form *sporangia*, asexual reproductive organs that produce motile *zoospores*. When the unicellular zoospores are released, they will swim for a period and, if they settle in a suitable environment, will germinate and grow to form a new plant. In some cases specialized multicellular asexual propagules are formed. For instance, lichens may form *isidia* or *soridia*, and liverworts may form *gemmae*. If the propagule breaks off and lands in a suitable environment, it will grow into a new plant.

Asexual reproduction may also occur in vascular plants. If a stem is laid horizontally on the ground, it may produce *adventitious roots*, which will allow that portion of the stem to grow as a separate plant. Similarly, some plants have roots that form *buds* and produce new stems at some distance from the original stem. The most dramatic examples of this are aspen groves in which all the trees are *clones* of one another. These natural phenomena are the basis of horticultural plant propagation by means of stem, leaf, or root cuttings.

Other plants form specialized structures for asexual propagation. For instance, strawberries produce *stolons*, specialized stems that grow out from a plant, then root and form new plantlets. *Bulb*-forming plants, such as gladiolus, frequently form new bulblets, and if a *rhizome* is split, such as on an iris, each half will continue to grow as a new plant. Some plants, such as kalenchoe, produce complete plantlets on the edges of leaves, which fall off and disperse to propagate the plant.

Marshall D. Sundberg

See also: Algae; Angiosperm life cycle; Angiosperm plant formation; Bacteria; Bryophytes; Chromosomes; Cloning of plants; DNA in plants; DNA replication; Fungi; Germination and seedling development; Hybridization; Lichens; Mitosis and meiosis; Nonrandom mating; Nucleus; Plant biotechnology; Plant life spans; Pollination; Seeds; Shoots.

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REPRODUCTIVE ISOLATING MECHANISMS

Categories: Evolution; genetics; reproduction and life cycles

Reproductive isolating mechanisms are genetically influenced, as opposed to factors such as geographic isolation. These built-in isolating mechanisms prevent interbreeding between species and thereby promote reproductive efficiency.

Reproductive isolating mechanisms prevent interbreeding between species. The term, which was first used by Theodosius Dobzhansky in 1937 in his landmark book *Genetics and the Origin of Species*, refers to mechanisms that are genetically influenced and built-in. Geographic isolation can prevent interbreeding among populations, but it is an external factor. The standard model for speciation requires that populations be geographically isolated long enough to diverge genetically. Later, if the geographic barriers break down, built-in isolating mechanisms maintain reproductive isolation between the divergent populations. As these mechanisms continue to prevent hybridization, continued divergence leads to new species.

Reproductive isolating mechanisms function only between sexually reproducing species. They have no applicability to forms that reproduce only by asexual means. *Hermaphrodites*, organisms with both male and female reproductive organs that reproduce only by self-fertilization (rare in animals, more common in plants), represent a distortion of the sexual process that produces essentially the same results as asexual reproduction. Many lower animals, many plants, and protists regularly employ both asexual and sexual means of reproduction, and the significance of isolating mechanisms in such forms is essentially the same as in normal sexual species.

Prezygotic Mechanisms

Reproductive isolating mechanisms are usually classified into two main groups. *Premating*, or *prezygotic*, mechanisms operate prior to mating, or the release of *gametes*, and therefore do not result in a waste of the reproductive potential of the individual. By contrast, *postmating*, or *postzygotic*, mechanisms come into play after mating, or the release of gametes, and could result in a loss of the genetic contribution of the individual to the next generation. This distinction is important in the theoretical sense, in that *natural selection* should favor genes that promote premating isolation. Genes that do not promote premating isolation presumably would be lost more often through mating with an individual from another species, which often leads to no offspring or infertile offspring, in turn leading to a reinforcement of premating isolation.

Ecological isolation (habitat isolation) often plays an important role in both animals and plants. Different forms may be adapted to different habitats in the same general area and may meet only infrequently at the time of reproduction. Different plant species may occur on different soils, on different drainage profiles or exposures, or at different altitudes. This type of isolation, although frequent and widespread, is often incomplete, as the different forms may come together in transitional habitats. The importance of ecological isolation, however, is attested by the fact that when *hybrid swarms* (groups of organisms that show signs of extensive hybridization) are produced between forms that normally remain distinct, they have often been found to result from disruption of the environment, usually by humans.

Mechanical isolation is a less important type of premating isolation in plants, though it does occur in some. Complex floral structures in certain plants (such as orchids) may favor one species of animal pollinator over others. Finally, temporal differences often contribute to premating isolation. The most common type of *temporal isolation* is seasonal isolation: Species may reproduce at different times of the year. One type of western pine normally sheds its pollen in February, while another does not shed its pollen until April. Differences can also involve the time of day. In one species of desert plant, the flowers open in the early morning, while in another species of the same genus the flowers open in the late afternoon. Such differences, as in the case of ecological isolation, are often incomplete but may be an important component of premating isolation.

Postzygotic Mechanisms

If premating mechanisms fail, postmating mechanisms can come into play. If gametes are released, there still may be a failure of fertilization (*intersterility*). In plants, the pollen may not germinate on the foreign stigma or the pollen tube may fail to develop. Fertilization failure is almost universal between remotely related species and occasionally occurs even between closely related species.

If fertilization does take place, other postmating mechanisms may operate. The hybrid may be inviable (*zygotic inviability*). In other cases, development may be essentially normal, but the hybrid may be ill-adapted to survive in any available habitat (*hybrid adaptive inferiority*). Even if hybrids are produced, they may be partially or totally sterile (*hybrid sterility*). Hybrids between closely related forms are more likely to be fertile than those between more distantly related species, but the correlation is an inexact one. The causes for hybrid sterility are complex and can involve genetic factors, differences in gene arrangements on the chromosomes that disrupt normal chromosomal pairing and segregation at meiosis, and incompatibilities between cytoplasmic factors and the chromosomes.

If the hybrids are fertile and interbreed or backcross to one of the parental forms, a subtler phenomenon known as *hybrid breakdown* sometimes occurs. It takes the form of reduced fertility or reduced viability in the offspring. The basis for hybrid breakdown is poorly understood but may result from an imbalance of gene complexes contributed by the two species.

A Fail-Safe System

In most cases of reproductive isolation that have been carefully studied, more than one kind of isolating mechanism has been found. Even though one type is clearly of paramount importance, it is usually supplemented by others. Should the predominant type fail, others may come into play. In this sense, reproductive isolation can be viewed as a fail-safe system.

A striking difference in the overall pattern of reproductive isolation between animals and plants is the much greater importance of premating isolation in animals and the emphasis on postmating mechanisms in plants. *Behavioral isolation*, together with other premating mechanisms, is highly effective in animals, and postmating factors usually function only as a last resort. In contrast, behavioral factors contribute little to premating isolation in plants. Pollen in many forms is widely distributed either by the wind or by unselective animal pollinators, and postmating factors consequently are much more likely to come into play. This difference is reflected in a much higher incidence of natural hybridization in plants as compared with animals.

John S. Mecham

See also: Gene flow; Genetic drift; Genetics: Mendelian; Genetics: mutations; Genetics: post-Mendelian; Hybrid zones; Hybridization; Nonrandom mating; Pollination; Population genetics; Species and speciation.

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RESISTANCE TO PLANT DISEASES

Categories: Anatomy; diseases and conditions; physiology

Plants have a number of defense mechanisms by which they can resist biotic or abiotic stresses that might cause their death or inhibit their growth. Such mechanisms are referred to as resistance.

Plants, the primary producers in all food chains, are besieged by a host of biological agents throughout their life cycles. Each species of plant is attacked by at least one hundred different kinds of mycoplasmas, viruses, bacteria, fungi, nematodes, and insects. In addition, regional weather patterns change, and plants are often faced with unfavorable environmental conditions such as heat, drought, or cold. Plants must contend with the chemicals used by people to deal with unwanted plants. These *herbicides* are designed to kill the plant or to restrict its growth.

When plants are exposed to *biotic* or *abiotic* stress, varying degrees of damage may occur, but many plants manage to protect themselves. Collectively, their *defense mechanisms* make up what is referred to as plant resistance. Although all plants possess some means of defense against stress, the term *resis-*

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tant plant is usually reserved for varieties that have the ability to produce a larger crop of good quality fruit than would other varieties placed under the same stress conditions.

Types of Resistance

Resistance is often categorized according to its intensity. An *immune cultivar* is one that will never be consumed or injured by a particular stress under any condition. Few, if any, cultivars are considered immune to biotic or abiotic factors known to induce stress in other cultivars of the same plant species. A *high-resistance cultivar* is one that exhibits only slight damage from a specific biotic or abiotic stressing agent under a given set of conditions. A *low-resistance cultivar* is one that demonstrates less damage from a stressing agent than the average for the species. *Susceptible* and *highly susceptible* cultivars show increasing damage from a biotic or abiotic agent greater than the average for the species.

Resistance also varies according to environmental conditions, genetic control, number of pests, and plant age. *Multiple resistance* refers to cultivars that are resistant to multiple factors. Resistance under field conditions (called *field resistance*) may be considerably different from the resistance observed in the laboratory or greenhouse.

Resistance may be controlled by a single gene (monogenic), by a few genes (oligogenic), or by many genes (polygenic). The terms "horizontal resistance" or "general resistance" are used when describing resistance that is expressed equally against all biotypes of a pest species, and "vertical resistance," or "specific resistance," refers to resistance expressed against only some of the biotypes of a pest species. Resistance may be expressed at any stage of the life cycle from seedling through maturity. On occasion, host plants may pass through a particularly susceptible stage of growth quickly, thereby avoiding infestation by a large number of pests.

Mechanisms of Resistance

The mechanisms of plant resistance are generally grouped into three main categories: *tolerance*, *nonpreference*, and *antibiosis*. Tolerance is the sum of all plant responses that give the species the ability to withstand a particular degree of stress. The term "tolerance" is particularly applicable to mechanisms of resistance associated with environmental stresses. Plants commonly develop tolerances to stresses such as heat, cold, drought, or salt. Nonpreference is a phenomenon in which the plant is merely ignored by a particular pest. The plant has no food or shelter to offer the pest and is not suitable for egg-laying; therefore, the plant is not a potential host. Antibiosis refers to a mechanism in which the plant exerts some deleterious action on the pest. For example, the plant may produce a substance that inhibits some essential function of the pest's biology, such as reproduction or development, usually leading to death of the pest.

Structural Defenses

Both structural and biochemical defenses can be preexisting or induced by stress. Preexisting defense structures include the waxy surfaces of many leaves, thickness of the cuticle that covers the epidermal cells, characteristics of openings into the plant, and thickness and toughness of the cell walls of the plant cells. After a pest invades a plant, inducible changes in structure can provide some degree of defense. After invasion by pests such as fungi, bacteria, viruses, and nematodes, some plants will form layers of cork tissue that seal off the invading organisms and prevent them from reaching the remainder of the plant.

Other structural defense strategies include the formation of structures called *tyloses* to seal off the infected vascular tissue or the deposition of gums around lesions. Both tyloses and gum deposits prevent the spread of the agent. In some instances, plants will form abscission layers that seal off a section of leaf and cause it to die along with the pest.

Biochemical Defenses

Although structural barriers provide some degree of defense against invading organisms, chemicals produced by the plant during or after the induction of stress appear to be much more important in conferring resistance. There are several preexisting biochemical defense systems. Although plants do not produce antibodies to specific invading pests, some type of immunological response appears to be operating. Plants that are resistant to specific pathogens do not contain the *antigens*, chemicals that induce the resistance response, that are found in the susceptible plants. Some cultivars maintain resistance by limiting the production of certain chemicals that are essential nutrients for invading pathogens. Other preexisting defense mechanisms include the presence in the plants' cells of chemicals that inhibit the growth of an invading pest or the release into the environment of chemicals that either inhibit or kill potential pathogens.

When injured by a biotic agent, chemicals, or environmental factors, plants respond with a series of biochemical reactions aimed at limiting the injury and healing the wound. This response is much more pronounced in resistant plants than in susceptible plants. The biochemical response to stress shows tremendous variation. Many resistant plants respond to a pest invasion by releasing phenolics or other toxic compounds. Fungi produce a group of toxic substances called *phytoalexins* in response to an invasion.

Many plants respond to stress by the induced synthesis of proteins and other enzymes that form an immune layer around the infected site. When resistant plants are confronted with the oxidative stress that usually accompanies environmentally induced stress, they increase the production of antioxidant enzymes. Enzymes produced by invading organisms are often responsible for the damage suffered by the host plant, but some resistant plants produce substances that either resist or inactivate these enzymes. Some invading organisms produce toxins that damage the host plant, and plants resistant to these organisms generally produce chemicals that detoxify the toxins. Other plants develop resistance by altering certain biochemical pathways or initiating a hypersensitive response.

Genetically Engineered Resistance

With the advent of recombinant DNA (deoxyribonucleic acid) technology in the 1970's, the development of new traits such as resistance was no longer limited to mutation or natural selection from a limited pool of genes. Scientists first developed transgenic animals and plants in the early 1980's, and industry has made widespread use of genetically modified organisms. Despite the beneficial applications, potential risks and ethical issues associated with the technology have led to controversy.

Genetic engineering has been used extensively in agriculture. Products of modified organisms are used to protect plants from frost and insects. In 1986 the U.S. Environmental Protection Agency approved the release of the first genetically modified crop plant; by the end of the 1990's, more than one thousand others had been field-tested. Plants have been designed to resist disease, drought, frost, insects, and herbicides as well as to improve the nutritional value or flavor of foods.

D. R. Gossett, updated by Bryan Ness

See also: Biopesticides; Biotechnology; Cloning of plants; Diseases and disorders; DNA: recombinant technology; Genetically modified foods; Herbicides; Integrated pest management; Pesticides; Plant biotechnology; RNA.

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RESPIRATION

Categories: Cellular biology; photosynthesis and respiration; physiology

All cells must have a source of energy in order to survive. Almost all cells utilize ATP as their energy currency. In other words, ATP is produced and stored up until it is needed to supply energy for metabolic activity. Respiration is the process by which cells oxidize a fuel, usually the simple sugar glucose, and use the energy released during this oxidation to produce ATP.

The term "metabolism" refers to the sum total of all the chemical activity that occurs within an organism. Metabolism can be further divided into two large categories, *anabolism* and *catabolism*. Anabolism refers to those metabolic reactions associated with the synthesis of molecules, such as proteins or carbohydrates, while catabolism includes those reactions involved in the degradation of molecules. Respiration is a catabolic process.

Carbohydrates, especially the simple sugars glucose and fructose, serve as the initial substrates for the respiratory process. In plants, these substrates are produced by *photosynthesis* in the chloroplasts. Solar energy is used to convert carbon dioxide and water into small sugar-phosphate molecules which are then combined to form fructose. Energy is required to form each carbon-to-carbon bond (called a *covalent bond*), and a specified amount of energy is stored in each covalent bond. In other words, solar energy is converted to chemical energy.

The fructose may directly enter *glycolysis*, the first series of reactions in cellular respiration, or it may be converted to glucose. The glucose may also enter glycolysis directly, or it may be combined with a fructose molecule to form sucrose (table sugar), which can be transported to other parts of the plant. Once sucrose reaches the target cells, it can be converted back to glucose and fructose, which can then be metabolized via glycolysis. Glucose can also be polymerized into large starch molecules, which can be stored. When the plant experiences an energy deficit, starches can be broken down to glucose molecules.

During respiration fuel molecules, such as glucose, undergo a series of reactions in which the molecule is oxidized into smaller molecules, and in aerobic respiration, the glucose will ultimately be degraded to carbon dioxide and water. As the molecules are degraded, the energy stored in the chemical bonds that held the glucose molecule together is released, and the cells trap this energy in the form of *adenosine triphosphate* (ATP) molecules. In a sense, the oxidation of glucose as a fuel is similar to the oxidation (burning) of any other organic fuel, such as gas, fuel oil, or coal, except the biological oxidation of glucose is a stepwise process and results in the formation of ATP. Each step requires an *enzyme*, an organic catalyst. There are many enzymes associated with respiration, but the three most common types are kinases, decarboxylases, and oxioreductases. *Kinases* catalyze reactions associated with ATP formation or utilization; *decarboxylases* catalyze decarboxylation reactions which remove chemical groups called carboxyls as carbon dioxide; and *oxioreductases* catalyze oxidation/reduction reactions. *Oxidation* is the removal of electrons from a molecule, and *reduction* is the addition of electrons. In general, oxidation involves the removal of two electrons and two hydrogen ions (H^+) from the substrate molecule. The release of H^+ into the cytosol would result in acidification of the cell; therefore, oxioreductases require the presence of *coenzymes* which will accept the electrons and H^+. In other words, these coenzymes are reduced as glucose is oxidized. The two most important coenzymes in respiration are *nicotine adenine dinucleotide* (*NAD*) and *flavin adenine dinucleotide* (FAD). The reduced forms of these coenzymes are NADH + H^+ and $FADH_2$, respectively.

Glycolysis and Fermentation

Glycolysis, the first series of reactions in the respiratory pathway, consists of nine or ten separate steps, depending on whether the initial substrate is fructose or glucose. Because sugar molecules are not very reactive, the first two or three steps in the process use two ATP molecules to convert the six-carbon glucose or fructose to a very reactive molecule called *fructose-1,6-bisphosphate*. This six-carbon compound is then broken down into the equivalent of two molecules of a three-carbon compound called *glyceraldehyde-3-phosphate* (*PGAL*). Each molecule of PGAL undergoes a series of reactions in which it is converted to *pyruvic acid*. During this conversion, one NADH + H^+ is formed, and enough energy is released to produce two ATP molecules per PGAL. In summary, glycolysis is the conversion of glucose to two molecules of pyruvic acid, two molecules of NADH + H^+, and a net gain of two ATP molecules (four were produced, but two were used to initiate the process). Glycolysis occurs in the cytosol and is entirely *anaerobic*, meaning that it occurs in the absence of oxygen.

In anaerobic organisms, such as yeast, each molecule of pyruvic acid is decarboxylated to produce carbon dioxide and a molecule called acetaldehyde. The NADH + H^+ produced during glycolysis is then used to convert the acetaldehyde to ethanol. This anaerobic process is called *fermentation*. Overall, the process of fermentation results in the conversion of glucose to two molecules of carbon dioxide, two molecules of ethanol, and a net gain of two ATP molecules.

The Krebs Cycle and Oxidative Phosphorylation

In aerobic plants, each molecule of pyruvic acid is transported to the matrix of the mitochondria where it is oxidatively decarboxylated to produce a carbon dioxide molecule, a molecule of NADH + H^+, and a compound called acetyl coenzyme A (acetyl CoA), which contains two carbon atoms from the initial glucose molecule. Acetyl CoA then enters a second series of reactions called the *Krebs cycle*, also known as the tricarboxylic acid cycle or the citric acid cycle. The two carbons from the glucose molecule combine with a four-carbon compound called *oxaloactic acid* to form a six-carbon compound called *citric acid*. The citric acid is decarboxylated twice, and the remaining four-carbon fragment is ultimately converted back to oxaloacetic acid. During this process, two molecules of carbon dioxide, three molecules of NADH + H^+, one $FADH_2$ molecule, and one ATP molecule are produced. During glycolysis, two molecules or pyruvic acid are produced per glucose; therefore, after two turns of the Krebs cycle, glucose is converted to six molecules of carbon dioxide, six (four net) ATP molecules, ten molecules of NADH + H^+, and two molecules of $FADH_2$.

A third series of reactions, referred to as *electron transport*, takes place within the mitochondrial membranes. The electrons and H^+ ions bound to the NADH + H^+ and $FADH_2$ are transferred to initial electron receptors and then passed through a series electron transporters, each with a lower *reduction potential* (the tendency to accept electrons). Several of these electron transporters are iron-sulfur containing proteins called cytochromes. Hence, this electron transport system is sometimes referred to as the cytochrome system. The final electron acceptor in this system is oxygen. When two electrons and H^+ ions are transferred to oxygen, a molecule of water is formed. This provides the cells with a safe means of removing excess H^+ ions, but more important, additional ATP is produced. As electrons are transported from NADH + H^+ and $FADH_2$ through the electron transport chain and ultimately to oxygen, energy is released. This energy can be used to synthesize ATP from ADP (adenosine diphosphate). Since the energy is stored in the phosphate bond (ADP to ATP) and occurs only in the presence of oxygen, the production of ATP during aerobic respiration is referred to as *oxidative phosphorylation*. Each mole of NADH + H^+ produced within the mitochondria results in the production of three moles of ATP via the electron transport system. The NADH + H^+ from glycolysis and $FADH_2$ enter the electron transport system downstream from the NADH + H^+ derived from inside the mitochondria. As a result, each mole of these molecules produces only two moles of ATP. The total ATP production per mole of glucose from electron transport and oxidative phosphorylation is thirty-two moles.

3 × 8 NADH + H^+ from within the mitochondria = 24;
2 x 2 NADH + H^+ from glycolysis = 4; 2 × 2 $FADH_2$
from the Krebs cycle = 4: 24 + 4 + 4 = 32.

Overall, aerobic respiration uses glycolysis, the Krebs cycle, and electron transport and results in the conversion of one mole of glucose to six moles of carbon dioxide, twelve moles of water and a net of thirty-six moles of ATP.

2 net ATPs from glycolysis + 2 ATPs from the Krebs
cycle + 32 ATPs from electron transport = 36 ATPs.

Each mole of ATP represents about 8,000 calories of energy; therefore the oxidation of one mole of glucose can produce a total of 288,000 calories of energy available for cellular work.

D. R. Gossett

See also: ATP and other energetic molecules; Carbohydrates; Energy flow in plants; Ethanol; Glycolysis and fermentation; Krebs cycle; Microbial nutrition and metabolism; Mitochondria; Oxidative phosphorylation; Photosynthesis.

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RHYNIOPHYTA

Categories: Evolution; paleobotany; *Plantae*; seedless vascular plants; taxonomic groups

When first proposed by Harlan Banks in 1968, the Rhyniophyta *were the first and oldest vascular land plants. The trimerophytes subsequently evolved from them.*

In 1908, Octave Lignier developed a model of what the sporophyte of the earliest vascular land plants might look like. The sporophyte is a diploid (2*n*) plant that produces spores in a sporangium, while its counterpart, the gametophyte, is a haploid (*n*) plant that bears the male (antheridia) and female (archegonia) sex organs. Lignier proposed that the first vascular land plants would consist of a forked, photosynthetic stem lacking both roots and leaves. At the point of branching, the fork looked like a capital Y. Running along the ground or just below the soil surface was a horizontal stem (rhizome) bearing hairlike filaments (rhizoids) on its lower surface that functioned in anchorage and absorption. Spores were produced either within the unmodified stem tips of some of the aerial branches or in a specialized reproductive structure, a thick-walled, elongate sporangium, that terminated some branch tips.

In 1912, some unique plant fossils were found in the Rhynie Chert (406 million to 401 million years old) in Scotland. The Rhynie Chert is a hot-spring chert formed when silica-saturated water from a hot spring flooded a low-lying marsh, seeped into the plants, and hardened within and about them. Because they are encased in chert, the Rhynie plants were the first fossil plants to yield both structural and anatomical data. Two of the plants, *Rhynia major* (now *Aglaophyton*) and *R. gwynne-vaughanii*, were reconstructed as near-perfect matches to Lignier's model of the earliest vascular land plant. With their discovery, the science of paleobotany came of age.

As knowledge of the rhyniophytes increased, a revision of the group seemed in order. As originally defined, the *Rhyniophyta* included both vascular (tracheophytes *Rhynia* and *Cooksonia pertoni*) and nonvascular plants that are intermediate between bryophytes and vascular plants (*Aglaophyton* and *Horneophyton lignieri*). These plants are placed in two groups, the *Rhyniophyta* and *Horneophyta*, respectively.

Horneophyta or Protracheophytes

Aglaophyton's rhizome was in contact with the ground at intervals, and rhizoids were concentrated at those positions rather than spread evenly along the axis. The tissue of the rhizome contained a fungus, representing the earliest known example of a plant-fungus symbiosis. The vast majority of land plants require this symbiotic relationship to live. The land plant provides the fungus with shelter within its cells and access to the products of photosynthesis. The fungus absorbs water and minerals from the soil, which it passes on to the land plant.

This partnership is so important to living plants that scientists were not surprised to find it very early in the fossil history of the land plants. Dense clusters of buds (possibly dormant stem tips) were found on the rhizome at the base of the aerial stems. The aerial stem was naked and branched by forking into two daughter axes of equal size. Elongate sporangia were borne at the tips of some aerial branches. The water-conducting cells of *Aglaophyton* lack the internal wall thickenings characteristic of tracheids (thick-walled, dead cells found in the xylem of vascular land plants) and resemble the thin-walled, water-conducting cells (hydroids) of the mosses. Because of the absence of tracheids, *Aglaophyton* is considered a nonvascular plant and must be removed from the *Rhyniophyta*. A male reproductive structure (*Lyonophyton rhyniensis*) represents the gametophyte of *Aglaophyton*.

Another nonvascularized sporophyte found in the Rhynie Chert was *Horneophyton*. Instead of having obvious sporangia, the spores of *Horneophyton* were produced within the stem tip and released by means of a terminal pore. Multicellular projections were found on the stem, which terminated in stomates. The aerial stems did not grow from a rhizome. The aerial stems each terminated in a bulbous, nonvascularized structure called a corm. Several corms were found attached to one another, but no vascular tissue connected them. As in *Aglaophyton*, the water-conducting cells were thin-walled and lacked internal wall thickenings. *Langiophyton mackiei* represents the female gametophyte of *Horneophyton*.

When gametophytes are known in the protracheophytes, they have an anatomical and structural complexity similar to that of their corresponding sporophytes. In contrast, the gametophytes of vascular land plants are small and inconspicuous (often subterranean). Scientists know more about the gametophytes of the plants of the Rhynie Chert than they do about almost all other groups of fossil plants.

Rhynia

Rhynia gwynne-vaughanii was reconstructed as a smaller version of *Aglaophyton*. The aerial stem of *Rhynia* was naked and branched by forking. The rhizome bore rhizoids. Thick-walled water-conducting cells (tracheids) were present. Although *Rhynia* was reconstructed bearing sporangia, none were originally found attached to the aerial stems. In addition to lacking sporangia, *Rhynia* had bumps along the aerial stem that were interpreted as female reproductive structures (archegonia). As a result, *Rhynia* was reinterpreted as the gametophyte of *Aglaophyton*. Subsequently, sporangia were found attached to *Rhynia*, making the plant a sporophyte once more. The sporangia were borne laterally along the stem on short side branches, and they were shed after releasing their spores. The gametophyte of *Rhynia* is unknown.

The small, circular vascular strands and fleshy stems associated with the rhyniophytes and horneophytes indicate that these plants did not grow very tall. Water pressing against the inside of the cell walls in their stems (turgor pressure) held these plants upright.

Cooksonia

The oldest vascular land plant (412 million to 406 million years old) and only cooksonioid with identifiable vascular tissue is *Cooksonia pertoni*. The aerial stems of *Cooksonia* branched by forking and bore at their branch tips sporangia shaped like kidney beans. Plants whose sporangia resemble those of *C. pertoni* are known from older sediments (414 million to 412 million years in age), but no vascular tissue has been found in their stems. The oldest fossil plant from the Western Hemisphere that resembles *Cooksonia* comes from Bathurst Island in the Canadian Arctic (420 million to 414 million years in age). No roots or rhizomes are known for any *Cooksonia*. If the older specimens of Cooksonia lacked vascular tissue, *Cooksonia* may not be a valid genus. These plants are best referred to collectively as cooksonioids, and plants showing these traits could be bryophytes, protracheophytes, or rhyniophytes.

Fossil Spores

Fossils spores are known from sediments that are about 40 million years older than those from which cooksonioids are recovered. The most abundant spores were not produced by the vascular land plants and are called cryptospores. Banded tubules and sheets bearing cell outlines (collectively called nematoclasts) are recovered with the cryptospores. Similar structures are produced by the sporangial epidermis of modern mosses (cellular sheets) and liverworts (banded tubes). The cryptospores had a worldwide distribution and showed limited diversity. These spores were probably produced by early bryophytes.

To identify the type of plant that produced a specific spore, researchers must find the spore within a sporangium. Although free spores are common, no spores are known from sporangia for the first 65 million years of land plant evolution. The presence of cryptospores and the occasional spore that might have been produced by a vascular land plant indicates that land plants first appeared about 500 million years ago. Most of the 65-million-year period from which sporangia are unknown was characterized by high sea levels, and little continental deposition occurred. The missing continental deposits are where the necessary sporangia would have been found. The oldest spores from continental deposits are about 435 million years old. Cryptospores are found in sporangia from England that are between 414 million and 412 million years old. Although they predominated early, cryptospores form a very minor component of the spore flora about by 414 million years ago. The decrease in the number of cryptospores reflects the growing importance (diversification) of the vascular land plants.

Ancestors of the Rhyniophytes

The first land plants, bryophytes, protracheophytes, and tracheophytes, evolved from green algal (charophycean) ancestors that lived in freshwater habitats whose appearance was unpredictable (not seasonal) and of short duration. Their algal ancestors were preadapted to life on land. They were resistant to microbial attack due to the structure of their cell walls. They had a genetic (heritable) basis for lowering or suspending metabolic activity during drought (dry conditions that could last for days or months) and desiccation (dry conditions that could last for decades). Their reproductive bodies did not dry out during air transport from one water body to another. The first to colonize the land successfully were the bryophytes. The protracheophytes and tracheophytes appeared after the bryophytes were well established on land.

Gary E. Dolph

See also: Adaptive radiation; Algae; *Charophyceae*; Evolution of plants; Fossil plants; Hornworts; Liverworts; Mosses; Paleobotany; Plant tissues; Seedless vascular plants; Shoots; Species and speciation; Stems; *Trimerophytophyta*; *Zosterophyllophyta*.

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RIBOSOMES

Categories: Cellular biology; genetics

Ribosomes are complex cellular structures found in all cells and are responsible for making proteins. They are composed of ribosomal RNA (rRNA) and protein and are most abundant in the cytoplasm, although some functional ribosomes can be found in the nuclei of eukaryotic cells. Chloroplasts and mitochondria also have their own ribosomes.

Ribosomes are responsible for synthesizing the proteins in all cells by a process called *translation*. It is called translation because ribosomes use messenger ribonucleic acids (mRNAs) as their guide and must "translate" the message contained in the nucleotides of mRNAs. The general structure of ribosomes is the same in all cells, but ribosomes of prokaryotes are smaller than ribosomes in the cytoplasm of eukaryotes. The ribosomes in chloroplasts and mitochondria are more similar to the smaller ribosomes of prokaryotes but are often smaller yet.

Ribosome Structure

Because ribosomes, and rRNAs, are so large, they are not described on the basis of their molecular weight but rather in *Svedbergs*, or Svedberg units. Svedbergs (denoted S) are a measure of how quickly a large molecule or aggregation of molecules sediment, or sink to the bottom of a centrifuge tube while being spun around. Higher S values mean faster sedimentation and thus greater mass. For example, prokaryotic ribosomes sediment at 70's, whereas eukaryotic ribosomes, which are larger, sediment at 80's. Svedbergs cannot be added together, because they are not directly related to mass but to a combination of mass and overall molecular size and shape. Consequently, if two molecules that are both 30's are joined together, their combined sedimentation rate would be about 50's or a little more but not 60's.

Prokaryotic ribosomes constitute three rRNAs and fifty-two different proteins. Like all ribosomes, they are composed of two subunits, referred to simply as large and small subunits. Large subunits have a sedimentation rate of 50's and are composed of a 23S rRNA, a 5S rRNA, and thirty-one proteins. Small subunits have a sedimentation rate of 30's and are composed of a single 16S rRNA and twenty-one different proteins. To function, a small and large subunit must come together.

Eukaryotic ribosomes are more complex, with four rRNAs and more than eighty proteins. Large subunits have a sedimentation rate of 60's and are composed of a 28S rRNA, a 5.8S rRNA, a 5S rRNA, and about forty-nine proteins. Small subunits have a sedimentation rate of 40's and are composed of a single 18S rRNA and about thirty-three proteins. Assembly of the subunits takes place in a region of the nucleus called the *nucleolus*. When completed, the subunits are transported through nuclear pores to the cytoplasm. Although translation of mRNAs takes place primarily in the cytoplasm, a small amount occurs in the nucleus.

Translation in Prokaryotes

Before translation can take place, *transcription* of a gene must occur. Transcription converts the deoxyribonucleic acid (DNA) code of a gene into a complimentary RNA code, in the form of an mRNA. Even while RNA polymerase catalyzes the joining of nucleotides for the mRNA, translation can begin. Translation includes three steps: initiation, elongation, and termination.

In *initiation*, special proteins called initiation factors (IFs) enable the small subunit of a ribosome to bind to an mRNA and form the initiation complex. Next, a special tRNA called fMet-tRNA (N-formylmethionyl-tRNA), which carries a specially modified amino acid derivative of methionine, binds to the start codon of the mRNA (AUG). This modified methionine is the first amino acid in all prokaryotic proteins, but many proteins are modified after transcription, often by removing the first few amino acids. Lastly, the large ribosomal subunit binds.

Elongation is a complex process in which the ribosome adds amino acids, one at a time, to the growing protein. Ribosomes have three sites where events in translation takes place. The A site (aminoacyl-tRNA site) is where new tRNAs, with their attached amino acids, bind to the ribosome and mRNA. The P site (peptidyl-tRNA site) is where the tRNA with the growing protein (polypeptide) is attached to the ribosome and the mRNA. The E site (exit site), only recently recognized, is where tRNAs leave the ribosome after they have completed their work.

The sequence of events in elongation can be difficult to visualize, but it is a cyclical process that repeats until elongation is done. The steps are as follows. First, while the tRNA with the growing protein (called a peptidyl-tRNA) rests in the P site, a tRNA with an amino acid (called an aminoacyl-tRNA) enters the A site and binds to the codon on the mRNA. Second, the peptidyl-tRNA attaches the growing protein to the amino acid on the aminoacyl-tRNA. Now the tRNA in the P site has no amino acids attached to it. Third, the tRNA in the P site now leaves the ribosome by passing through the E site. Fourth, as the tRNA leaves the P site, the tRNA at the A site (now a peptidyl-tRNA) is translocated (moved) to the P site by moving the mRNA over one codon, leaving the A site open for the next aminoacyl-tRNA to attach. These steps repeat until the stop codon, near the end of the mRNA, is reached. Many of the events of elongation were long believed to be catalyzed by proteins in the ribosome. It is now known that some of the ribosome's catalytic properties are due to the rRNAs, which, as a result, are sometimes called *ribozymes*.

The stop codon is not recognized by any of the tRNAs. *Termination* occurs when some special proteins called *releasing factors* bind to the ribosome. When they bind, the protein that is attached to the tRNA in the P site is released from the tRNA, the tRNA leaves through the E site, and the two subunits come apart.

Translation in Eukaryotes

The process of translation in eukaryotes varies only in minor details from translation in prokaryotes, and these differences are due to the greater complexity of eukaryotic mRNA and ribosomes. Eukaryotic mRNA must go through extensive processing after being transcribed, including intron excision/exon splicing and addition of a special 5′ cap and a 3′ poly-adenosine tail. Eukaryotic mRNA cannot be translated until these modifications are completed. Although some mRNA is translated in the nucleus, most must be transported to the cytoplasm first. Consequently, transcription and translation are completely separate processes, unlike their coupling in prokaryotes.

Initiation in eukaryotes involves a larger number of initiation factors. Once the small ribosomal subunit binds, it then starts at the 5′ end of the mRNA and searches for the start codon (AUG). When the start codon is found, a methionyl-tRNA binds to the ribosome and the start codon of the mRNA. In eukaryotes, like in prokaryotes, the first amino acid in all proteins is methionine, but in eukaryotes it is not a N-formyl-methionine. Elongation and termination are essentially the same in both eukaryotes and prokaryotes. As in prokaryotes, completed proteins are typically modified in various ways before being used by the cell.

Many ribosomes will typically translate an mRNA simultaneously. An mRNA with several ribosomes lined up along it, all of them translating at once, is often called a *polyribosome*. Polyribosomes are observed in both eukaryotes and prokaryotes.

Distribution in Eukaryotic Cells

After being synthesized in the nucleolus, a few ribosomes will function for an unknown length of time in the nucleus. Most, though, are transported to the cytoplasm as separate subunits. Once in the cytoplasm, ribosomes will either bind to endoplasmic reticulum (ER), in regions called rough ER because of the fuzzy appearance of these areas in electron micrographs, or they will remain free in the cytoplasm. Ribosomes bound to the rough ER specialize in making proteins that will either be embedded in membranes or transported in vesicles to the Golgi complex. The different fates of proteins made at the rough ER are determined by special *signal sequences*, sequences of amino acids at the beginning of proteins which are typically removed later.

Ribosomes that are free in the cytoplasm make proteins of various kinds that are needed for processes occurring in the cytoplasm. Regardless of location, ribosomes are usually found disassembled, and the two subunits come together only when needed for translation. Cells have anywhere from several thousand ribosomes to as many a few million in cells that have particularly high rates of protein synthesis.

Bryan Ness

See also: Angiosperm cells and tissues; Cell cycle; Cell theory; Chloroplasts and other plastids; Cytoplasm; Cytoskeleton; Cytosol; DNA: historical overview; DNA in plants; DNA replication; Endomembrane system and Golgi complex; Endoplasmic reticulum; Eukaryotic cells; Membrane structure; Microbodies; Nucleus; Oil bodies; Peroxisomes; Photosynthesis; Plant cells: molecular level; Plasma membranes; Respiration; RNA.

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RICE

Categories: Agriculture; economic botany and plant uses; food

Rice, the starchy seeds of an annual cereal grass, is the most commonly consumed food grain for a majority of the world's population.

The rice plant, *Oryza sativa*, is a member of the grass family, classified into *indica* and *japonica* varieties. World production of rice exceeds 500 million tons. Most countries—particularly in Asia—cultivate rice for domestic consumption, so less than 5 percent enters the export market. The United States generates only about 2 percent of world rice production, but almost half of U.S. production is exported. Rice cultivation almost certainly began in India, where it dates back to about 3000 B.C.E. During medieval times it spread westward to southern Europe.


Digital Stock

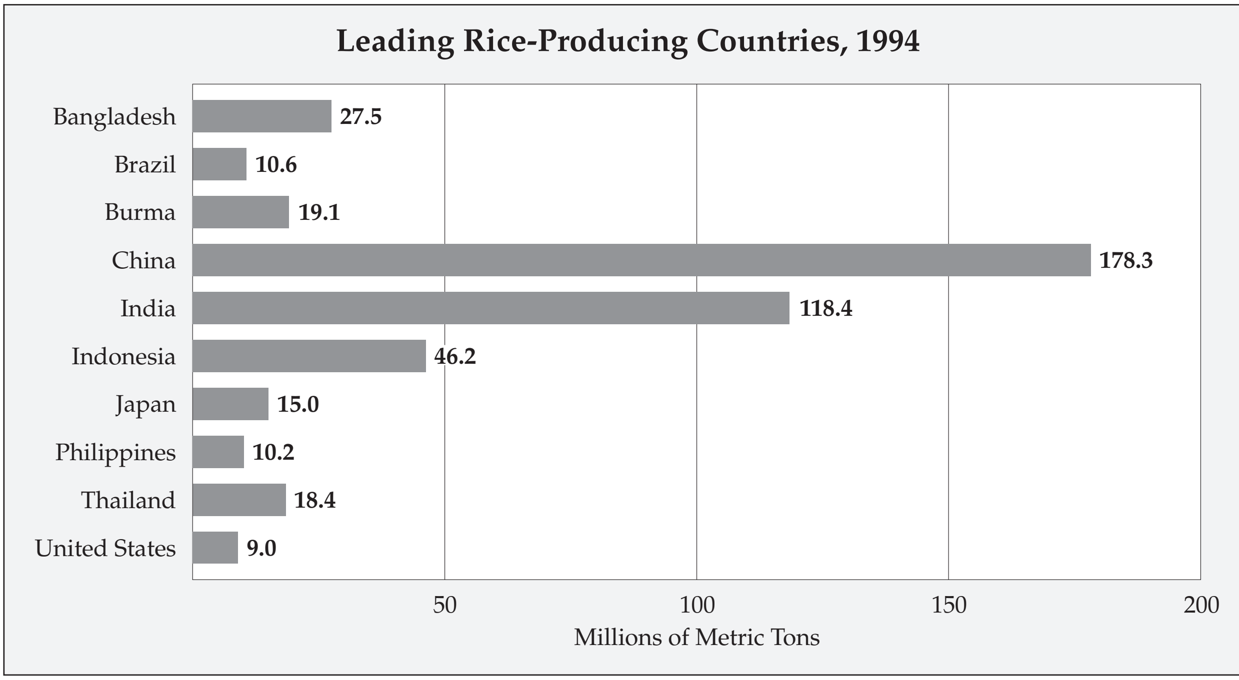
Rice paddies in Indonesia.

Cultivation

Monsoon tropics are ideal for indica rice, which is commonly cultivated in China and Southeast Asia. The plants can adapt to uncertain conditions. The japonica type of rice requires precise water control as well as weed and insect control. It is cultivated in temperate zones such as the United States, Australia, Japan, Korea, and certain parts of China.

Rice is self-pollinated, and the grain is enclosed in the *palea*, or hull. Harvested but unmilled rice is called *paddy* or rough rice. Milling of rough rice by any of several processes yields the polished grain that is ready for consumption. Rough rice contains approximately 10 percent protein, 65 percent starch, 2 percent lipids, 5 percent minerals, and 18 percent hull/bran. The unhulled whole rice kernel also contains thiamine, niacin, and riboflavin. Parboiled rice can be stored for long periods.

The International Rice Research Institute in the Philippines has contributed significantly to the development



Note: World total for 1994 was approximately 535 million metric tons.
Source: U.S. Department of Commerce, *Statistical Abstract of the United States, 1996*, 1996.

of high-yielding types of rice, beginning in the mid-1960's. The development of these plants is considered a significant part of the 1960's *Green Revolution* in agriculture. Some of these varieties demand complete irrigation systems year-round that help keep the soil submerged under about 6 inches (15 centimeters) of water. Next to corn, rice provides the farmer with the greatest yield when plants are cultivated with the necessary care. The crop grows well in irrigated and flooded areas.

Cooked rice is mostly consumed in its whole grain form. Puffed rice and flaked rice are common breakfast cereals, and rice flour is used in bakery products. Laundry starch is made from rice starch. Rice hull is used in cattle feed as well as fertilizers. The rice plant produces oil for food and industry and thatching material for roofs and mats. The Japanese alcoholic beverage sake is made from a process that involves the fermentation of rice.

Wild Rice

The plant commonly known as wild rice, *Zizania aquatica*, is actually a separate genus found in North America. Like rice, wild rice is an annual grass, and it grows mostly in lakes and streams. Lakes in Minnesota, Wisconsin, and southern Canada provide a good harvest of wild rice. Wild rice, once a staple of the diet of American Indians in those regions, has become a popular side dish.

Mysore Narayanan

See also: African agriculture; Agriculture: world food supplies; Alternative grains; Aquatic plants; Asian agriculture; Australian agriculture; Caribbean agriculture; Central American agriculture; Green Revolution; Grains; High-yield crops; Hybridization; North American agriculture; Pacific Island agriculture; Plant biotechnology; Plant domestication and breeding; South American agriculture.

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RNA

Categories: Cellular biology; genetics

Ribonucleic acid (RNA), a molecule that plays many roles in the effective usage of genetic information, exists in several forms, each with its own unique function. RNA functions in the process of protein synthesis, during which information from DNA is used to direct the construction of a protein, and possesses enzymatic and regulatory capabilities.

Ribonucleic acid (RNA) is a complex biological molecule that is classified along with deoxyribonucleic acid (DNA) as a *nucleic acid*. Chemically, RNA is a polymer (long chain) consisting of subunits called *ribonucleotides* linked together by phosphodiester bonds. Each ribonucleotide consists of three parts: the sugar ribose (a five-carbon simple sugar), a negatively charged phosphate group, and a nitrogen-containing base. There are four types of ribonucleotides, and the differences between them lie solely in which of four possible bases they contain. The four bases are adenine (A), guanine (G), cytosine (C), and uracil (U).

The structures of DNA and RNA are very similar, but there are three important differences. The sugar found in the nucleotide subunits of DNA is *deoxyribose*, which is related to but differs slightly from the ribose found in the ribonucleotides of RNA. In addition, while DNA nucleotides also contain four possible bases, there is no uracil in DNA; instead, DNA nucleotides may contain a different base, called thymine (T). Finally, while DNA exists as a double-stranded helix in nature, RNA is almost always single-stranded.

Folding of RNA Molecules

The significance of many types of RNA lies in the order of their nucleotides, which represents information transcribed from DNA. This nucleotide order is called the *primary structure* of the molecule. An important aspect of many biological molecules, however, is the way their primary structures fold to create a three-dimensional shape. A single strand of DNA, for example, associates with another strand in a particular way to form the famous double helix, which represents its actual three-dimensional shape in nature. Similarly, protein molecules, especially enzymes, must be folded into a very specific three-dimensional shape if they are to perform their functions; loss of this shape will cause their inactivation.

Since RNA is single-stranded, it was recognized shortly after the discovery of some of its major roles that its capacity for folding is great and that this folding might play an important part in the functioning of the molecule. The nucleotides in an RNA molecule can form hydrogen-bonded *base pairs*, according to the same rules that govern DNA base pairing. Cytosine binds to guanine, and uracil binds to adenine. What this means is that in a particular single-stranded RNA molecule, complementary portions of the molecule are able to fold back and form base pairs with one another. These are often local interactions, and a common structural element that is formed is called a "hairpin loop" or "stem loop." A hairpin loop is formed when two complementary regions are separated by a short stretch of bases so that when they fold back and pair, some bases are left unpaired, forming the loop. The net sum of these local interactions is referred to as the RNA's secondary structure and is usually important to an understanding of how the RNA works. All *transfer RNAs* (tRNAs), for example, are folded into a secondary structure that contains three stem loops and a fourth stem arranged onto a "cloverleaf" shape.

Finally, local structural elements may interact with other elements in long-range interactions, causing more complicated folding of the molecule in space. The cloverleaf arrangement of a tRNA undergoes further folding so that the entire molecule takes on a roughly L-shaped appearance. An understanding of the three-dimensional shape of an RNA molecule is crucial to understanding its function. By the late 1990's, the three-dimensional structures of many tRNAs had been worked out, but it had proven difficult to do X-ray diffraction analyses on most other RNAs because of technical problems. More advanced computer programs and alternate structure-determining techniques have now enabled research in this field to proceed.

Three Classes of RNA

While all RNAs are produced by transcription, several classes of RNA are created, and each has a particular function. By the late 1960's, three major classes of RNAs had been identified, and their respective roles in the process of protein synthesis had been elucidated. In general, protein synthesis refers to the assembly of a protein using information encoded in DNA, with RNA acting as an intermediary to carry information and assist in protein building. In 1956, Francis Crick, one of the scientists who had discovered the double-helical structure of DNA, referred to this information flow as the "central dogma," a term that continues to be used.

Messenger RNA (mRNA) is the molecule that carries a copy of the DNA instructions for building a particular protein. It usually represents the information provided by a single gene and carries this information to the ribosome, the site of protein synthesis. This information must be decoded so that it will specify the order of amino acids in a protein. Nucleotides are read in groups of three (*codons*). In addition to the information required to order amino acids, the mRNA contains signals that tell the protein-building machinery where to start and stop reading the genetic information.

Ribosomal RNA (rRNA) exists in three distinct sizes and is part of the structure of the ribosome. The three ribosomal RNAs interact with many proteins to complete the ribosome, the cell structure that directs the events of protein synthesis. One of the functions of the rRNA is to interact with mRNA at a particular location and orient it properly so that reading of its genetic code can begin at the correct location. Another rRNA acts to facilitate the transfer of the growing polypeptide chain from one tRNA to another (peptidyl transferase activity).

Transfer RNA (tRNA) serves the vital role of decoding the genetic information. There are at least twenty and usually fifty to sixty different tRNAs in a given cell. On one side, they contain an "anticodon" loop, which can base-pair to the mRNA codon according to its sequence and the base-pairing rules. On the other side, they contain an amino acid binding site, to which is attached the appropriate amino acid for its anticodon. In this way, tRNA allows the recognition of any particular mRNA codon and matches it with the appropriate amino acid. The process continues until an entire new protein molecule has been constructed.

Split Genes and mRNA Processing

In bacterial genes, there is a colinearity between the segment of a DNA molecule that is transcribed and the resulting mRNA. In other words, the mRNA sequence is complementary to its template and is the same length, as would be expected. In the late 1970's, several groups of scientists made a seemingly bizarre discovery regarding mRNAs in eukaryotes (organisms whose cells contain a nucleus, including all living things that are not bacteria or archaebacteria): The sequences of mRNAs isolated from eukaryotes were not collinear with the DNA from which they were transcribed. The coding regions of the corresponding DNA were interrupted by seemingly random sequences that served no immediately obvious function. These *introns*, as they came to be known, were apparently transcribed along with the coding regions (*exons*) but were somehow removed before the mRNA was translated. This completely unexpected observation led to further investigations that revealed that mRNA is extensively processed, or modified, after its transcription in eukaryotes.

After a eukaryotic mRNA is transcribed, it contains all of the intervening sequences and is referred to as immature, or a "pre-mRNA." Before it can become mature and functional, three major processing events must occur: splicing, the addition of a "cap," and the addition of a "tail."

The process of splicing is a complex one that occurs in the nucleus with the aid of the "spliceosome," a large complex of RNAs and proteins that identify intervening sequences and cut them out of the pre-mRNA. In addition, the spliceosome must rejoin the sequences from which the intron-encoded nucleotides were removed so that a complete, functional mRNA results. The process must be extremely specific, since a mistake that caused the removal of only one extra nucleotide could change the protein product of translation so radically that it might fail to function.

While splicing is occurring, two other vital events are being performed to make the immature mRNA ready for action. A so-called cap, which consists of a modified guanine, is added to one end of the pre-mRNA by an unconventional linkage. The cap appears to function by interacting with the ribosome, helping to orient the mature mRNA so that translation begins at the proper location. A tail, which consists of many adenines (often two hundred or more), is also attached to the other end of the pre-mRNA. This so-called poly-A tail, which virtually all eukaryotic mRNAs contain, seems to be involved in determining the relative stability of an mRNA. These important steps must be performed after transcription in eukaryotes to enable the creation of a mature, functional messenger RNA molecule that is now ready to be translated. Most mRNAs must be transported out of the nucleus before they are used to make proteins, but about 10 to 15 percent of the mRNAs produced remain in the nucleus, where they are used to make proteins.

Other Specialized Functions

The traditional roles of RNA in protein synthesis were originally considered the only roles RNA was capable of performing. RNA in general, while considered an important molecule, was thought of as a "helper" in translation. This all began to change in 1982, when the molecular biologists Thomas Cech and Sidney Altman, working independently and with different systems, reported the existence of RNA molecules that had catalytic or enzymelike activity, meaning that RNA molecules can function as enzymes. Until this time, it was believed that all enzymes were protein molecules. The importance of these findings cannot be overstated, and Cech and Altman ultimately shared the 1989 Nobel Prize in Chemistry for the discovery of these RNA enzymes, or *ribozymes*. Both of these initial ribozymes catalyzed reactions that involved the cleavage of other RNA molecules—that is, they acted as nucleases. Subsequently, many ribozymes have been found in various organisms, from bacteria to humans. Some of them are able to catalyze different types of reactions, and there are new ones reported every year. Thus ribozymes are not a mere curiosity but play an integral role in the molecular machinery of many organisms. Their discovery also gave rise to the idea that at one point in evolutionary history, molecular systems composed solely of RNA performing many roles existed in an "RNA world."

At around the same time as these momentous discoveries, still other classes of RNAs were being discovered, each with its own specialized functions. In 1981, Jun-Ichi Tomizawa discovered *RNAI*, the first example of what would become another major class of RNAs, the *antisense RNAs*. The RNAs in this group are complementary to a target molecule (usually an mRNA) and exert their function by binding to that target via complementary base pairing. These antisense RNAs usually play a regulatory role, often acting to prevent translation of the relevant mRNA to modulate the expression of the protein for which it codes.

Another major class of RNAs, the *small nuclear RNAs* (snRNAs), was also discovered in the early 1980's. Molecular biologist Joan Steitz was working on the autoimmune disease systemic lupus when she began to characterize the snRNAs. There are six different snRNAs, now called U1-U6 RNAs. These RNAs exist in the nuclei of eukaryotic cells and play a vital role in mRNA splicing. They associate with proteins in the spliceosome, forming so-called *ribonucleoprotein complexes* (snRNPs), and play a prominent role in detecting proper splice sites and directing the protein enzymes to cut and paste at the proper locations.

It has been known since the late 1950's that many viruses contain RNA, and not DNA, as their genetic material. This is another fascinating role for RNA in the world of biology. The viruses that cause influenza, polio, and a host of other diseases are RNA viruses. Of particular note are a class of RNA viruses known as *retroviruses* because they have a particularly interesting life cycle. Retroviruses, which include human immunodeficiency human immunodeficiency virus (HIV), the virus that causes acquired immunodeficiency syndrome (AIDS) in humans, use a special enzyme called reverse transcriptase to make a DNA copy of their RNA instructions when they enter a cell. That DNA copy is inserted into the DNA of the host cell, where it is referred to as a *provirus*, and never leaves. Clearly, understanding the structures and functions of the RNAs associated with these viruses will be important in attempting to create effective treatments for the diseases associated with them.

An additional role of RNA was noted during the elucidation of the mechanism of DNA replication. It was found that a small piece of RNA, called a primer, must be laid down by the enzyme primase before DNA polymerase adds DNA nucleotides to this initial RNA sequence, which is subsequently removed.

Matthew M. Schmidt

See also: Chloroplast DNA; DNA: historical overview; DNA in plants; DNA replication; Gene regulation; Genetic code; Genetics: mutations; Mitochondrial DNA; Nucleic acids; Proteins and amino acids.

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ROOT UPTAKE SYSTEMS

Categories: Anatomy; physiology; transport mechanisms; soil

Root uptake systems are processes by which root cells transport water and nutrients from the soil, across the root surface, and to the tissues that will move the water and nutrients throughout the plant.

Fertile soil is a complex mixture of a variety of minerals, many different types of organic matter in different stages of decay, and a host of living microorganisms. This complex medium holds a large quantity of water, which it supplies to plants. In addition to water, the soil supplies the plants with the thirteen mineral nutrients required for normal growth and development. These nutrients (and the ionic forms taken up by the root) are nitrogen, phosphorus, potassium, sulfur, calcium, magnesium, iron, manganese, boron, chlorine, zinc, copper, and molybdenum. Varying amounts of these mineral nutrients exist both as constituents of the soil particles and as dissolved ions in the soil

PhotoDisc

Most plant roots extend below the soil surface.

water. Root uptake systems are responsible for taking these nutrient ions and water from the soil and moving them into the root tissues.

Root Structure

Most plant roots extend below the soil surface as either a *fibrous root system* or *taproot system*. In a fibrous root system, the major root branches numerous times, and each branch divides again and again, until a meshlike network is formed within the soil. This system does not penetrate very deep into the soil, but it does cover considerable area close to the surface.

In a taproot system, only small secondary lateral roots branch off the main root (the taproot) as it grows downward into the soil. The taproot may extend several meters in depth. Along the outer periphery of either of these root systems, large numbers of small *filamentous root fibers* and *root hairs* can be found. The root hairs are filamentlike projections of the epidermal (outer layer) cells. These root hairs, in conjunction with the cells of the filamentous root fibers, are responsible for the vast majority of water and nutrient uptake.

Each root cell, as is the case in all plant cells, is surrounded by a porous cell wall. Immediately inside the cell wall is a semipermeable membrane, which regulates the movement of ions and molecules into the *cytosol* of the cell. This semipermeable membrane is a fluid mosaic structure composed primarily of lipid and protein. A double layer of lipid provides the basic stable structure of the membrane. The protein is then interspersed periodically throughout the lipid bilayer. Some of these proteins, called *peripheral proteins*, penetrate only one of the layers of lipid, while *integral proteins* extend through both lipid layers to interface with the environment both inside and outside the cell. The rate and extent of water and ion movement through membranes are largely determined by this structural configuration.

Ion Uptake Mechanisms

Uptake of ions across membranes is accomplished by three mechanisms: *simple diffusion*, *facilitated diffusion*, and *active transport*. The first two are passive processes, with no direct input of cellular energy required. The latter, as the name indicates, is an active process requiring the cell to expend energy.

In its simplest analysis, diffusion is the net movement of suspended particles down a *concentration gradient*. Thus, certain ions dissolved in the soil solution will move into the root cell cytosol as long as the external concentration is higher than the concentration inside the cell.

Because of the lipid nature of the membrane, the rate of this movement will be determined by the *lipid solubility* of the particle. Those particles with high lipid solubility will diffuse across the membrane much faster than those with low lipid solubility.

Many nutrients exhibit low lipid solubility, yet still diffuse across the membrane. This is accomplished by facilitated diffusion. The ion with low lipid solubility combines with a membrane protein, which then facilitates its uptake across the membrane.

In both free and facilitated diffusion, the particles move down a concentration gradient. In numerous instances, however, the ion concentration of the root cell cytosol is greater than the concentration of the ion in the soil solution. The ion will nevertheless continue to accumulate within the root tissues.

Diffusion of any sort cannot account for this "uphill" movement against a concentration gradient. In this instance, the nutrient ion will combine with a membrane protein referred to as a *carrier*. This protein carrier will transport the particle across the membrane. Uptake mediated by this protein carrier system is called active transport and requires the input of energy supplied by the hydrolysis of adenosine triphosphate (ATP), the cell's primary energy currency.

Osmotic Potential

Regardless of the mechanism utilized to transport ions into the root cytosol, the final result is the establishment of an *osmotic potential* across the membrane. Osmotic potential is a measure of the tendency of water to move across a semipermeable membrane in response to a difference in solute concentration. The addition of a solute to water lowers its osmotic potential, and water will always move from the side of the membrane containing the solution with the lower solute concentration (higher osmotic potential) to the side of the membrane containing the solution with the higher solute concentration (lower osmotic potential). Hence, the uptake of the mineral ions by the plant root cells establishes a lower osmotic potential within the cytosol than exists in the soil solution, and water flows across the membrane into the cell.

In order for the water and ions to move across the root from the epidermal layer to the internal transport vessels called *xylem*, several layers of *cortex cells* and the *endodermis* must be crossed. There are two pathways water and ions can take. One is through the cytosol of the epidermal cells, cortical cells, and endodermal cells by means of the *plasmodesmata*, which are cytoplasmic strands that pass between plant cells, thereby connecting the cells as microscopic "bridges." These plasmodesmata provide a means by which the cytosol from all cells can exist as a continuous mass referred to as the *symplast*, and transport through this system is called *symplastic transport*.

A second pathway, referred to as *apoplastic transport*, occurs through the apoplast (the region of continuous cell walls among cells). Because this apoplast is freely permeable to water and ions, the cells of the epidermis, cortex, and endodermis are in intimate contact with the soil water. Apoplastic transport, however, cannot occur across the endodermis because of the presence of an impermeable waxy layer in the cell walls called the *Casparian strip*. Thus, water and ions can travel through the apoplast until reaching the endodermis. There, movement into the endodermal cytosol by one of the three mechanisms mentioned above is required.

After passing the Casparian strip, the water and ions can move back into the apoplast. Although there is some disagreement among plant scientists as to which pathway is most important, it is highly probable that both pathways are involved. Regardless of whether the transport across the root is apoplastic or symplastic, the water and ions reach the xylem tubes within the interior of the root, where subsequent transport throughout the plant can take place.

D. R. Gossett

See also: Active transport; Angiosperm cells and tissues; Cells and diffusion; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Plant tissues; Roots; Vesicle-mediated transport; Water and solute movement in plants.

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ROOTS

Categories: Anatomy; physiology

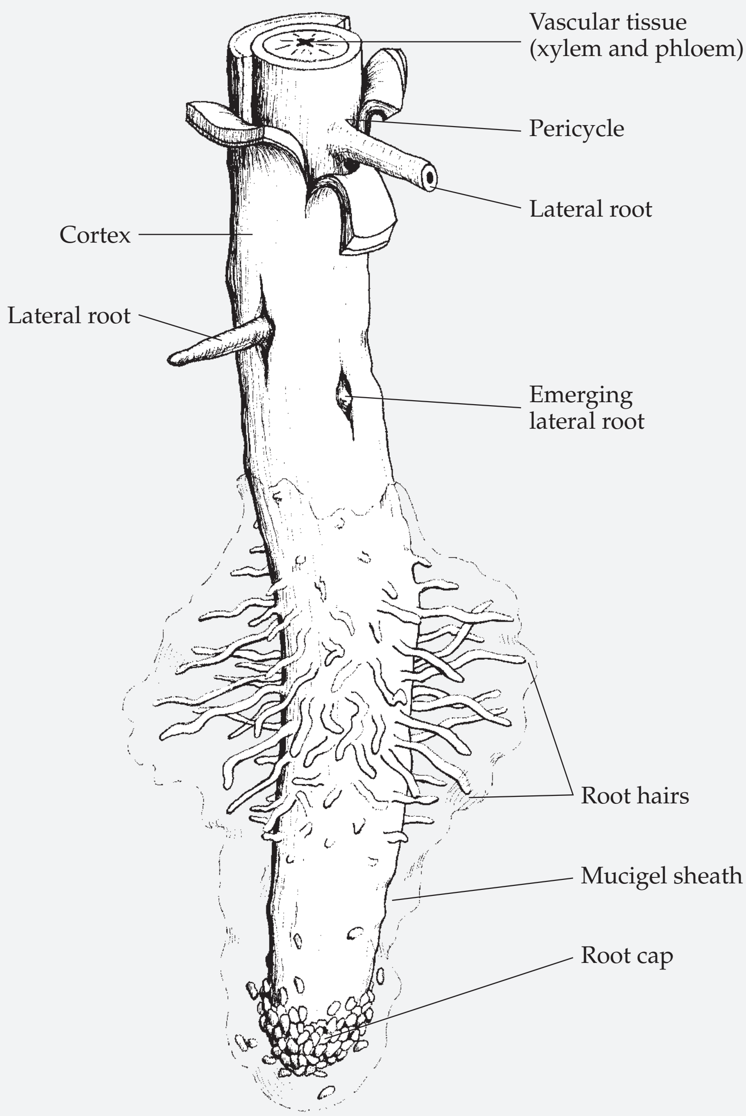
Roots are those underground portions of a plant that store food, absorb water and minerals from the soil, and anchor the plant in the earth.

Roots account for more than 80 percent of plants' biomass in ecosystems such as tundra and shortgrass prairies. In many plants, roots are longer and spread wider than the shoots. The extensive root systems of plants are effective collectors of water and minerals necessary for the life of the plant.

Root Cap and Quiescent Center

The root's structure facilitates each of its functions. Tips of roots are covered by a thimble-shaped *root cap*. At the base of the root cap is a *meristem* that produces cells that form the cap. The meristem pushes cells forward into the cap, which protects the tip of the growing root as it forces its way

Parts of a Root



Kimberly L. Dawson Kurnizki

through the soil. As these cells move through the cap, they differentiate into rows of *columella cells*. Columella cells contain *plastids* that sediment, in response to gravity, to the lower side of the cell. This sedimentation is how roots perceive gravity.

Surrounding the outside of the root cap are *peripheral cells*. Peripheral cells produce and secrete large amounts of a slimy, water-soluble substance called *mucigel*. Mucigel has several important functions. It protects roots from desiccation and contains compounds that diffuse into the soil and inhibit growth of other roots. Mucigel also lubricates roots as they force their way between soil particles. Soil particles cling to mucigel, thus increasing the root's contact with the soil, which helps roots absorb water.

Just behind the root cap is the *quiescent center*, which is made up of five hundred to one thousand seemingly inactive cells. Cells of the quiescent center divide only about once every twenty days, while those of the adjacent meristem divide as often as twice per day. Cells of the quiescent center become active when the tip of the root is damaged. When this occurs, the quiescent cells divide rapidly to form cells to repair the damaged root tip. The quiescent center also organizes the patterns of primary growth in roots.

Subapical Region

The *subapical region* of roots consists of three zones: the *zone of cellular division*, the *zone of cellular elongation*, and the *zone of cellular maturation*. These regions of the root intergrade and are not sharply defined. The zone of cellular division surrounds the quiescent center and is a dome-shaped meristem 0.5 to 1.5 millimeters behind the root tip. Thus, the meristem of a root is subterminal and is made of small, multisided cells. Meristematic cells divide between one and two times per day. In some plants, the meristem produces almost twenty thousand new cells per day. The rate of these divisions is influenced by hormones such as *ethylene*.

The zone of cellular elongation is 4 to 15 millimeters behind the root tip. Cells in this zone elongate rapidly by filling their vacuoles with water. As a result, the elongating zone is easily distinguished from the root cap and zone of cellular division by its long, vacuolate cells. Cellular elongation in the elongating zone pushes the root cap and apical meristem through the soil as fast as 2 to 4 centimeters per day. Cellular elongation is typically inhibited by the hormone *auxin* and stimulated by low concentrations of ethylene.

Cells behind the elongating zone do not elongate. Elongation begins the process of cellular differentiation, or specialization. Differentiation is completed in the zone of cellular maturation, which is 1 to 5 centimeters behind the root tip. The maturation zone is distinguished by the presence of numerous root hairs—as many as forty thousand per square centimeter. Root hairs increase the surface area of the root by a factor of several thousands and are usually less than 1 millimeter long. They live only a few days and form only in the mature, nonelongating region of the root. Because root hairs are fragile extensions of epidermal cells, they usually break off when plants are transplanted.

All mature tissues of roots form behind the zone of cellular maturation. The root is surrounded by an *epidermis*, which is usually only one cell thick. Epidermal cells usually lack a cuticle. The epidermis covers all of the root except the root cap and typically has no openings.

Cortex

Immediately inside the epidermis is the *cortex*. The cortex occupies most of a root's volume and consists of three concentric layers: the *hypodermis*, storage *parenchyma cells*, and the *endodermis*. The hypodermis is a waxy, protective layer that slows outward movement of water. Thus, the hypodermis helps roots retain water and nutrients that have been absorbed.

Most of the cortex consists of thin-walled parenchyma cells that store carbohydrates. These cells are separated by large intercellular spaces occupying as much as 30 percent of the root's volume. The innermost layer of the cortex is the endodermis. Unlike other cortical cells, endodermal cells are packed tightly together and lack intercellular spaces. Their radial and transverse walls, furthermore, are impregnated with a *Casparian strip* of lignin and suberin. If endodermal cells are compared to bricks in a brick wall, then the Casparian strip is analogous to the mortar surrounding each brick. The Casparian strip prevents inward movement of water and nutrients through the cell wall and intercellular spaces. The endodermis functions somewhat like a valve that regulates movement of nutrients.

Collectively, the tissues inside the cortex are called the *stele*, which consists of the *pericycle*, *vascular tissues*, and sometimes a *pith*. The *pericycle* is the outermost layer of the stele and is a meristematic layer of cells one to several cells thick; it produces secondary, or lateral, roots.

Inside the pericycle is the root's vascular tissue, which consists of *xylem* and *phloem*. Vascular tissues transport water, minerals, and sugars throughout the plant and differentiate in response to auxin, a plant hormone, coming from the shoot. Roots of most dicotyledons (dicots) and gymnosperms have a lobed, solid core of primary xylem in the center of the root. Roots of monocots and a few dicots have a ring of vascular tissue that surrounds a pith. Bundles of primary phloem differentiate between lobes of xylem. In dicots and gymnosperms, a *vascular cambium* later forms between the xylem and phloem and produces secondary growth that thickens the root.

Types of Root Systems

Different kinds of plants often have different kinds of root systems. Most gymnosperms and dicots have a *taproot system* consisting of a large primary root and smaller branch roots. In plants such as the carrot, fleshy taproots store large amounts of carbohydrates. Not all taproots store food. Long taproots of plants such as poison ivy and mesquite are modified for reaching water deep in the ground rather than storing food. Many plants have very long taproots. Engineers digging a mine in the southeastern United States uncovered the taproot of a mesquite tree more than 50 meters down.

Most monocots such as corn and other grasses have a *fibrous root system* that consists of an extensive mass of similarly sized roots. Most of these roots are *adventitious roots*, which form on organs other than roots themselves. Fibrous roots of some plants are edible—for example, sweet potatoes are fleshy parts of fibrous root systems of ipomoea (morning glory) plants. Plants with fibrous root systems reduce erosion because their root systems are extensive and cling tightly to soil particles.

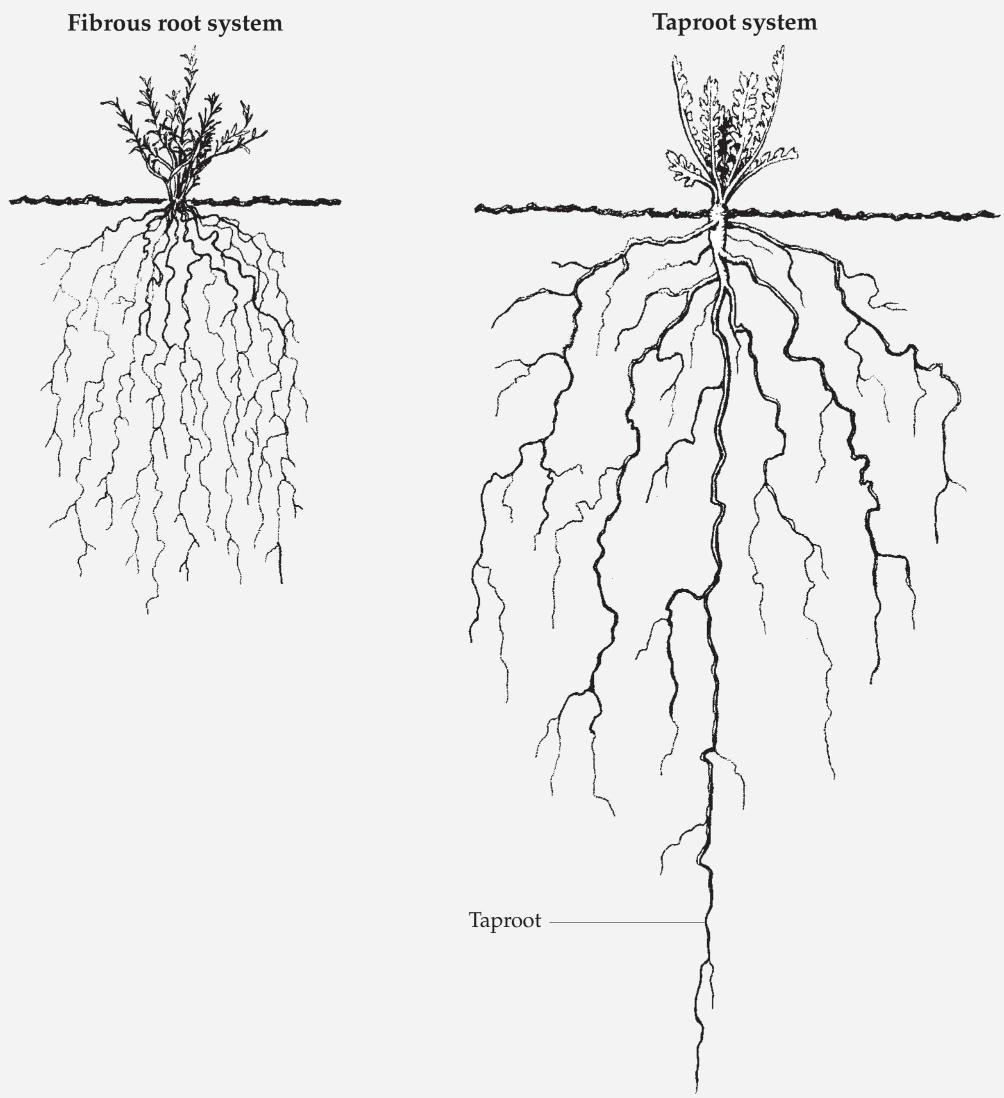
Adventitious roots are common in ferns, club mosses, and horsetails. In plants such as tree ferns, adventitious roots form in stems, grow down through the cortex, and finally emerge at the base of the stem. Adventitious roots are a primary means of *asexual reproduction* in many plants. For example, prairie grasses and forests of quaking aspen trees are often derived from a single individual propagated by adventitious roots. Humans use adventitious roots to propagate plants such as raspberries, apples, and brussels sprouts. Formation of adventitious roots is controlled by hormones such as auxin, which is often an ingredient in "rooting" compounds sold commercially.

Functions

The structure of a root relates directly to its four primary functions: *absorption*, *anchorage*, *conduction*, and *storage*. For example, most water and nutrients are absorbed by root hairs in the zone of maturation of the root. The water thereafter moves through the root either inside cells or in spaces between cells. Water seeping between cells finally encounters the endodermis, which is the primary barrier to absorption. The Casparian strip in the endodermis ensures that water and nutrients enter the stele via the plasmodesmata (narrow strands of cytoplasm that connect the cytoplasms of adjacent cells). Most nutrients are absorbed and accumulate in the apical 0.3 to 0.5 meter of the root.

Few nutrients are absorbed past a few centimeters beyond the root tip because these parts of the

Two Root Systems



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root lack root hairs and have a waxy endodermis. These nonabsorptive regions of roots anchor plants and may later produce branch roots. Water and dissolved nutrients absorbed by roots move to the shoot in xylem. Roots receive nutrients from the shoot via the phloem. These nutrients either are used for growth or are stored in cortical cells for future use.

Roots of many plants are modified for special functions. For example, roots of plants such as beets, radishes, dandelions, and cassava store large amounts of starch. Sweet potato roots store carbohydrates as sugars. Roots of other plants are used for asexual reproduction.

Roots of cherry, apple, and teak possess adventitious buds that form shoots called *suckers*. When separated from the parent plant, suckers become new individuals. Adventitious buds are a common means of propagating many other plants. For example, most groups of creosote bushes are clones derived from a single plant. Some of these clones are more than twelve thousand years old—meaning that the first seed germinated approximately four thousand years before humans began writing.

The roots of many plants minimize competition for water and nutrients by growing in different parts of the soil. For example, mesquite trees growing in deserts often have taproots more than 20 meters long that obtain water from the underground water table. Nearby cacti, however, survive in the same environment by producing a shallow root system that spreads as far as 30 meters. Cactus roots do not reach the water table; rather, they quickly absorb water after the infrequent and often heavy rains that occur in the desert.

Roots can protect the plant from other organisms. Most root defenses against soil pathogens are chemical rather than structural. Roots often secrete noxious chemicals that inhibit the growth of pathogens and other organisms, including other plants, in some cases.

Prop roots are aerial roots that grow into the soil. They are common in plants such as corn and banyan trees. Banyan trees produce thousands of prop roots that grow down from horizontally oriented stems and form pillarlike supports.

Environmental Influences

The growth and distribution of roots are controlled by several environmental factors. For example, the short days and cooler temperatures of winter typically cause roots to become inactive. Microbes living in the soil also affect how roots grow. Most microbes in soil live within 10 micrometers of the root and secrete compounds that significantly affect growth and distribution of roots. These compounds can affect the anatomy, morphology, number of root hairs, and branching patterns of root systems.

Microbes also affect how plants absorb and transport minerals from the soil. Plants growing in sterile soil absorb fewer minerals than those growing in soil containing microbes. Beneficial fungi called *mycorrhizae* live in and on roots of almost all plants in a form of mutualism, meaning that both the plant and the fungus benefit from the association. The mycorrhizae absorb nutrients from the environment, while the host plant provides the fungus with carbohydrates, amino acids, vitamins, and other organic substances. Plants with mycorrhizae tolerate drought and other types of stress better than uninfected plants.

Roots of legumes such as beans are often infected with *Rhizobium* (from *rhiza*, the Greek word for "root"), a genus of the nitrogen-fixing bacteria. Swellings in response to these infections are called *nodules*. Bacteria receive carbohydrates and other substances from the host, while the host plants receive large amounts of usable nitrogen from the bacteria.

Many organisms compete with roots to collect nutrients and water in the soil. For example, 1 gram of fertile soil contains approximately 10^9 bacteria, 10^6 actinomycetes (a group of fungilike bacteria), 10^5 fungi, and 10^3 algae. Plants have evolved several different strategies for competing with these organisms. One is to produce an extensive root system consisting of many roots that permeate the soil. Most roots grow in the upper 3 meters of soil, however, where nutrients are most abundant.

The narrow zone of soil surrounding a root and subject to its influence is called the *rhizosphere*. Roots modify the rhizosphere by secreting organic matter, compressing the soil, and absorbing nutrients. As a result of these effects, the rhizosphere is significantly different from bulk soil. It usually contains large amounts of energy-rich molecules. These molecules are eaten by fungi and bacteria.

Roots tend to grow best in moist, loosely packed soil. Roots of many plants grow two to four times faster in loose, sandy soil than in tightly packed clay. The slow growth of roots in poorly aerated soil is probably caused by the accumulation of ethylene, a plant hormone that slows root growth.

Roots of plants that grow in wet areas are usually small and modified for gas exchange. They possess small amounts of xylem, lack root hairs, and contain large intercellular spaces, thereby improving ventilation. Roots of aquatic plants are also modified for gas exchange. For example, the black mangrove produces specialized roots called *pneumatophores*, which grow up into the air, where they function like snorkels through which oxygen diffuses to submerged roots.

Epiphytes, including some bromeliads and orchids, are plants that grow on other plants but are not parasites. Adaptations among these "air plants" include a thickened root epidermis which protects the cortex and retards water loss. The "flower pot plant" (*Dischidia rafflesiana*) grows a "pot" that collects water and debris; the plant's aerial roots grow into the pot, where they can absorb the minerals collected there.

Roots of plants that grow in dry areas are often extensive and modified for rapid transport of water. They contain large amounts of xylem, which allows them to move water rapidly to the shoot after rainfall. Plants such as witchweed and broomrape use their roots to parasitize other plants. Witchweed is a red-flowered plant that infects grains such as corn and sorghum; it is the second leading cause of cereal famine in Africa.

Randy Moore, updated by Elizabeth Slocum

See also: Angiosperm cells and tissues; Bulbs and rhizomes; Gas exchange in plants; Germination and seedling development; Growth and growth control; Liquid transport systems; Nitrogen fixation; Plant tissues; Root uptake systems; Water and solute movement in plants.

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RUBBER

Category: Economic botany and plant uses

Rubber is a product of rubber tree bark or a macromolecule or polymer of repeated chains of carbon and hydrogen atoms. Rubber's properties of extensibility, stretchability, toughness, and resilience make it a useful commodity in applications ranging from tires to clothing.

The name "rubber" originates from the material's ability to erase pencil marks; its chemical designation is *polyisoprene* with several isomers. About 60 to 65 percent of the rubber produced today is synthetic. When explorer Christopher Columbus arrived in Haiti in 1492 he found Indians playing a game with a ball made from the *latex* of rubber. American Indians were also known to have used latex for making footwear, bottles, and cloaks. By 1735 latex had been described as *caoutchouc* by a French geographical expedition in South America.

The role that rubber could play in clothing and footwear attracted the attention of chemists and inventors throughout the world in the late eighteenth and mid-nineteenth centuries. Charles Macintosh and Thomas Hancock, working as colleagues, discovered two separate means of using rubber in fabrics and footwear. Macintosh found that placing rubber between layers of fabric resulted in a fabric with no sticky and brittle surfaces. Hancock developed the rubber masticator, which welded rubber scraps to be used for further manufacturing.

The dramatic increase in the use of rubber that occurred in the twentieth century is attributable largely to the development of the automobile industry and advances in industrial technology. Although rubber's percentage of use compared with other elastomers decreased from the end of World War II to the late 1970's, the development of radial automobile tires in Europe in the late 1940's and their popularization in the United States in the late 1960's resulted in increased use of natural rubber.

Origin of Rubber

The early use of rubber involved all-natural rubber formed from a number of different plant species belonging to the *Euphobiaceae* family, of which the rubber tree (*Hevea brasiliensis*), native to Brazil, has become the exclusive commercial source. As a coagulated milk substance, rubber is obtained from a fluid in latex vessels located in the bark of the tree. A number of other tropical and subtropical plant species also contain such latex vessels, including *Manihot*, *Castilla*, the Russian dandelion, guayule

Image Not Available

(*Parthenium argentatum*), and *Funtumia elastica*.

Both the Russian dandelion and guayule were widely used during World War II. Research has continued on guayule, a plant native to the southwestern United States and northern Mexico. Similarly, *Funtumia elastica*, native to West and Central Africa, has received some research attention. Guayule, used by American Indians, is still considered a possible alternative rubber source to synthetic rubber in North America, particularly the southwestern United States.

Today the production of natural rubber is based on *Hevea brasiliensis*, which is grown mostly in tropical and subtropical environments. While production is concentrated in developing countries, consumption occurs mostly in industrialized countries. Between 1955 and 1988 production of rubber more than doubled, with Malaysia the leading world producer and the United States the world's largest consumer.

Growing Rubber Plants

Trees for commercial rubber plantations are vegetatively propagated by means of bud grafting. The bud from a high-yielding tree is cut and inserted under the bark of a rootstock. Upon a successful take, the bud grows, and the rootstock is topped or removed at the point of growth. It is then transplanted from the nursery to the field. The tree is ready for tapping in five to seven years, when tree girth reaches 50 centimeters at 1.60 meters from ground level. Crown budding may also be done before budded stumps are transferred to the field. This type of budding is used to provide a crown that is tolerant of or resistant to disease or wind damage. Stand density in rubber plantations ranges from 250 trees to 400 trees per hectare at an average spacing of about 6 meters by 6 meters.

Rubber grows best in deep, well-drained soil but can be grown on a wide range of soils. Rainfall should exceed 2,000 millimeters yearly, evenly distributed without any marked dry season. Temperature should average 25 to 28 degrees Celsius, with high (80 percent) humidity and bright sunshine of about six hours per day year-round. These conditions exist in the major rubber-producing countries of the world.

In *Hevea*, latex is obtained from latex vessels called secondary *laticifers*. The quantity of laticiferous tissue in the tree is determined by a number of anatomical factors, such as vessel rings, size of laticifers, girth of trees, and the distribution of latex and latex vessel rows. The flow of latex and, subsequently, the yield of a rubber tree is dependent on these anatomical features.

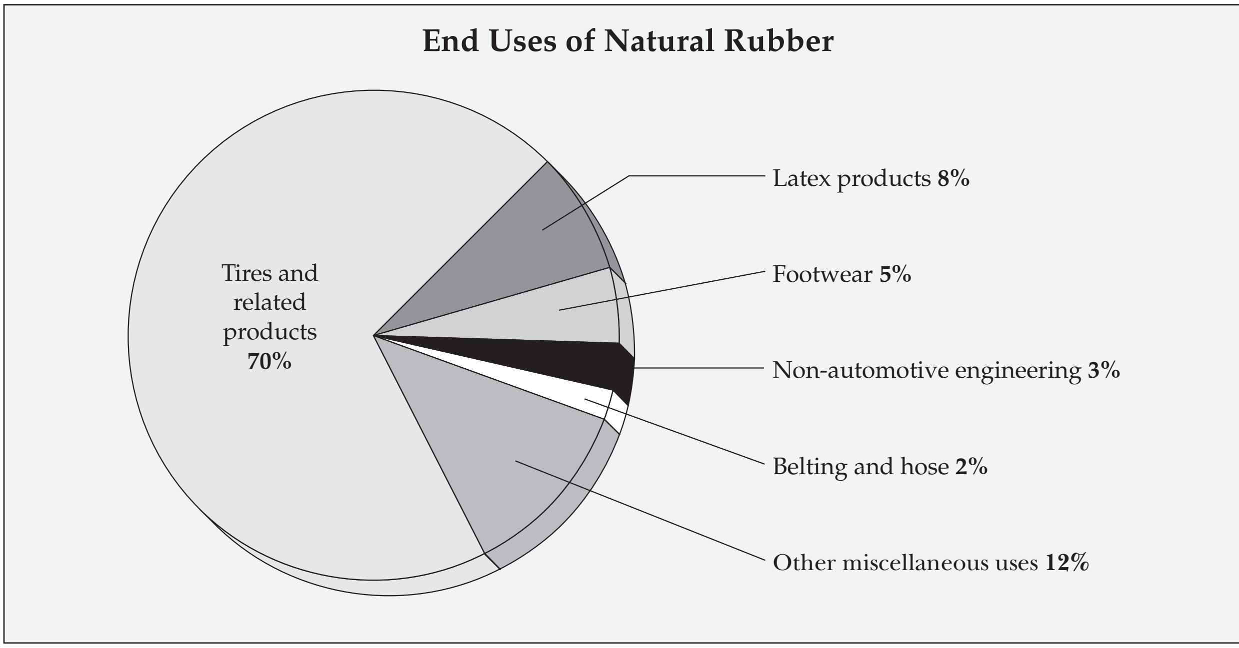
Latex Processing

Until about 1913 Brazil was the major producer of natural rubber, obtained mostly from wild rubber trees growing in the jungles of the Amazon basin. In the early twentieth century, plantation production of rubber began, based on the work of Henry N. Riley in Singapore around 1890. Riley developed the "tapping" method for extracting latex from *Hevea*. Later improvements to this method included the mechanization of the tapping knife.

During tapping, a slice of bark is systematically removed from one side (panel) of the tree, starting from an upper left corner and shaving to a lower right corner, with care being taken not to damage the cambium. The cut usually has an angle of 25 to 30 degrees. Once the cut is made, latex flows into a collecting cup through a spout inserted on the tree. Generally, tapping is done from just before sunrise to about 10:00 A.M., to take advantage of maximum turgor pressure within the tree in the early morning hours. Stoppage of latex flow is attributable to a coagulum that plugs latex vessels.

About four to five hours after tapping, the latex is collected from the trees. Field latex or cuplumps and "tree-lace" latex (strips or sheets of latex coagulated on a tapping cut) are collected and taken to a factory, laboratory, or small-holder processing center. At the processing center, latex is sieved to remove foreign objects, such as stones, branches, and leaves, and is then blended by the addition of water or dilute acetic or formic acid. About 10 percent of the latex is shipped as latex concentrate, following blending. Concentrates of natural rubber latex are obtained by the process of centrifugation and creaming. Meanwhile, the remainder of the latex and field coagulum are processed, either into conventional types of rubber or into technically specified rubber (TSR).

A number of fundamental weaknesses associated with manufactured rubber were resolved in 1839 with the development of vulcanization by Charles Goodyear, an American inventor. Vulcanization is the process of treating natural rubber with sulfur and lead and subjecting the compounds to intense heat, resulting in what Goodyear first called "fire proof gum" but later called vulcanized rubber.



Source: Adapted from R. E. Brice and K. P. Jones, in *Natural Rubber Science and Technology*, edited by A. D. Roberts, 1988.

Current vulcanization technology is a modification of Goodyear's invention. New forms of vulcanization are available based on diurethanes, which are stable at processing temperatures as high as 200 degrees Celsius or more. Vulcanized rubber can then be processed into a wide range of applications, including tires, fabrics, bridge constructions, and other latex products such as adhesives and footwear.

Future Uses of Natural Rubber

There is continuing interest and effort on the part of research scientists and natural rubber producers to find new uses for natural rubber. Thus, projections for new uses range from snowplow blades to earthquake-resistant building construction materials. Although many proposed uses are engineering applications, there are other applications in the area of wood products that may eventually make the large acreages of rubber plantations important sources for environmental restoration, given the increasing deforestation that is taking place in the natural rubber-producing areas of the world. In rubber plantations that are more than forty years old, the regeneration of secondary forests with associated wildlife species occurs frequently. Thus, natural rubber is both an important industrial crop species and a major renewable resource.

Synthetic Rubber

Much of what people typically consider rubber today is actually synthetic rubber. Synthetic rubber is a polymer of several hydrocarbons; its basis is monomers such as butadiene, isoprene, and styrene. Almost all monomers for synthetic rubber are derived from petroleum and petrochemicals. The emulsion polymerization process occurs at very high temperatures. There are different types of synthetic rubbers, three of which are dominant in the rubber industry. These are styrene-butadiene rubber (SBR), polyisoprene rubber (IR), and polybutadiene rubber (BR). Unlike natural rubber, synthetic rubber is produced mainly in industrialized countries. The United States is the world's leading producer.

Theoretically, synthetic rubber production dates back to 1826, when scientist Michael Faraday indicated that the empirical formula for synthetic rubber was $(C_5H_8)_x$. The technology for synthetic rubber production was not developed until 1860, however, when Charles Williams found that natural rubber was made of isoprene monomers. Great interest in using synthetic rubber as a substitute for natural rubber began during World War II, when the Germans were looking for alternatives to natural rubber. The severe shortages of natural rubber during and immediately after the war stimulated significant research in synthetic rubber and its technology. Today, synthetic rubber is used in a wide range of applications, and it constitutes 60 to 65 percent of the total rubber produced and consumed.

Oghenekome U. Onokpise

See also: Asian agriculture; Asian flora; Central American flora; Forest management; Metabolites: primary vs. secondary; Plants with potential; South American flora; Vacuoles.

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RUSTS

Categories: Diseases and conditions; fungi; pests and pest control; poisonous, toxic, and invasive plants; taxonomic groups

Rust fungi belong to the taxonomic class Teliomycetes *within the basidiosporic phylum and include some seven thousand known species, all plant parasites, with many being extremely important plant pathogens.*

Rust diseases have caused serious problems for centuries and continue to cost billions of dollars annually worldwide. Important examples include: leaf, stem, and crown rusts of wheat, barley, and oats; the blister, fusiform, and gall rusts of pines; coffee rust; many field crop rusts, such as soybean, peanut, sunflower, and flax rusts; and rusts of many horticultural crops and ornamental plants, such as cedar-apple rust, bean rust, and rose rust.

Symptoms and Signs

Symptoms, the visible effects on a host caused by rust diseases, are often less noticeable than are the signs of infection, that is, the visible presence of a pathogen, such as reproductive spores. Symptoms such as bushy overgrowths, *witches' brooms* (dense clusters of shoots), and large galls are more common in some tree hosts than in herbaceous hosts. In most herbaceous rusts and the foliar rusts of some trees, such as coffee and poplar, little, if any, distortion of the host occurs. Most noticeable are the rust's reproductive spores borne in various types of pustules (or sori) that rupture leaf and stem epidermis. Loss of water vapor through ruptured epidermis can cause wilt symptoms during hot, dry periods. Several kinds of spores and pustules may develop during different stages of the rust's life cycle. Combined results of parasitism, water loss, cell death, and other effects on the host can result in significant reductions in yield.

Life Cycle and Related Spore Stages

Rust fungi have a complex life cycle that may contain up to five different spore types, or stages, each performing specific functions in the cycle. Some rust species lack one or more spore stage or stages. *Autoecious* forms of rusts, such as bean rust, complete their life cycle on one host species. *Heteroecious* rusts require two unrelated hosts on which to complete their life cycle. *Puccinia graminis*, the wheat stem rust pathogen, which produces all five spore stages on two unrelated hosts, is a good example of a rust with the heteroecious life cycle.

Distribution and Dissemination

Initial distribution of rusts between continents, especially if separated by oceans, is often the result of human activity, such as the inadvertent introduction of the pathogen on seeds, cuttings, or other plant parts. Once established in a region, rusts are most often spread locally and long distance by wind-blown urediniospores. In North America, south-to-north dispersal of urediniospores of wheat stem and leaf rust fungi occurs annually from Mexico and south Texas through the Great Plains into Canada. Coffee rust, long absent in the Western Hemisphere, rapidly spread across South and Central America by wind dispersal following its 1970 introduction into Brazil.

Obligate Parasitism

Although a few rusts can be grown on chemically defined, nonliving nutrients, most rusts require a living host on which to grow and reproduce. Consequently, rusts are termed *obligate parasites* or *biotrophs*, in contrast to the majority of plant pathogens, which are *facultative parasites* or *heterotrophs*. Those can grow and reproduce on many nutritional media in culture, in dead plant tissue, or as parasites of living plants. Within infected host tissue, rust fungi grow primarily as filamentous hyphae in intercellular spaces between host cells. Rusts obtain nutrition through specialized branches, haustoria, that extend into and absorb nutrients from living host cells. Those absorbed nutrients are then transported through intercellular hyphae to expanding or spore-producing portions of the rust colony.

Image Not Available

Disease Control

Typically, total control of rust diseases is impossible, both biologically and economically; hence, the usual goal is management of rust diseases, not control. Several different management methods are commonly pursued, depending on the host, the type of rust involved, its major means of dissemination, and economics or aesthetic value of the host plant or crop. The ideal and most cost-effective management tool is host resistance, either naturally present in the host population or resulting from plant breeding.

Wheat Stem Rust: Five Stages

Stage	*Spore-Bearing Structure*	*Spores*	*Spores' Nuclear Condition*
0	Pycnia, bearing[1]	Pycniosporesand receptive hyphae	Haploid (*n*)
I	Aecia, bearing[1]	Aeciospores	Dikaryotic (*n* + *n*)
II	Uredinia, bearing[2]	Urediniospores	Dikaryotic (*n* + *n*)
III	Telia, bearing[2]	Teliospores	Dikaryotic, later diploid (2*n*)
IV	Basidia, bearing	Basidiospores[3]	Haploid (*n*)

1. Produced on the barberry host.
2. Produced on the wheat or barley host.
3. Produced upon germination of teliospores, on crop debris or on soil.

Breeding for rust resistance has been especially important in rusts of cereals and other major agronomic plants. Unfortunately, many resistant varieties, or cultivars, may eventually succumb to new, more virulent or aggressive strains or races of the pathogen that arise by natural selection from populations of the pathogen in nature. Foliar fungicide sprays can be cost-effective management tools for rusts of some cereal crops, beans, coffee, and roses. In some instances, removing or eradicating the alternate host, such as common barberry, in heteroecious rusts has controlled such diseases but has usually proven ineffective economically.

Larry J. Littlefield

See also: Basidiosporic fungi; Diseases and disorders; Fungi; Parasitic plants; Resistance to plant diseases.

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SAVANNAS AND DECIDUOUS TROPICAL FORESTS

Categories: Biomes; ecosystems; forests and forestry

Savannas are areas of continuous grass or sedge cover beneath trees that range from scattered, twisted, and gnarled individuals to open woodlands. Deciduous tropical forests have continuous to open forest cover and undergo a leafless period during a seasonally lengthy dry season.

Where the annual rainfall in tropical regions is less than 2,000 millimeters and three to six months out of the year are dry, savannas and deciduous forests are common. Both savannas and deciduous tropic forests often occur where the annual rainfall is less than that of savannas. Together, the two biomes are referred to here as the *dry tropical biome*.

A pronounced pattern of seasonally wet and dry periods is the most important factor affecting the distribution of these types of plant cover. Higher soil fertility favors forest over grasses and savanna such as in the cerrado of Brazil, which occurs only on certain geological formations and low-nutrient soils. Fire has been a dominant feature of these biomes, and human influences—fires, agriculture, and grazing of animals—have interacted with climate to produce a varied landscape.

The dry tropical biome is most geographically widespread on the continents of Africa, South America, and Australia, with smaller enclaves in Asia. The world's largest expanses of dry forest—the Brachystegia woodland across Central Africa, the *cerrado* (savanna) and *caatinga* (dry forest) of the Amazon basin, and much of interior Australia—are notable examples. "Elephant grass savanna," with tall grasses up to 4 meters tall and scattered trees, occurs exclusively in Africa. In the West Indies, dry forest occurs in rain-shadow zones on the leeward sides of islands affected by the tradewinds.

Plant Adaptations and Diversity of Life-Forms

As the rainfall decreases below 2,000 millimeters, and especially below 1,000 millimeters, the height of the forest decreases and the proportion of trees that are deciduous increases. In the dry tropics, leaf fall occurs in response to drought, and therefore the lengthy dry season becomes a selective pressure to which plants have adapted. Tree leaves tend to be compound, with small leaflets that help plants exchange heat with their surroundings better than large, simple leaves; rates of leaf respiration and transpiration are thereby reduced. Sclerophyllous leaves are common, aiding in moisture retention, and the drier, more open woodlands may have cacti or other succulents.

The dry forest is far less species-rich than the rain forest, but the diversity of life-forms and the proportion of endemics are greater. For example, dry forests may contain xerophytic (dry-adapted) evergreens, either obligatively or facultatively deciduous trees, trees with photosynthetic bark, plants that use the crassulacean acid metabolism (CAM) photosynthesis as well as C_3 and C_4 dicots, grasses, bromeliads, lianas, epiphytes, and hemiparasites. Trees from *Fabaceae* (the legume family) are the most well-represented family among trees.

Dry forests contain a higher proportion of wind-dispersed species than wetter forests, and many trees will have their flowering and fruiting controlled by the duration and intensity of the dry season. Synchronous flowering within and among species is common, and many produce seed during the dry season. Flowers are often conspicuous and visited by specialized pollinators such as hawkmoths, bats, and bees.

It is incorrect to generalize about savannas and dry tropical forests because, although they both occur in the drier tropics, the two vegetation types occur in different habitats and are adapted differently to their respective environments.

Trees of the cerrado in northeast Brazil are deeply rooted, tap groundwater, and have high rates of transpiration. Drought here is atmospheric, as water is always available below 2 meters of soil depth. The deciduous caatinga of central Brazil, however, receives only 500 millimeters of rain yearly, and transpiration of trees is low. Here, trees suffer significant water deficits during the long, dry season, are truly xerophytic, and exhibit classic adaptations to drought.

Trees of the cerrado have a number of adaptations that confer resistance to fire. These include a thick, corky bark, the ability to form adventitious roots from buds on roots following the burning of the stem, and the cryptophyte or hemicryptophyte life-form (cryptophytes produce buds underground). Many herbaceous species are induced to flower by fire.

Human Impacts and Conservation

Fires have occurred in the Brazilian cerrado for thousands of years based on carbon 14 dating of charcoal fragments. Fire is thus an environmental factor to which the vegetation has become adapted. Yet, the human influence has been to increase the incidence of fire. The cerrado has changed as a result to a more open form of plant cover with fewer trees and shrubs. In addition, timber extraction, charcoal production, and ranching have altered the savanna landscape. The ability of belowground organs to survive such types of disturbance has increased the ability of the cerrado to persist. Yet it is estimated that 50 percent of the cerrado has been destroyed, much of this the result of clearing for agriculture since the 1960's.

Because of better soils and fewer pests, humans in tropical areas of Central America have mostly chosen the dry and moist life zones as places to live rather than the wetter rain-forest zones. As a result, dry forest ecosystems have been subject to massive disturbance. Today, only a small fraction of the original dry forest remains. Fire has been used as a means of clearing the forest for farming, but, unlike the savanna, the dry forest is not adapted to fire. At Guanacaste, Costa Rica, a well-known tropical conservation project, restoration of dry forest, is dependent on controlling annual fires set by farmers and

Corbis

Savannas are landscapes of dense grass and scattered trees, such as these yellow fever trees growing in Nakura National Park in Kenya. Common on the continent of Africa, savannas are also found in India, Australia, and the northern part of South America.

ranchers and supporting the return of forest vegetation to dry areas. In Africa, large areas of dry forest are burned annually by farmers, and areas of dense, dry forest have been converted to more open forest or even savanna. Sustainable land-use systems are urgently needed for dry tropical regions.

Allan P. Drew

See also: African flora; Australian flora; Biomes: types; Biomes: definitions and determinants; Biomes: types; Central American flora; Community-ecosystem interactions; Drought; Slash-and-burn agriculture; South American flora; Sustainable agriculture.

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SEEDLESS VASCULAR PLANTS

Categories: Evolution; paleobotany; *Plantae*; seedless vascular plants; taxonomic groups

Seedless vascular plants possess vascular tissues (xylem and phloem) for transport of materials through the body but do not produce seeds bearing dormant embryos as part of the reproductive process. They are among the oldest of land plants.

Modern seedless vascular plants include species from several different phyla, including the club mosses, spike mosses, and quillworts of the phylum *Lycophyta*, the horsetails of the phylum *Sphenophyta*, the whiskferns of the phylum *Psilotophyta*, and the great diversity of ferns in the phylum *Pterophyta*. Lycophytes, sphenophytes, and psilotophytes are generally referred to as *fern allies*. Carolus Linnaeus used the word *Cryptogamia* (from the Greek *kryptos*, meaning "hidden," and *gamos*, meaning "marriage," or reproduction) as an inclusive taxonomic category for a wide range of organisms such as bryophytes, ferns, fern allies, algae, and fungi whose sexual reproductive parts were concealed from observation. The term *cryptogam* in modern usage refers to plants that do not produce seeds.

Origin and Relationships

Theories on the origin of vascular plants suggest that they probably arose from an ancestor in the group of nonvascular plants known as the bryophytes. Fossil spores from the Ordovician period (about 500 million years ago) are linked to the earliest land plants, which were likely an early liverwort (phylum *Hepatophyta*) or hornwort (phylum *Anthocerophyta*). The most derived bryophytes, the mosses (phylum *Bryophyta*), share an ancestor with the line that gave rise to vascular plants. A line that gave rise to the phylum *Lycophyta* appears to have diverged early in vascular plant development, soon after the advent of phloem and the rise of the dominance of the branching sporophyte generation. The remaining line diverged into a branch that gave rise to modern sphenophytes (horsetails) and ptero-

Seedless Vascular Plants: Phyla and Characteristics

Phylum	*Status*	*Anatomical Characteristics*	*Reproduction Exhibits*
Lycophyta	Living	Stems, roots, leaves, some branching	Homospory, heterospory
Psilotophyta	Living	Stems, no leaves or roots, branching	Homospory
Pterophyta	Living	Stems, roots, leaves, no branching	Homospory, minimal heterospory
Rhyniophyta	Extinct	Stems, no leaves or roots, often branching	Homospory
Sphenophyta	Living	Stems, roots, leaves, no branching	Homospory, some (extinct) heterospory
Trimerophytophyta	Extinct	Stems, no leaves or roots, branching rare	Homospory
Zosterophyllophyta	Extinct	Stems, no leaves or roots, often branching	Homospory, some heterospory

Source: Some data adapted from Peter H. Raven et al., *Biology of Plants*, 6th ed. (New York: W. H. Freeman/Worth, 1999).

phytes (ferns) and a branch that gave rise to modern seed plants.

Seedless vascular plants are well represented in the fossil record. *Cooksonia*, a representative of the extinct phylum *Rhyniophyta*, is thought to be one of the earliest vascular plants, dating to the mid-Silurian period (around 430 million years ago). Numerous other examples dating to the Devonian period (around 400 million years ago) are well documented.

Life Cycle and Gametophyte Anatomy

Seedless vascular plants express the typical life cycle pattern called *alternation of generations* found in many algae and members of the kingdom *Plantae*. As in all vascular plants, the diploid sporophyte generation, which produces haploid spores for the asexual reproductive phase, is dominant. Haploid spores are produced by meiosis in special structures called sporangia (singular, sporangium). In psilotophytes, some lycophytes, the sphenophytes, and the pterophytes, only one kind of spore is produced in a phenomenon called *homospory*. Sexually reproducing haploid gametophytes that have both male and female sex organs arise from these spores. In some lycophytes, two kinds of spores are produced in a phenomenon called *heterospory*. Large spores called megaspores are produced in megasporangia. Megaspores develop into female gametophytes. Small spores called microspores are produced in microsporangia. Microspores develop into male gametophytes.

The haploid gametophytes of seedless vascular plants, which produce gametes (sex cells) for the sexual reproductive phase, are independent and smaller than the sporophytes. Gametophytes range in size from a few millimeters to a few centimeters in length or diameter, while sporophytes can range in size from a few millimeters to several meters in height. Since there is a distinct difference between the appearance of the sporophyte and the gametophyte, these organisms are said to express *heteromorphy*. In psilotophytes and some lycophytes, gametophytes are nonphotosynthetic and underground, while in most of the other groups gametophytes grow on the soil surface and are photosynthetic. Underground gametophytes must rely on mutualistic fungi in mycorrhizal relationships to supply them with energy and carbon sources for growth and development.

Gametes are produced by mitotic cell division. Male gametes are produced in organs called *antheridia* (singular, *antheridium*). Sperm cells are multiflagellated and require liquid water for transmission to the female organs of a nearby plant. Eggs are produced in organs called *archegonia* (singular, *archegonium*). Sperm cells swim through the neck of the archegonium and into a swollen region at the base called the venter, which contains the egg. Fertilization results in the production of a diploid zygote, which develops into an embryo that then grows into a sporophyte.

Sporophyte Anatomy

According to the fossil record, the earliest vascular plants were quite similar in structure to the modern genus *Psilotum*, of the phylum *Psilotophyta*: the whiskferns. The *Psilotum* sporophyte lacks true leaves and roots (that is, the organs lack vascular tissue). Small, nonvascularized flaps of tissue called prophylls are found on the stem of *Psilotum*, which some theorize either are reduced leaves or may be suggestive of the evolutionary origin of leaves—that is, that true leaves are the result of the evolutionary vascularization of prophylls. The other living psilotophyte genus, *Tmesipteris*, possesses true leaves, each with a single vein, referred to as microphylls. Other groups produce either the one-veined microphylls or megaphylls that have numerous, often branched veins. The most dramatic leaf expression in seedless vascular plants is found in the delicate, pinnately compound, megaphyllous fronds of many of the ferns in phylum *Pterophyta*. In lycophytes, sporangia are produced on specialized leaves called sporophylls. Some interpret the spore-bearing sporangiophores that make up the cones of sphenophytes to be specialized leaves, as well.

The aerial stem of *Psilotum* exhibits a primitive pattern of isotomous dichotomous branching, with two equal branches arising from one branch point, or node. Other seedless vascular plants may show different patterns: For example, lycophytes often show an unequal dichotomous branching pattern, or anisotomy.

In most cryptogams, aerial stems arise from underground stems called rhizomes. Rhizomes of psilotophytes have many rhizoids, rootlike epidermal extensions, to aid in absorption of water and mineral nutrients. The sporophytes of all other groups of seedless vascular plants possess vascularized roots for absorption and anchorage.

The vascular tissues of all members of this broad group include the primitive type of xylem called tracheids and the primitive type of phloem called sieve cells. The vascular cylinder, or stele, of *Psilotum* is composed of a solid core of xylem surrounded by a layer of phloem. This arrangement is called a *protostele*. Variations on the protostele pattern are common in the roots, rhizomes, and shoots of members of the *Lycophyta*. Protosteles are the most common stele types found in vascular plant roots, in general.

The shoot steles of sphenophytes and pterophytes are composed of a ring of xylem surrounding a pith made of parenchyma tissue. A ring of phloem surrounds the xylem ring. This arrangement is called a *siphonostele*. Variations on the siphonostele pattern are common in the shoots of all vascular plants from the sphenophytes through the seed plants.

The endodermis is a layer of cells that surrounds the vascular cylinder of roots and rhizomes and some shoots in certain psilotophytes; it is is usually localized in the roots and rhizomes of lycophytes, sphenophytes, and pterophytes. The waterproofing suberin deposited in the Casparian strip of the endodermis regulates water flow to the vascular tissue.

Lycophyta

Fossil evidence suggests that the phylum *Lycophyta*, the lycophytes, arose during the Devonian period. There are between ten and fifteen genera, consisting of about one thousand species, divided among three broad groups: the club mosses of the order *Lycopodiales*, the spike mosses of the order *Selaginellales*, and the quillworts of the order *Isoetales*. All possess microphylls; however, the homosporous club mosses differ significantly from the heterosporous spike mosses and quillworts. Some extinct lycophytes were woody and grew to tree size. Lycophytes were among the dominant species during the Carboniferous period (around 350 million years ago), during which the plants that eventually became coal deposits were produced.

Sphenophyta

Phylum *Sphenophyta* arose during the Devonian period and reached its peak during the late Devonian and Carboniferous periods. Among the largest sphenophytes were members of the genus *Calamites*, treelike plants that exceeded 18 meters (60 feet) in height and nearly 0.5 meter (18 inches) in basal stem diameter. There are fifteen living herbaceous species in the only remaining genus, *Equisetum*, the horsetails.

Psilotophyta

The fossil record is incomplete regarding the ancestry of modern psilotophytes, so it is difficult to assign a date of origin. Although once considered to possess characteristics that allied them to the most primitive vascular plants, molecular studies have suggested that psilotophytes are possibly closely related to pterophytes (ferns), perhaps representing a reduction from an early fern ancestor. The phylum includes only two living genera, consisting of a total of six to eight species.

Pterophyta

Pterophytes, or ferns, arose during the Devonian period and reached the height of abundance and diversity during the Carboniferous. Today, there are about eleven thousand species of ferns ranging in size from a few millimeters across (such as *Azolla*) to several meters in height (such as *Dicksonia*). Excluding flowering plants, ferns are the most abundant and diverse plants on earth, exhibiting a variety of growth habits, from floating aquatics to tropical epiphytes to temperate terrestrial plants. They are important both ecologically and economically, serving as habitat and food sources for many organisms. Humans use ferns as food, fuel, and decoration.

Darrell L. Ray

See also: Bryophytes; Evolution of plants; Ferns; Hornworts; Horsetails; Liverworts; Lycophytes; Mosses; Mycorrhizae; Plant tissues; Psilotophytes; Reproduction in plants; *Rhyniophyta*; *Tracheobionta*; *Trimerophytophyta*.

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SEEDS

Categories: Anatomy; reproduction and life cycles

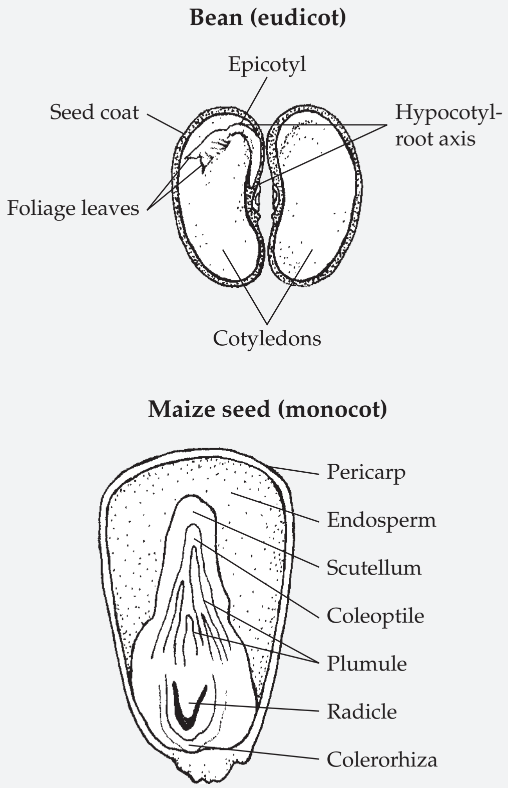
A seed is a mature, fertilized plant ovum containing an embryo, a food supply, and a protective covering called the testa, or seed coat.

A mature seed typically consists of a mature plant *ovum* containing a minute, partially developed young plant, the *embryo*, surrounded by an abundant supply of food and enclosed by a protective *seed coat*. Seed plants are divided into two main groups: the *gymnosperms*, primarily cone-bearing plants such as pine, spruce, and fir trees, and the *angiosperms*, the flowering plants. The gymnosperms have naked *ovules* which, at the time of *pollination*, are exposed directly to the pollen grains. Their food supply in the seed is composed of a female gametophyte, rather than the endosperm found in angiosperms.

In angiosperms, seeds develop from ovules that are enclosed in a protective *ovary*. The ovary is the basal portion of the *carpel*, typically a vase-shaped structure located at the center of a flower. The top of the carpel, the *stigma*, is sticky, and when a pollen grain lands upon it, the grain is firmly held. The germinating pollen grain produces a *pollen tube* that grows down through the stigma and *style* into the ovary and pierces the ovule.

Two male sperm nuclei are released from the pollen grain and travel down the pollen tube into the ovule. One of the sperm nuclei fuses with an egg cell inside the ovule. This fertilized egg divides many times and develops into the embryo. The second male nucleus unites with other parts of the ovule and develops into the *endosperm*, a starchy or fatty tissue that is used by the embryo as a source of

Seeds: Eudicots vs. Monocots



Kimberly L. Dawson Kurnizki

In angiosperm seeds, the embryo may have either one or two cotyledons. Angiosperms with one cotyledon are plants called monocots; those with two cotyledons are called eudicots (formerly dicots). A typical example of a eudicot is the bean (Phaseolus vulgaris), *whereas a typical monocot is corn, or maize* (Zea mays).

food during germination. Angiosperm seeds remain protected at maturity. While the seed develops, the enclosing ovary also develops into a hard shell, called a seed coat or *testa*, often enclosed in a fibrous or fleshy fruit.

Structure

Although the characteristics of different plant seeds vary greatly, some structural features are common to all seeds. Each seed contains an embryo with one, two, or several *cotyledons*. In angiosperm seeds, the embryo may have either one or two cotyledons. Angiosperms with one cotyledon are plants are called *monocots*; those with two cotyledons are called *eudicots* (formerly *dicots*). A typical example of a monocot is corn, or maize (*Zea mays*), whereas the bean (*Phaseolus vulgaris*) is a typical eudicot. In gymnosperms, the embryo may have between two and sixteen cotyledons; for example, the embryo of Scots pine (*Pinus sylvestris*) possesses eight cotyledons.

Immediately below the cotyledons is the *hypocotyl*, at the tip of which lies the growing point of the root. Above the cotyledons lies the *epicotyl*, which consists of a miniature shoot tip and leaves. Upon germination of the seed, the epicotyl develops into the stem and leaves of the new young plant. Almost all seeds carry with them a supply of food, which in angiosperms is the endosperm. Although the embryo is usually surrounded by the endosperm, in some seeds (such as maize) embryos and endosperm lie side by side. In the seeds of the pea family (*Leguminosae*), the food reserves of the endosperm are absorbed by the embryo, resulting in enlarged cotyledons. Gymnosperm seeds differ from those of angiosperms in the origin of their stored food. In gymnosperms the stored food is provided by a female gametophyte housed with the embryo inside the seed, whereas in angiosperms the food reserve is the endosperm.

All seeds are surrounded by a seed coat, the testa. Variability in the appearance of the testa is considerable, and these variations are used by taxonomists as an aid in distinguishing among different genera and species. The testa is of great importance to the seed; it is often the only barrier protecting the embryo from the external environment. The seed coats of some plants swell and produce a jellylike layer in response to contact with water. The gel retains water needed by the seed for germination. Cotton fibers are formed as extensions from some of the outermost cells of the seed coat in cotton plants (*Gossypium*). The seed coats of nutmeg contain aromatic substances.

Size and Chemistry

The range of seed size is extreme—more than nine orders of magnitude. The largest known seed is that of the double coconut (*Lodoicea maldivica*); the seed and fruit together weigh as much as 27 kilograms. At the other end of the scale, the dustlike seeds of some orchids, begonias, and rushes weigh only about 5 milligrams per seed. It is thought that the size of seed displayed by each species represents a compromise between the requirements for dispersal (which would favor smaller seeds that can be borne on wind or picked up by animals) and the requirements for establishment of the seedling (which would favor larger seeds that can adhere to a growth medium).

The chemical composition of seeds varies widely among species. In addition to the normal compounds found in all plant tissues, seeds contain unique food reserves that are used to support early seedling growth. About 90 percent of plant species use *lipids* (fats and oils) as their main seed reserves. The cotyledons of soybeans and peanuts are rich in oil, whereas in other legumes such as peas and beans, *starch* is the reserve material. Sixty-four percent of the weight of a castor bean is derived from the oil stored in the endosperm. In seeds of cereal crops, the endosperm stores much starch; in corn it can be up to 80 percent of the weight of the seed. All seeds, particularly legumes, also store protein as a reserve substance.

Dispersal

A seed can be regarded as a vessel in which lies a partially developed young plant in a condition of arrested growth, waiting for the correct conditions for growth to resume. Successful reproduction depends on seed dispersal to places appropriate for germination to occur. During the evolutionary history of plants, seeds and fruits have developed a great variety of specialized structures that enhance seed dispersal.

Wind is one major means of seed distribution. Very small seeds, such as the dustlike seeds of orchids, heathers, and some rushes and grasses, are dispersed by wind. Such seeds have been recovered from the atmosphere by airplanes at elevations up to 1,000 meters. Heavier seeds have evolved a variety of structures to ensure wind dispersal. For example, some members of the daisy family, such as dandelions, bear numerous one-seeded fruits to which are attached a feathery, tuftlike structure that acts as a parachute. Similar structures aid in the dispersal of the seeds of many other plants, such as cattails and milkweeds. Heavier seeds, such as those of ash, maple, and pine trees, have developed large, flat wings that allow the seeds to fly in a propeller-like manner for a considerable distance from the parent plant.

Often adaptations for wind dispersal of seeds can be seen not only in the seed's structure but also in structures of the parent plant. Many plants offer their seeds to the wind by bearing them on long flower stalks that tower above the surrounding vegetation. Tumbleweed bushes are small and almost spherical. When mature, they develop a weakness of the main stem at soil level. Wind can break the stem of the bush from which, as it rolls over the ground, the seeds are shaken loose and are scattered.

The seeds or fruits of many plants are dispersed by sticking to the outsides of birds or land animals.

Digital Stock

The size of seed displayed by each species is thought to represent a compromise between the requirements for dispersal (which would favor smaller seeds that can be borne on wind, as are these dandelion seeds, or picked up by animals) and the requirements for establishment of the seedling (which would favor larger seeds that can adhere to a growth medium).

Seeds are transported in mud that sticks to the feet of animals. The large number of species whose seeds show no obvious special dispersal adaptation are probably spread in this manner. Many seeds, however, can attach themselves to a passerby by means of adhesive substances, hooks (such as the fruit of bedstraw), or burrs (such as the seeds of the burdock plant).

Some plant species have seeds that are adapted for dispersal by animals and birds that transport them internally. The attractive and tasty fleshy fruits and berries of plants can be considered an adaptation to aid in seed dispersal. The seeds of most fruits eaten by animals and birds have a digestion-resistant coat. The animal deposits excrement containing seeds at a location at some distance from the parent plant, where the seeds grow into new plants. In some species, germination will not even occur unless the seed has passed through an animal's digestive tract. The presence of seeds in bird droppings is responsible for the appearance of some plants on remote, barren, volcanic islands. Various animal behaviors, including the collecting behavior of ants and the seed-burying activities of mice, squirrels, and jays, also aid in seed dispersal.

Several plants have evolved mechanisms that expel seeds explosively away from the parent plant. The pods of *Impatiens*, for example, develop strongly unbalanced tension forces as they ripen. When the pod is fully mature, the tension is so intense that the slightest disturbance causes the pod to split open, violently expelling the seeds.

Dormancy

Seeds are adapted for conditions other than geographic dispersal. When a seed arrives at its destination after dispersal, conditions may not be suitable for establishment of the plant. The delaying mechanism which prevents germination under adverse conditions is called *dormancy*. Seeds can remain in a condition of dormancy for varying lengths of time, depending on the species, until the correct balance of oxygen, moisture, and temperature triggers germination.

Viability varies greatly from species to species and may last only a few weeks or many years. Seeds of the cocoa plant are viable for only ten weeks. Some seeds, however, remain viable for decades or even hundreds of years. Seeds of the Indian lotus have been shown to remain viable for almost one thousand years. No claims for long-term viability have surpassed those made for the Arctic lupine, however: Seeds of this species have been successfully germinated after having been buried in the Arctic tundra for ten thousand years.

Iain Miller and Randy Moore

See also: Angiosperm life cycle; Dormancy; Flower structure; Fruit: structure and types; Germination and seedling development; Gymnosperms; Plant life spans; Pollination; Reproduction in plants.

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SELECTION

Categories: Evolution; genetics

Selection refers to any process by which some individuals are allowed to reproduce at the expense of others, leading to a shift in the composition of a population over generational time.

In the context of animal and plant breeding by humans, the process of selection is referred to as *artificial selection*. In the wild, it is referred to as *natural selection* and is viewed by scientists as the principal means by which *adaptations* (traits that promote the survival and reproduction of organisms) arise and new species evolve over geological time frames.

Natural Selection

In *On the Origin of Species by Means of Natural Selection*, published in 1859, Charles Darwin presented arguments for two related theories. The first argument documents evidence for evolution on the basis of an extensive study of biogeographical, embryological, and fossil data. Within ten years of its publication, nearly all individuals who today would be considered scientists were convinced that evolution had occurred.

Darwin's second argument develops the case for what he identified as the chief mechanism of evolution: his theory of natural selection. This argument elegantly draws attention to the probabilistic consequences of three conditions in nature. First, organisms vary from one another in ways that affect their ability to survive and reproduce. Second, at least some of this variation is heritable. Third, there is *competition*, owing to the fact that organisms produce more offspring than can possibly survive. Darwin's genius was to recognize that as a consequence of these conditions, members of a population possessing favored variations would be more likely to leave offspring than those that did not, and as such, the composition of the population as a whole would change over generational time in the direction of the favored form.

Evidence

In addition to evidence for the existence of the above conditions in nature, Darwin also gave indirect evidence in support of the long-term consequences of these conditions he had deduced. In addition to thought experiments, he developed an analogy between artificial and natural selection. He pointed out that during the relatively short time that pigeon and dog species had been domesticated, breeders had been able, by picking which individuals were allowed to reproduce, to create new varieties as distinct in appearance as true species in nature. Darwin then drew attention to the fact that conditions in nature (coupled with the occasional introduction of new variants by mutation) operating over geological time periods could have a similarly dramatic effect on populations in the wild.

Although the vast time and spatial frames involved make it difficult to observe directly the origin of new adaptations and species, many field experiments in the years since Darwin first wrote have confirmed both the power and ubiquity of natural selection in nature. A particularly important example in the context of botany was provided in the late 1960's by Janis Antonovics and others, who demonstrated that the evolution of heavy metal tolerance in many plant species was the result of natural selection. Other contemporary areas of research on selection include the study of *developmental plasticity*, or the ability of an organism to respond to environmental conditions during its development, as occurs when a growing sapling forms leaves to maximize its light exposure in the presence of partial shading by other trees in a forest. This ability is itself the object of natural selection.

Genotypes vs. Phenotypes

Although evolution is often discussed in terms of a change in the frequency of genes in a population, in fact, natural selection acts directly on the *phenotypes* (observable characteristics of organisms) and only indirectly on the *genotypes* (the specific forms of the gene, or *alleles*, an individual has inherited from its parents) responsible for them. While often portrayed as a process that removes genetic variability from populations, natural selection can promote variability, as occurs when the population exists in an environment where one form of a trait is advantageous in some areas but another form is advantageous in other areas. Such processes may lead to *clines*, or gradations, in the frequencies of genes over the range of the population.

Ecosystems

The foregoing has discussed selection with reference to isolated populations. In ecosystems composed of multiple populations of distinct species, natural selection can promote the evolution of *ecotypes*, or populations having a distinct set of characteristics unique to the region they inhabit and the mode of life they pursue. Natural selection can favor the *coevolution* of populations of distinct species with one another. This occurs in the evolution of predator and prey species, in which, for example, the origin of an adaptation that allows a predator to consume a grass species that was previously toxic to it changes the selective environment of the prey species, leading to the evolution of entirely new plant defenses.

Convergent vs. Divergent Evolution

The presence of common selective conditions in distinct locations may lead to the independent evolution of similar characteristics in separate species; that is, *convergent evolution*. A good example is provided by cacti in North and South American deserts and euphorbs in African deserts: Both have thornless leaves with a similar structure that has evolved to maximize water retention. Natural selection can also lead to a partitioning of resource space, a phenomenon known as *divergent evolution*, in which distinct populations of a species evolve divergent modes of life. This may reflect the imposition of a barrier that prevents interbreeding or competition among cohabiting populations leading to a partitioning of niche space. A good example is the common mistletoe, *Viscum album*, a parasitic higher plant having three distinct races that specialize on deciduous trees, firs, and pines.

David W. Rudge

See also: Adaptations; Clines; Coevolution; Competition; Evolution: convergent and divergent; Evolution: historical perspective; Evolution of plants; Genetic drift; Genetics: Mendelian; Genetics: mutations; Genetics: post-Mendelian; Plant domestication and breeding; Population genetics; Species and speciation.

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SERPENTINE ENDEMISM

Category: Soil

Serpentine endemics are plants that grow only in serpentine soils. These uncommon soils present serious challenges to plants and are often sparsely covered with dwarfed vegetation.

Serpentine rock is one form of *ultramafic rock*, an uncommon rock found in mountain-building zones. Soils derived from ultramafic rock are called serpentine soils. The most important chemical characteristics of ultramafic rock and of the serpentine soils formed from it are high magnesium concentrations; low calcium concentrations; low calcium/magnesium ratios; low concentrations of other macronutrients (such as nitrogen, phosphorus and potassium); high concentrations of toxic heavy metals (such as nickel, chromium, and cobalt); and low micronutrient (molybdenum, boron) concentrations. All these factors are detrimental to plant growth.

Physical factors also tend to be harsh in serpentine soils. They are rocky and low in humus (the organic matter formed from decomposing plants), and temperatures tend to fluctuate widely. In part, these physical factors are caused by the chemical factors discussed above and their restriction of plant growth. Sparse plant cover results in less plant material to decompose, thus less humus; and a greater plant cover would mitigate temperature changes. Whatever their causes, these physical factors further restrict plant growth. Not all serpentine soils have all these characteristics, but those present combine in various ways to severely restrict plant growth on serpentine soils.

Plants of Serpentine Soils

Many plant species cannot grow in serpentine soils. Others can grow in serpentine soils or in other soils, but the serpentine varieties are often dwarfed and require special adaptations. Still others, the serpentine endemics, grow only in serpentine soils. Two examples are *Quercus durata*, a shrubby oak that grows in some western serpentines, and *Aster depauperatus*, a small aster of some Appalachian serpentine soils.

One common adaptation of serpentine plants is a high tolerance for nickel, the most troublesome of the serpentine heavy metals. A second is the ability to use calcium efficiently in the presence of excess magnesium. Magnesium is an essential nutrient, but in high concentrations it interferes with the plant's use of calcium, another essential nutrient. These two adaptations are widespread among serpentine endemics, suggesting that they are two of the adaptations important to serpentine endemics. Additional adaptations are probably necessary because a plant growing on serpentine must overcome all of the soil's troublesome characteristics.

Competition may explain why these plants are unable to grow in more favorable soils. Many serpentine endemics cannot compete with other plants outside the serpentine environment and are thus excluded from nonserpentine soils. Because most plants cannot grow in serpentine soil, serpentine endemics are freed from competition and can grow successfully in those soils.

Because they only occur on these uncommon soils, serpentine endemics are especially susceptible to extinction. Preservation efforts have focused on some of these areas and their plant life.

Carl W. Hoagstrom

See also: Adaptations; Agronomy; Halophytes; Nutrient cycling; Selection; Soil.

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SHOOTS

Category: Anatomy

"Shoot" is a term used to refer collectively to the stem and associated leaves of a vascular plant.

The *stem* of a vascular plant is typically a cylindrical, aboveground axis that grows upright, away from the pull of gravity. Young stems are green and photosynthetic, and in some plants, such as horsetails and most cacti, the stems are the primary site of photosynthesis. In most plants, however, the primary function of the stem is to support leaves in a position where they are well exposed to light. The part of the stem where a leaf attaches is a *node*. The section of stem between nodes is an *internode*. Internode elongation spaces the leaves and is responsible for most of the increase in length of the stem every growing season.

The cylindrical shape of the stem is a structural adaptation that provides maximum strength per volume of tissue. The *vascular tissues*, which contain tough, thick-walled fiber cells, contribute to the strength of the stem. In non-seed plants, such as ferns, these tough cells form a core in the center of the stem with softer tissues around them. In seed plants, such as conifers and flowering plants, the vascular tissues tend to lie in a subperipheral ring below the surface, surrounding a softer core of tissue. This is analogous to the arrangement of steel reinforcing bars in a column of reinforced concrete. In gymnosperms and dicots, the vascular tissues are formed in a single ring. In monocots, strands of vascular tissue form throughout the stem but even so tend to be more numerous and more tightly packed around the periphery of the stem.

Leaves are lateral appendages of the stem that are typically flattened to expose a maximum amount of surface area to sunlight. They are the primary site of photosynthesis in most vascular plants. The flattened portion of the leaf is the *blade*, or *lamina*. In some plants, such as grasses, the lamina appears to attach directly to the stem. In most plants, however, there is a stemlike stalk, the *petiole*, that extends the lamina away from the stem. In many cases the cells of the petiole enable the blade to be repositioned to maximize exposure to light. The *leaf base* is the attachment zone where the leaf connects to the stem. In some plants the cells of the leaf base enlarge to form *stipules* on each side of the petiole. The leaf base merges with the node. One or more *axillary buds* arise in the angle formed by this merger.

Shoot Development

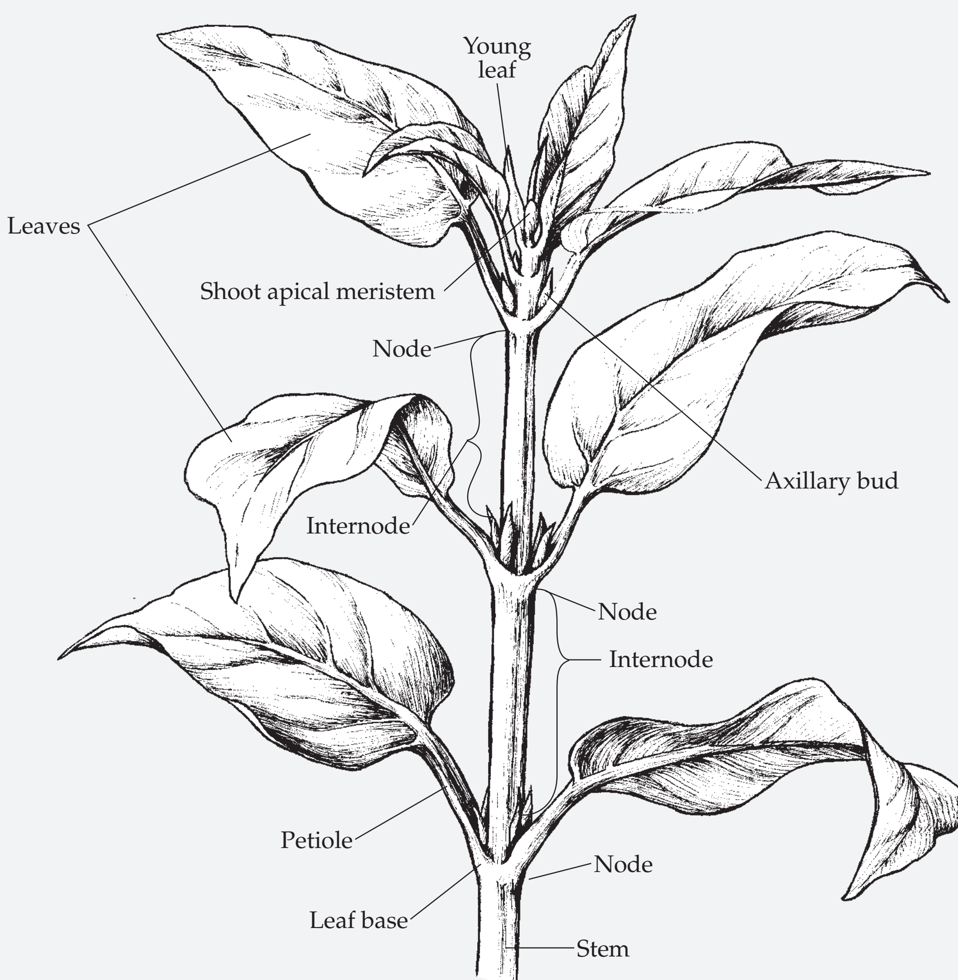
At the tip of every shoot is a *terminal bud*. If the leaves of this bud are carefully peeled away, a tiny, rounded dome of tissue is exposed—the *shoot apical meristem*. A meristem is a region of the plant where cell division is concentrated. Cell division and differentiation in the shoot apical meristem produce the tissues that form the stem and leaves of that shoot.

The structure of the shoot apical meristem varies, depending on the plant being examined. Seedless vascular plants, such as ferns, have a large, pyramidally shaped apical cell that ultimately gives rise to all the cells and tissues of the shoot. The seed plants have a multicellular apical meristem differentiated into several zones. Each zone is associated with one of three primary meristems that form the tissues of the shoot system. A surface layer of cells covers the dome and differentiates into *protoderm*, the primary meristem that forms *epidermal cells*. The epidermis is a continuous protective layer that covers the stem and leaves of the shoot system. Within the apical meristem, certain cells begin to elongate and form the *procambium*, the primary meristem that forms vascular tissues. The remainder of the internal cells of the apical meristem become ground meristem, the primary meristem that forms ground tissues, such as cortex and pith.

As the apical meristem grows and new cells are formed, the dome of tissue enlarges. This growth is not symmetric; rather, surface or subsurface cells of a localized region will proliferate more rapidly than the rest to form a small bulge of tissue. This bulge is the first sign of initiation of a new leaf, a *leaf primordium*. As the leaf primordium enlarges, the protoderm also proliferates to maintain a continuous covering over the developing leaf that is contiguous with the developing stem. This continuity is maintained as cells differentiate into mature epidermal cells.

After initiation of a leaf primordium, the shoot apical meristem continues to grow, and procambium begins to differentiate within the developing node. These procambial cells connect to already formed procambium in older portions of the stem to form the template for the vascular system of the stem. Simultaneously, as the leaf primordium enlarges, procambial strands differentiate in the leaf base region. Further development is bidirectional. Cells from the basal end of each strand differentiate into the node and connect with the already-formed

Parts of the Shoot



Kimberly L. Dawson Kurnizki

procambium there. Cells from the upper end of each strand continue to develop into the enlarging leaf primordium. In this way the vascular tissues of the leaf and stem are integrated into a continuous system. Similarly, the ground tissues of leaf and stem are continuous as the leaf primordia are initiated and develop.

Specialized Shoots

Specialized shoots are usually associated with storage or vegetative reproduction. *Bulbs*, such as onions, have a shortened stem with enlarged, overlapping, fleshy leaves. *Tubers*, such as potatoes, are subterranean storage shoots with thick, starch-filled stem cells and undeveloped leaves subtending axillary buds (the "eyes"). *Rhizomes* are horizontal shoots running on, or below, the soil surface. Their leaves are typically much reduced.

Marshall D. Sundberg

See also: Angiosperm cells and tissues; Bulbs and rhizomes; Cloning of plants; Growth habits; Leaf anatomy; Leaf arrangements; Stems; Plant tissues; Thigmomorphogenesis; Tropisms; *Tracheobionta*.

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SLASH-AND-BURN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; environmental issues

Slash-and-burn agriculture, also called swidden agriculture, is a practice in which forestland is cleared and burned for use in crop and livestock production. While yields are high during the first few years, they rapidly decline in subsequent years, leading to further clearing of nearby forestland.

Slash-and-burn agriculture has been practiced for many centuries among people living in tropical *rain forests*. Initially, this farming system involved small populations. Therefore, land could be allowed to lie *fallow* (unplanted) for many years, leading to the full regeneration of the *secondary forests* and hence a restoration of the ecosystems. During the second half of the twentieth century, however, several factors led to drastically reduced fallow periods. In some places such fallow systems are no longer in existence, resulting in the transformation of forests into *shrub* and *grasslands*, negative effects on agricultural productivity for small farmers, and disastrous consequences to the environment.

Among the factors that have been responsible for reduced or nonexistent fallow periods are increased population in the tropics, increased demand for wood-based energy, and, perhaps most important, the increased worldwide demand for tropical commodities during the 1980's and 1990's, especially for products such as palm oil and natural rubber. These last two factors have helped industrialize slash-and-burn agriculture, which was practiced for centuries mainly by small farmers. Ordi-

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narily, small farmers are able to control their fires so that they are similar to a small forest fire triggered by lightning in the northwestern or southeastern United States. However, the continued reduction in fallow periods, coupled with increased burning by *subsistence farmers* and large agribusiness, especially in Asia and Latin America, is resulting in increased environmental concern.

While slash-and-burn agriculture seldom takes place in temperate regions, some agricultural burning occurs in the Pacific Northwest of the United States, where it is estimated that three thousand to five thousand agricultural fires are set each year in Washington State alone. These fires also create problems for human health and the environment.

Habitat Fragmentation

One of the most easily recognized results of slash-and-burn agriculture is *habitat fragmentation*, which leads to a significant loss of the vegetation needed for the maintenance of effective *gaseous exchange* in tropical regions and throughout the world. For every acre of land lost to slash-and-burn agriculture, 10 to 15 acres (4 to 6 hectares) of land are fragmented, resulting in the loss of habitat for wildlife, plant species, and innumerable macro- and microorganisms yet to be identified. This also creates problems for management and wildlife conservation efforts in parts of the world with little or no resources to feed their large populations. Fragmentation has also led to intensive discussions on *global warming*. While slash-and-burn agriculture by itself is not completely responsible for global warming, the industrialization of the process could make it a significant component of the problem, as more and more vegetation is fragmented.

Human Health

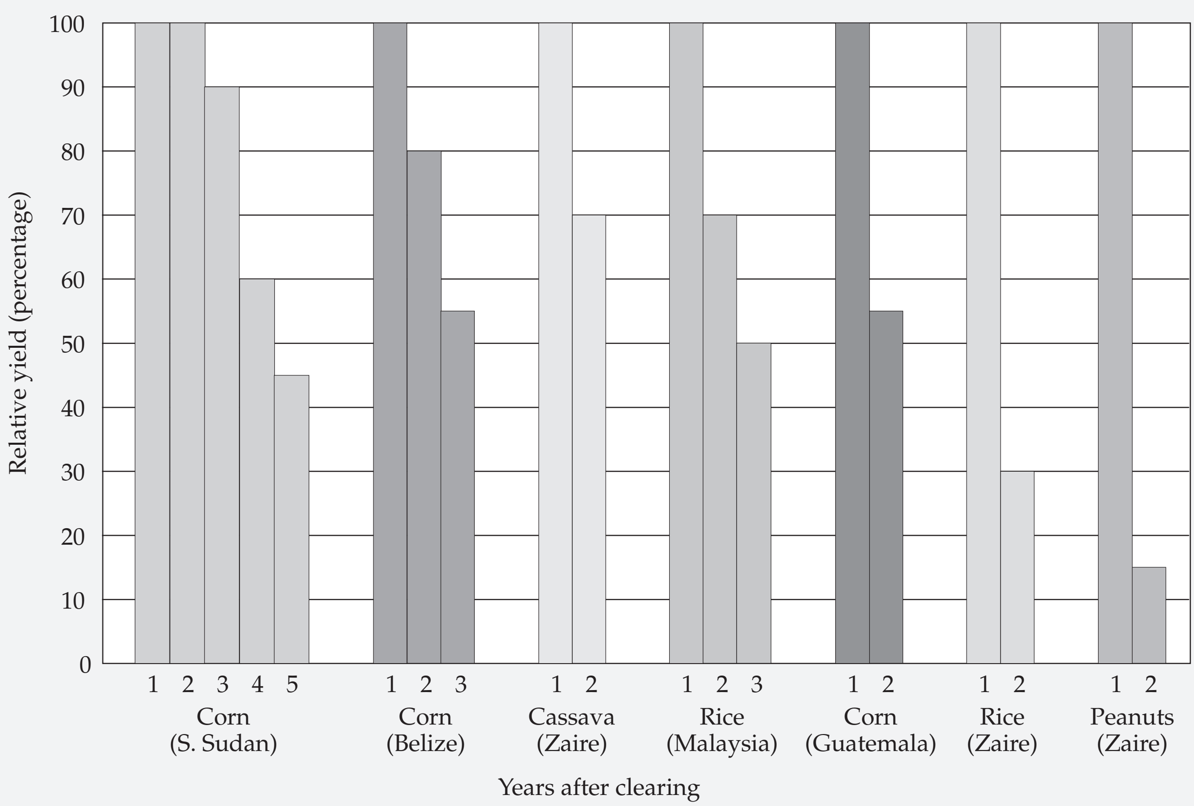
The impact of slash-and-burn agriculture on human health and the environment is best exemplified by the 1997 Asian fires that resulted from such practices. Monsoon rains normally extinguish the fires set by farmers, but a strong El Niño weather phenomenon delayed the expected rains, and the fires burned out of control for months. Thick smoke caused severe health problems. It is estimated that more than 20 million people in Indonesia alone were treated for asthma, bronchitis, emphysema, and eye, skin, and cardiovascular problems as a result of the fires. Similar problems have been reported for smaller agricultural fires.

Three major problems are associated with air pollution: *particulate matter*, *pollutant gases*, and *volatile organic compounds*. Particulate compounds of 10 microns or smaller that are inhaled become attached to the alveoli and other blood cells, resulting in severe illness. Studies by the U.S. Environmental Protection Agency (EPA) and the University of Washington indicate that death rates associated with respiratory illnesses increase when fine particulate air pollution increases. Meanwhile, pollutant gases such as carbon monoxide, nitric oxide, nitrogen dioxide, and sulfur dioxide become respiratory irritants when they combine with vapor to form *acid rain* or fog. Until the Asian fires, air pollutants stemming from the small fires of slash-and-burn agriculture that occur every planting season often went unnoticed. Thus, millions of people in the tropics experience environmental health problems because of slash-and-burn agriculture that are never reported.

Soil and Water Quality

The loss of vegetation that follows slash-and-burn agriculture causes an increased level of soil *erosion*. The soils of the humid tropics create a hard pan underneath a thick layer of organic matter. Therefore, upon the removal of vegetation cover, huge areas of land become exposed to the torrential rainfalls that occur in these regions. The result is severe soil erosion. As evidenced by the impact of Hurricane Mitch on Honduras during 1998, these exposed lands can give rise to large mudslides that can lead to significant loss of life. While slash-and-burn agriculture may not be the ultimate cause for sudden mud slides, it does predispose these lands to erosional problems.

Declining Crop Yields with Successive Harvests on Unfertilized Tropical Soils



Source: Data adapted from John Terborgh, *Diversity and the Tropical Rain Forest*. New York: W. H. Freeman, 1992.

Associated with erosion is the impact of slash-and-burn agriculture on water quality. As erosion continues, *sedimentation* of streams increases. This sedimentation affects stream flow and freshwater discharge for catchment-area populations. Mixed with the sediment are minerals such as phosphorus and nitrogen-related compounds that enhance algal growth in streams and estuaries, which depletes the supply of oxygen that aquatic organisms require to survive. Although fertility is initially increased on noneroded soils, nutrient deposition and migration into drinking water supplies continues to increase.

Controlling Slash-and-Burn Agriculture

Given the fact that slash-and-burn agriculture has significant effects on the environment not only in regions where it is the mainstay of the agricultural systems but also in other regions of the world, it has become necessary to explore different approaches to controlling this form of agriculture. However, slash-and-burn agriculture has evolved into a sociocultural livelihood; therefore, recommendations must be consistent with the way of life of a people who have minimal resources for extensive agricultural systems.

Among the alternatives are new *agroecosystems* such as *agroforestry systems* and *sustainable agricultural systems* that do not rely so much on the slashing and burning of forestlands. These systems allow for the cultivation of agronomic crops and livestock within forest ecosystems. This protects soils from being eroded. Another possibility is the education of small rural farmers, absentee landlords, and big agribusiness concerns in developing countries to understand the environmental impact of slash-and-burn agriculture. While small rural farmers may not have the resources for renovating utilized forestlands, big business can organize ecosystems restoration, as has been done in many developed nations of the world.

Oghenekome U. Onokpise

See also: Agriculture: modern problems; Air pollution; Deforestation; Erosion and erosion control; Forest fires; Rain-forest biomes; Rain forests and the atmosphere; Soil degradation; Sustainable agriculture.

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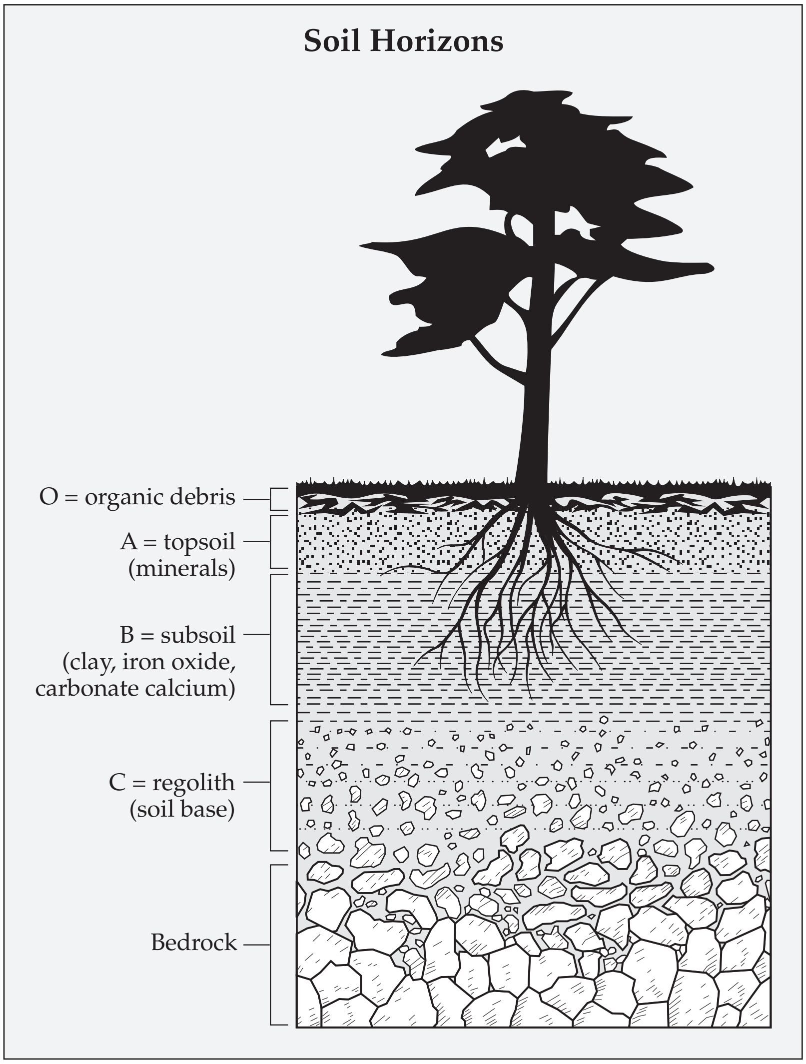
SOIL

Categories: Nutrients and nutrition; soil

Soil is a product of the physical and chemical breakdown of the earth's surface into small fragments, including sand, silt, and clay. Soil contains the products of organic matter decomposition—the composting of dead plant and animal debris.

Soils are classified on the basis of *soil profile* and *soil formation*. They can be grouped according to a number of characteristics, including agronomic use, color, organic matter content, texture, and



moisture condition. Typical soil is about 45 percent minerals and about 5 percent organic matter. The other 50 percent of soil consists of pores that hold either water or air. The liquid portion of soil contains dissolved minerals and organic compounds, produced by plants and microorganisms. The gases found in soil often are the same as those found in the air above it. Soil can support plant life if climate and moisture are suitable. It is a changing and dynamic body, adjusting to conditions of climate, topography, and vegetation. In turn, soil influences plant and root growth, available moisture, and the nutrients available to plants. While "the soil" is a collective term for all soils, "a soil" means one individual soil body with a particular length, depth, and breadth.

Soil Profile

In a typical soil, the top layer is usually dark with decomposing organic matter; the layers below are sand, silt, clay, or some combination of the three. Soil scientists classify soils on the basis of soil profile and soil formation.

Typically the top soil layer is called the *O horizon*, or organic matter horizon. It has rotten logs, leaf litter, and other recognizable bits of plants and animals. Underneath the O horizon is the *A horizon*. It is characterized by thoroughly decomposed organic matter. Water passing through the A horizon carries clay particles and organic acids through it into the *B horizon*. Clay or organic substances passing into the B horizon glue soil particles together, forming soil aggregates. Soil aggregates—granular, columnar, and so on—are indicators of a mature, healthy soil. The lowest level of the soil profile is the *C horizon*. It contains bedrock or soil parent material that shows little or no evidence of plant growth or soil formation.

Soil Formation

Soil formation takes hundreds, even thousands, of years. Parent material, climate, organisms, topography, and time all contribute. Sources of parent material include igneous, sedimentary, and metamorphic rocks (fragments of which may be deposited by water, wind, and ice), and plant and animal deposits.

Soil formation is the result of the physical, chemical, and biochemical breakdown of parent material. It also reflects the processes of weathering and change within the soil mass. Many substances are added to soil—rain, water from irrigation, nitrogen from bacteria, sediment, salts, organic residues, and a variety of substances created by humans. However, many substances are also removed from the soil—water-soluble minerals, clay, plants, carbon dioxide, and nitrogen. Other transformations also are occurring: Organic matter is decomposing, and minerals are solubilizing and changing chemical form. Clays and soluble salts that move along with the soil water cause color and chemical changes in the soil.

Parent material is a primary determinant of soil type or soil classification. All soils at the lowest category of soil classification are distinct if the parent material differs. The differences in parent materials—weathering rates, the plant nutrient content, and soil texture resulting from parent material breakdown—contribute to the formation of distinctive soils. For example, sandstone yields sandy soil with low fertility.

Chemical Weathering

Soils slowly change color and density as a result of wetting and drying, warming and cooling, and freezing and thawing. During *weathering*—the rubbing, grinding, and moving of rocks by water, wind, and gravity—rocks are split into smaller and smaller fragments. Soil is composed of fragments 2 millimeters or less in diameter.

The expansion force of water as it freezes is sufficient to split minerals. However, water also is involved in chemical weathering—solution, hydrolysis, carbonation, reduction, oxidation, and hydration. A simple example of solution, the dissolving of minerals in liquid, is the dissolving of salt in water. The salts then move along with the liquid. In hot arid climates, salts can move to the surface as water evaporates, creating salt flats. In wetter climates, salts can move through the soil, depleting it of necessary plant nutrients and contaminating groundwater.

Hydrolysis is the splitting of a water molecule to form hydroxides and soluble hydroxide compounds, such as sodium hydroxide. *Hydration* is the addition of water to minerals in rock. When a mineral such as hematite (an oxide of iron) hydrates, it expands, softens, and changes color. *Carbonation* is the reaction of a compound with carbonic acid, a weak acid produced when carbon dioxide dissolves in water. Water often contains carbonic acid and other organic acids produced by organic matter decomposition. These acids increase the power of the water to disintegrate rock. *Oxidation* is the addition of oxygen to a mineral, and *reduction* is the removal of oxygen from a mineral.

Biological Weathering

Biological weathering is a combination of physical and chemical disintegration of rocks to produce soil. The roots of plants can crack rocks and break them apart. Plant roots also produce carbon dioxide, which combines with water to produce carbonic acid. Carbonic acid dissolves certain minerals, speeding the breakdown of parent material and chemically changing the soil.

Plants and animals also add humus (organic matter) to soil, increasing its fertility and water-holding capacity and speeding rock weathering. Animals such as earthworms, ants, prairie dogs, gophers, and moles also contribute to soil aeration and fertility by mixing the soil. In areas where animal populations are large, they can influence both the formation and destruction of soil.

Climate and Topography

Climate also influences soil formation indirectly through its action on vegetation. Soils in arid climates have sparse vegetation, less organic matter, and little soil profile development. Wet soil, however, usually has thick vegetation and high organic matter, and therefore a deep soil profile.

The shape of the land is referred to as its topography. Each landform—valleys, plains, hills, and mountains—is covered with a crazy quilt of different soil types. For example, the steep sides of the Sandia Mountains near Albuquerque, New Mexico, which are severely eroded by wind and summer rains, contain a variety of soil types—forest soils, sandy soils, and rocky soils. Sand, silt, and clay eroded from the mountains and nearby extinct volcanoes combine in the moist and fertile Rio Grande Valley. The valley has deep sandy soils, layered sand and clay soils, and soils eroded by flash floods.

Soils located in similar climates that develop from similar parent material on steep hillsides usually have thin A and B horizons because less water moves through the soil. Similar materials on shallower slopes allow more water to pass through them. Topography and climate work together either to allow or to prohibit plant growth and organic matter deposition. Without moisture, plants cannot grow to impede soil erosion, and soil development is slow. With moisture, plants can grow, hold the soil in place, add organic matter to the soil, and speed soil development.

The age of a soil may be reckoned in tens, hundreds, or thousands of years. Under ideal conditions, a soil profile may develop in two hundred years; however, under less favorable conditions soil development may take several thousand years.

Soil Classification

Scientists have identified and classified soils for hundreds of years. Soils can be grouped according to agronomic use, color, organic matter content, texture, moisture condition, and other characteristics. Each of these groupings serves a particular purpose. U.S. soil scientists adopted a system of soil classification on January 1, 1965, that was based on the knowledge they had about soil genesis, morphology, and classification. The U.S. system is divided into six categories: order, suborder, great group, subgroup, family, and series. *Soil taxonomy* is patterned after the worldwide system of plant and animal taxonomy, which contains phylum, class, order, family, genus, and species.

Changes to the system have proceeded through a number of major revisions or approximations.

The Twelve Soil Orders in the U.S. Classification System

Soil Order	*Features*
Alfisols	Soils in humid and subhumid climates with precipitation from 500 to 1,300 millimeters (20 to 50 inches), frequently under forest vegetation. Clay accumulation in the B horizon and available water most of the growing season. Slightly to moderately acid soils.
Andisols	Soils with greater than 60 percent volcanic ash, cinders, pumice, and basalt. They have a dark A horizon as well as high absorption and immobilization of phosphorus and very high cation exchange capacity.
Aridisols	Aridisols exist in dry climates. Some have horizons of lime or gypsum accumulations, salty layers, and A and slight B horizon development.
Entisols	Soils with no profile development except a shallow A horizon. Many recent river floodplains, volcanic ash deposits, severely eroded areas, and sand are entisols.
Gelisols	Soils that commonly have a dark organic surface layer and mineral layers underlain by permafrost, which forms a barrier to downward movement of soil solution. Common in tundra regions of Alaska. Alternate thawing and freezing of ice layers results in special features in the soil; slow decomposition of the organic matter due to cold temperatures results in a peat layer at the surface in many gelisols.
Histosols	Organic soils of variable depths of accumulated plant remains in bogs, marshes, and swamps.
Inceptisols	Soils found in humid climates that have weak to moderate horizon development. Horizon development may have been delayed because of cold climate or waterlogging.
Mollisols	Mostly grassland soils, but with some broadleaf forest-covered soils with relatively deep, dark A horizons, a possible B horizon, and lime accumulation.
Oxisols	Excessively weathered soils. Oxisols are over 3 meters (10 feet) deep, have low fertility, have dominantly iron and aluminum oxide clays, and are acid. Oxisols are found in tropical and subtropical climates.
Spodosols	Sandy leached soils of the cool coniferous forests, usually with an organic or O horizon and a strongly acidic profile. The distinguishing feature of spodosols is a B horizon with accumulated organic matter plus iron and aluminum oxides.
Ultisols	Strongly acid and severely weathered soils of tropical and subtropical climates. They have clay accumulation in the B horizon.
Vertisols	Soils with a high clay content that swell when wet and crack when dry. Vertisols exist in temperate and tropical climates with distinct dry and wet seasons. Usually vertisols have only a deep self-mixing A horizon. When the topsoil is dry, it falls into the cracks, mixing the soil to the depth of the cracks.

The system can be used to classify soils anywhere in the world, especially with the addition of a new soil order, the andisols. The new soil classification continues to be tested, and minor modifications may be anticipated. The approximation being used as of 1997 treated soil as a collection of three-dimensional entities that can be grouped based on similar physical, chemical, and mineralogical properties. The minimum volume of soil that scientists consider when they classify a soil is the pedon, which can range from 1 to 10 meters square and is as deep as roots extend into a soil.

By 1999, the U.S. soil classification system recognized twelve soil *orders*. The differences among orders reflect the dominant soil-forming processes and the degree of soil formation. Each order is identified by a word ending in "-sol." Each order is divided into suborders, primarily on the basis of properties that influence soil genesis, are important to plant growth, and reflect the most important variables within the orders. The last syllable in the name of a suborder indicates the order. An example is "aquent," meaning water, plus "-ent," from "entisol."

Suborders are distinctive to each order and are not interchangeable between orders. Each suborder is divided into great groups on the basis of additional soil properties and horizons resulting from differences in soil moisture and soil temperature.

Great groups are denoted by a prefix that indicates a property of the soil. An example is "psammaquents" ("psamm" referring to sandy texture and "aquent" being the suborder of the entisols that has an aquic moisture regime). Soil scientists have identified more than three hundred great groups in the United States. Great groups are distinguished on the basis of differing horizons and soil features. The differing soil horizons include those with accumulated clay, iron, or organic matter and those hardened or cemented by soil cultivation or other human activities. The differentiating soil features include self-mixing of soil due to clay content, soil temperature, and differences in content of calcium, magnesium, sodium, potassium, gypsum, and other salts.

There are more than twenty-four hundred *subgroups*, and each great group is divided into three kinds of *subgroups*: a *typic* subgroup, an *intergrade* subgroup, and an *extragrade* subgroup. The typic subgroup represents the central spectrum of a soil group. The intergrade subgroup represents soils with properties like those of other orders, suborders, or great groups. The extragrade subgroup represents soils with some properties that are not representative of the great group but do not indicate transitions to any other known kind of soil. Each subgroup is identified by one or more adjectives preceding the name of the great group.

Families are established within a subgroup on the basis of physical and chemical properties and other characteristics that are important to plant growth or that are related to the behavior of soils that are important for engineering concerns. Among the properties and characteristics considered are particle size, mineral content, temperature regime, depth of the root zone, moisture, slope, and permanent cracks. A family name consists of the name of a subgroup preceded by terms that indicate soil properties. Several thousand families have been identified in the United States.

Finally, the *series* is the lowest soil category, with more than nineteen thousand recognized in the United States as of 1999. A series might share one or more properties with those of an entire family, but for at least one property only a narrower range is permitted.

Texture, Structure, and Consistency

Soil texture is determined by the percent of sand, silt, and clay in a soil sample. Most fertile or productive soils have a loam texture, or about equal amounts of sand, silt, and clay, and a high organic matter content (about 5 to 10 percent). Soil texture determines the water-holding and nutrient-holding capacity of a soil. Thus, clay soils have a high nutrient-holding capacity, but they waterlog easily. Sandy soils have a lower nutrient-holding capacity but dry out easily. Farmers base their plans of how to fertilize and irrigate their crops partly on the texture of the soil.

Soil structure refers to how soil particles are glued together to form aggregates. During soil formation, soil particles are glued together with clay, dead microorganisms, earthworm slime, and plant roots, and they form air and water channels. Plants need these channels so they can absorb nutrients, water, and air. Soil structure may be destroyed when farmers cultivate wet or waterlogged soils with heavy farm machinery. Destroying soil structure makes a soil unsuitable for plant growth.

Soil consistency is the "feel" of a soil and the ease with which a lump can be crushed in one's fingers.

Common soil consistencies are loose, friable, firm, plastic, sticky, hard, and soft. Clay soils, for example, are sticky or plastic when they are wet, but they become hard or harsh when they are dry. The best time to work a clay soil is when it is soft or friable. Sandy soils, on the other hand, do not become plastic or sticky when they are wet or hard or harsh when they are dry. They have a tendency to stay loose, which makes them easier to work. Loam and silt loam soils are intermediate in behavior. When farmers are trying to determine whether to work the soil or wait for better soil moisture conditions, they usually check the soil consistency.

Aeration and Moisture

Soil aeration relates to the exchange of soil air with atmospheric air. Growing roots need oxygen and are constantly expiring carbon dioxide. Unless there is a continuous flow of oxygen into soil and carbon dioxide out of the soil, oxygen becomes depleted. When their oxygen supply is cut off, the roots will die.

Soil moisture refers to water held in soil pores. A plant draws water from soil the same way a child draws water from a cup with a straw. When the cup is full, it is easy for the child to draw up the water, but as the cup empties, the child must work harder to get water. Similarly, plants draw water from soil easily when the soil has plenty of water. As the soil dries, however, plants must work harder to pull water out of the soil until they reach wilting point.

Fertility

Plants absorb many of the nutrients they need from soil, including phosphorus, potassium, calcium, magnesium, sulfur, boron, chlorine, cobalt, copper, iron, manganese, molybdenum, and zinc. They may obtain carbon, hydrogen, and nitrogen from the air and water.

Soil testing services give farmers specific fertilizer and lime recommendations based on soil texture and chemical analysis. Farmers use soil tests to determine if their soil has enough essential nutrients for a crop to grow. The absence of one essential nutrient can limit overall crop growth. Nitrogen, phosphorus, and potassium are commonly applied to the soil as commercial fertilizer and manure. Calcium and magnesium are applied as lime, which is also used to reduce the acidity of soil and to increase the solubility of some minerals. Manure and other organic matter added to soils increase water-holding and nutrient-holding capacity and therefore boost crop yields.

Agricultural extension services offer guidelines for the maximum amounts of manure, sewage sludge, fertilizer, and other chemicals that farmers should apply to soils. Farmers are encouraged to apply nitrogen fertilizer in small applications at times when plants are growing rapidly. This soil management practice decreases deep percolation losses that could pollute groundwater.

With an understanding of soil characteristics, farmers and gardeners can learn to manage a wide variety of soils. Some soils are naturally fertile and need few amendments to promote high crop yields. Other soils, whether because of their parent material or climate, are naturally infertile and might best be used for purposes other than agriculture. Like the water and the air, the soil is a crucial natural resource. From an airplane, all soils look about the same, but from an ant's view, soils are all different. Differences in soil type make huge differences to plants, animals, humans, and the environment.

J. Bradshaw-Rouse, updated by Christina J. Moose

See also: Agronomy; Composting; Hydroponics; Nutrients; Soil conservation; Soil contamination; Soil degradation; Soil management; Soil salinization.

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SOIL CONSERVATION

Categories: Environmental issues; soil

Soil conservation is the effort by farmers and other landowners to prevent the buildup of salts and fertilizer acids in the soil, as well as the loss of topsoil from wind erosion, water erosion, desertification, and chemical deterioration. This can be achieved by implementing management practices to maintain soil quality and reduce pollution.

According to the United Nations Environment Programme, approximately 17 percent of the earth's vegetated land is degraded, which poses a threat to agricultural production around the world. The introduction of minerals, metals, nutrients, fertilizers, pesticides, bacteria, and pathogens suspended in *topsoil runoff* into waterways is a significant source of water pollution and is a threat to fisheries, wildlife habitat, and drinking water supplies. The introduction of soil particles into the air through wind *erosion* is a significant source of air pollution.

Threats and Responses

The Industrial Revolution of the nineteenth century and the population explosion of the twentieth century encouraged people to till new land, cut down forests, and disturb soil for the expansion of towns and cities. The newly exposed topsoil quickly succumbed to erosion from rainfall, floods, wind, ice, and snow. The Dust Bowl, which occurred in the Great Plains in the United States during the 1930's, is one example of the devastating effects of wind erosion.

Hugh Hammond Bennett, the so-called father of soil conservation, lobbied for congressional establishment of the United States Soil Conservation Service (approved in 1937) and the establishment of voluntary Soil Conservation Districts in each state. Bennett was named the first chief of the U.S. Soil Conservation Service in 1937. On August 4, 1937, the Brown Creek Conservation District in Bennett's home county, Anson County, North Carolina, became the first Soil Conservation District in the United States. Local landowners voted to establish the district by three hundred to one, proving that farmers were concerned about soil conservation. A reporter for the *Charlotte Observer* newspaper sought out the one negative voter; after having the program explained to him, he changed his opinion. By 1948, more than twenty-one hundred districts had been established nationwide. They were eventually renamed Soil and Water Conservation Districts. There are more than three thousand such districts in the United States.

The U.S. Food Security Act of 1985 authorized the Conservation Reserve Program to take land highly susceptible to erosion out of production and required farmers to develop soil conservation plans for the remaining susceptible land. The Natural Resource Conservation Service estimates that the loss of topsoil was nearly cut in half, reduced from 1.6 billion tons per year to 0.9 billion tons. The European Community and Australia also adopted soil conservation measures during the 1990's.

Practices

Soil conservation practices include covering the soil with *vegetative cover*, reducing *soil exposure* on tilled land, creating wind and *water barriers*, and installing *buffers*. Vegetative cover slows the wind at ground level, slows water runoff, protects soil particles from being detached, and traps blowing or floating soil particles, chemicals, and nutrients. Because the greatest wind and water erosion damage often occurs during seasons in which no crops are growing or natural vegetation is dormant, soil conservation often depends on permitting the dead residues and standing stubble of the previous crop to remain in place until the next planting time. An-


PhotoDisc

Soil conservation practices include protecting soil particles from becoming detached and trapping blowing or floating soil particles, chemicals, and nutrients.

nual tree-foliage loss serves as a natural ground mulch in forested areas. Planting grass or legume cover crops until the next planting season, or as part of a *crop rotation* cycle or *no-till planting* system, also reduces erosion.

Modern no-till and *mulch-till planting* systems reduce soil exposure to wind and rain, while plowing the land brings new soil to the surface and buries the ground cover. No-till systems leave the soil cover undisturbed before planting and insert crop seeds into the ground through a narrow slot in the soil. Mulch-till planting keeps a high percentage of the dead residues of previous crops on the surface when the new crop is planted. Row crops are planted at right angles to the prevailing winds and to the slope of the land in order to absorb wind and rainwater runoff energy and trap moving soil particles. Crops are planted in small fields to prevent avalanching caused by an increase in the amount of soil particles transported by wind or water as the distance across bare soil increases. As the amount of soil moved by wind or water increases, the erosive effects of the wind and water also increase. Smaller fields reduce the length and width of unprotected areas of soil.

Wind and water barriers include tree plantings and crosswind strips of perennial shrubs and 1-meter-high (3-foot-high) grasses, which act as wind breaks to slow wind speeds at the surface of the soil. The protected area extends for ten times the height of the barrier. In *alley cropping*, which is used in areas of sustained high wind, crops are planted between rows of larger mature trees. Contour strip farming on slopes, planting grass waterways in areas where rainwater runoff concentrates, and planting 3-meter-wide (10-foot-wide) grass field borders on all edges of cultivated or disturbed soil are additional methods for reducing wind speed and rainwater runoff and trapping soil particles, chemicals, and nutrients.

Buffers filter runoff to remove sediments and chemicals. Riparian buffers are waterside plantings of trees, shrubs, and grasses, usually 6 meters (20 feet) in width. Riparian buffers planted only in grass are called *filter strips*. Grassed waterways, field borders, water containment ponds, and contour grass strips are other types of soil conservation buffers.

Gordon Neal Diem

See also: Agriculture: modern problems; Agronomy; Composting; Erosion and erosion control; Hydroponics; Nutrients; Slash-and-burn agriculture; Soil; Soil contamination; Soil degradation; Soil management; Soil salinization; Sustainable agriculture.

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SOIL CONTAMINATION

Categories: Environmental issues; pollution; soil

Soils contaminated with high concentrations of hazardous substances pose potential risks to human health and the earth's thin layer of productive soil.

Productive soil depends on bacteria, fungi, and other soil microbes to break down wastes and release and cycle nutrients that are essential to plants. Healthy soil is essential for growing enough food for the world's increasing population. Soil also serves as both a filter and a buffer between human activities and natural water resources, which ultimately serve as the primary source of drinking water. Soil that is contaminated may serve as a source of water pollution through *leaching* of contaminants into groundwater and through *runoff* into surface waters such as lakes, rivers, and streams.

The U.S. government has tried to address the problem of soil contamination by passing two landmark legislative acts. The Resource Conservation and Recovery Act (RCRA) of 1976 regulates hazardous and toxic wastes from the point of generation to disposal. The Comprehensive Environmental Response, Compensation, and Liability Act

(CERCLA) of 1980, also known as Superfund, identifies past contaminated sites and implements remedial action.

Sources of Contamination

Soils can become contaminated by many human activities, including fertilizer or pesticide application, direct discharge of pollutants at the soil surface, leaking of underground storage tanks or pipes, leaching from landfills, and atmospheric deposition. Additionally, soil contamination may be of natural origin. For example, soils with high concentrations of heavy metals can occur naturally because of their close proximity to metal ore deposits. Common contaminants include inorganic compounds such as nitrate and heavy metals (for example, lead, mercury, cadmium, arsenic, and chromium); volatile hydrocarbons found in fuels, such as benzene, toluene, ethylene, and xylene BTEX compounds; and chlorinated organic compounds such as polychlorinated biphenyls (PCBs) and pentachlorophenol (PCP).

Contaminants may also include substances that occur naturally but whose concentrations are elevated above normal levels. For example, nitrogen- and phosphorus-containing compounds are often added to agricultural lands as *fertilizers*. Since nitrogen and phosphorus are typically the limiting nutrients for plant and microbial growth, accumulation in the soil is usually not a concern. The real concern is the leaching and runoff of the nutrients into nearby water sources, which may lead to oxygen depletion of lakes as a result of the *eutrophication* encouraged by those nutrients. Furthermore, nitrate is a concern in drinking water because it poses a direct risk to human infants (it is associated with blue-baby syndrome).

Contaminants may reside in the solid, liquid, and gaseous phases of the soil. Most will occupy all three phases but will favor one phase over the others. The physical and chemical properties of the contaminant and the soil will determine which phase the contaminant favors. The substance may preferentially adsorb to the solid phase, either the inorganic minerals or the organic matter. The attraction to the solid phase may be weak or strong. The contaminant may also *volatize* into the gaseous phase of the soil. If the contaminant is soluble in water, it will dwell mainly in the liquid-filled pores of the soil.

Contaminants may remain in the soil for years or wind up in the atmosphere or nearby water sources. Additionally, the compounds may be broken down or taken up by the biological component of the soil. This may include plants, bacteria, fungi, and other soil-dwelling microbes. The volatile compounds may slowly move from the gaseous phase of the soil into the atmosphere. The contaminants that are bound to the solid phase may remain intact or be carried off in runoff attached to soil particles and flow into surface waters. Compounds that favor the liquid phase, such as nitrate, will either wind up in surface waters or leach down into the groundwater.

Metals display a range of behaviors. Some bind strongly to the solid phase of the soil, while others easily dissolve and wind up in surface or groundwater. PCBs and similar compounds bind strongly to the solid surface and remain in the soil for years. These compounds can still pose a threat to waterways because, over long periods of time, they slowly dissolve from the solid phase into the water at trace quantities. Fuel components favor the gaseous phase but will bind to the solid phase and dissolve at trace quantities into the water. However, even trace quantities of some compounds can pose a serious ecological or health risk. When a contaminant causes a harmful effect, it is classified as a pollutant.

Treatments

There are two general approaches to cleaning up a contaminated soil site: treatment of the soil in place (*in situ*) or removal of the contaminated soil followed by treatment (*non-in situ*). In situ methods, which have the advantage of minimizing exposure pathways, include biodegradation, volatilization, leaching, vitrification (glassification), and isolation or containment. Non-in situ methods generate additional concerns about exposure during the process of transporting contaminated soil. Non-in situ options include thermal treatment (incineration), land treatment, chemical extraction, solidification or stabilization, excavation, and asphalt incorporation. The choice of methodology will depend on the quantity and type of contaminants, and the nature of the soil. Some of these treatment technologies are still in the experimental phase.

John P. DiVincenzo

See also: Agronomy; Composting; Environmental biotechnology; Hydroponics; Nutrients; Soil; Soil conservation; Soil degradation; Soil management; Soil salinization.

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SOIL DEGRADATION

Categories: Environmental issues; soil

A decline in soil quality, productivity, and usefulness due to natural causes, human activities, or both, is known as soil degradation. It is often caused by unfavorable alterations in one or all of a soil's physical, chemical, and biological attributes.

In 1992, for the first global study of soil degradation, the World Resources Institute in Washington, D.C., reported that 3 billion acres of land worldwide had been seriously degraded since World War II. They also stated that 22 million acres of once usable land could no longer support crops.

Natural Processes and Human Activities

Of the total acreage lost to soil degradation, almost two-thirds is in Asia and Africa; most of the loss is attributable to water and wind *erosion* resulting from agricultural activities, *overgrazing*, *deforestation*, and firewood collection. There are also seriously degraded soils in Central America, where degradation is caused primarily by deforestation and overgrazing. In Europe, industrial and urban wastes, pesticides, and other substances have poisoned soils in much of Poland, Germany, Hungary, and southern Sweden. In the United States, the U.S. Department of Agriculture estimates that a quarter of the nation's croplands have been depleted through deep plowing, removal of crop residue, conversion to permanent pasture, and other conventional agricultural practices. Although unwise management practices contribute significantly to soil degradation, soil degradation also involves three natural soil processes: physical, chemical, and biological degradation.

Physical Degradation

Physical soil degradation involves deterioration in soil structure, leading to compaction, crusting, accelerated erosion, reduced water-holding capacity, and decreased aeration. Soil *compaction* is the compression of soil particles into a smaller volume. Excessively compacted soil suffers from poor aeration and reduced gas exchange, which can restrict the depth of root penetration. Soil compaction also causes accelerated runoff and erosion of soils.

Crusting is the formation of a hard layer a few millimeters or a few tens of millimeters thick at the soil surface. Crusts affect drainage, leading to waterlogging at the soil surface and to salinity or alkalinity problems. Once crusts called *duricrusts* form, soil moisture recharge declines, and vegetation cannot root. Sheet and gully erosion increases as the land fails to absorb precipitation. Hard layers can also form below the cultivation depth and are called *hard pans* (other names are plow soles, traffic pans, and plow pans). These compacted layers can restrict root growth, making crops and trees vulnerable to drought and lodging (falling over).

Chemical Degradation

Chemical degradation comprises changes in soil's chemical properties that regulate nutrient availability. *Nutrient depletion* is the major factor in chemical soil degradation. Soil nutrient depletion may be caused or exacerbated by many factors, including *monocropping*, leaching of nutrients, and salt buildup.

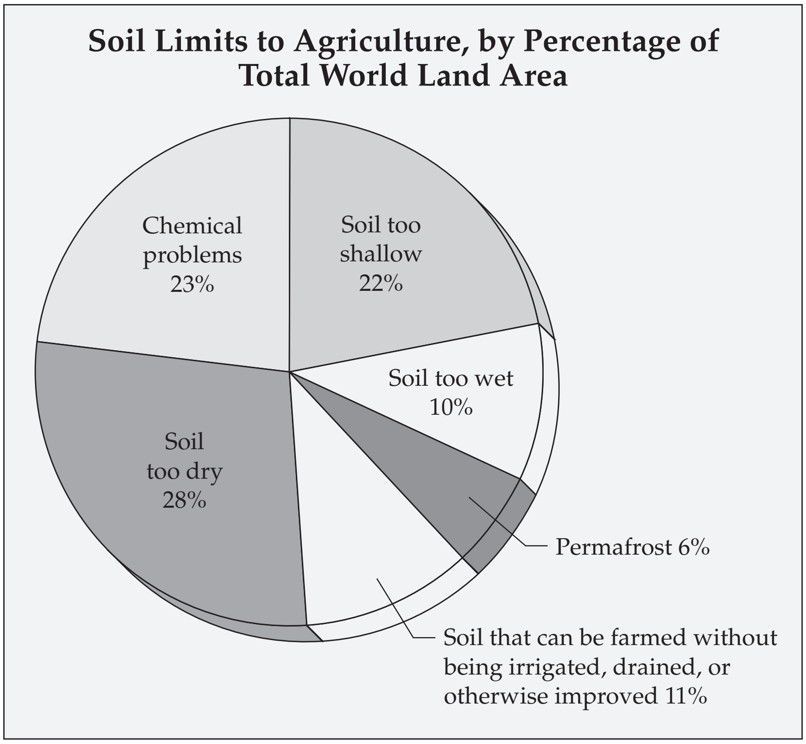
A historic example of nutrient depletion is the depletion of soils in the southeastern United States by the growing of cotton. As late as 1950, "King Cotton" was the most valuable farm commodity produced in Alabama, Arkansas, Georgia, Louisiana, Mississippi, South Carolina, Tennessee, and Texas. In the eighteenth and nineteenth centuries, the growing of cotton ruined soil fertility as it spread westward from the Atlantic to the Texas panhandle. Cotton growth without regard to topography in hilly regions contributed to soil erosion. Topsoil was eventually removed from many fields, which further depleted nutrients. One reason that peanuts became a major crop in the South is that they are *nitrogen-fixing* plants that can grow in soils depleted of nitrogen by cotton.

Nutrient *leaching* is another problem. Continuous irrigation can leach nutrients and cause salt buildup in soils where drainage is poor. Leaching can move essential but soluble nutrients past the root zone deeper into the soil and into groundwater. In addition, the water used to irrigate soil often contains salts that can accumulate to toxic levels and inhibit plant growth where evaporation occurs readily. Thick crusts of salt on farmland in Pakistan, Australia, Ethiopia, Sudan, and Egypt have made soil unfit for crops.

Laterization refers to the product and process of wetting and drying that leads to the irreversible consolidation and hardening of aluminum and iron-rich clays into hard pans, sometimes of great thickness, called *plinthitic materials* (Greek *plinthos* means "brick"). Laterization is particularly common in the humid and subhumid tropics.

PhotoDisc

Of the total acreage lost to soil degradation, most of the loss is attributable to water and wind erosion resulting from agricultural activities, overgrazing, deforestation, and firewood collection. Soil compaction also causes accelerated runoff and erosion of soils.



Source: United Nations Food and Agriculture Organization (FAOSTAT Database, 2000).

For example, peat soils that are drained decompose rapidly and subside. In drier climates, the loss of organic matter reduces the soil's moisture-holding capacity and lowers soil fertility, which leads to lower crop yields and thus to less organic matter being returned to the soil.

Tropical rain forests such as those of the Amazon basin in South America seem lush, so people widely assume tropical soils to be fertile and high in organic matter. Although tropical forests do produce considerable organic matter, the amount that stays in the soil is surprisingly small, and the soils actually have low nutrient levels. Soil microorganisms in the rain forest break down the organic matter and release nutrients that are absorbed by growing plants. However, warm temperatures and high rainfall cause accelerated nutrient loss if plants are absent. Nutrients that would buffer the pH of the soil are lost. Consequently, the clearing of rain forests exposes the soil to erosion, leaching, acidification, and rapid nutrient depletion.

Biological Degradation

The loss of organic matter and soil nutrients needed by plants can occur in any environment, but it is most dramatic in hot, dry regions. Organic matter is important in maintaining soil structure, supporting microorganisms, and retaining plant nutrients. Because organic matter is near the soil surface, it is generally the first soil component to be lost. Organic matter may be lost through brush fires, stubble-burning, overgrazing, or the removal of crops, fodder, wood, and dung. Loss of organic matter can be accelerated when soil moisture is reduced, when soil aeration is increased, or both.

J. Bradshaw-Rouse

See also: Agronomy; Composting; Deforestation; Erosion and erosion control; Fertilizers; Grazing and overgrazing; Herbicides; Hydroponics; Monoculture; Nutrients; Pesticides; Slash-and-burn agriculture; Soil; Soil conservation; Soil contamination; Soil management; Soil salinization.

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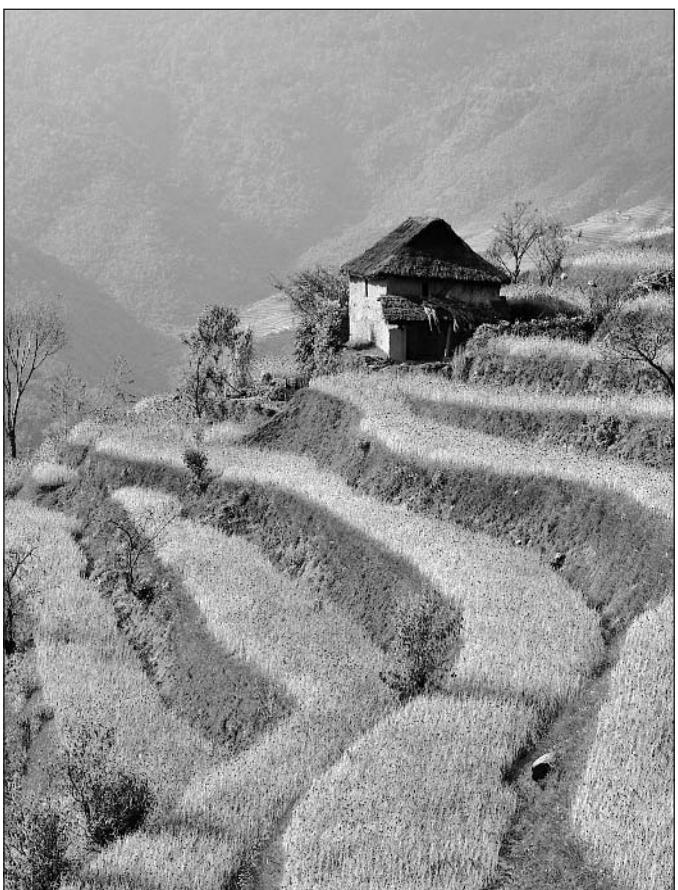
SOIL MANAGEMENT

Categories: Agriculture; disciplines; environmental issues; soil

Tillage, conservation, and cropping practices are soil management techniques that are used to preserve soil resources while optimizing soil use.

Soils are managed differently depending on their intended use. Soil management groups are soil types with similar adaptations or management requirements for specific purposes, such as use with crops or cropping rotations, drainage, fertilization, forestry, highway engineering, and construction. In managing soil for agriculture, soil management includes all tillage and planting operations, cropping practices, fertilization, liming, irrigation, herbicide and insecticide application, and other treatments conducted on or applied to the soil surface for the production of plants.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Soil management extends to the way in which soils are manipulated. Terraces, for example, are raised horizontal strips of earth constructed along the contour of a hill to slow the movement of downward-flowing water.

Tillage

The most basic aspect of soil management is the way in which it is cultivated or tilled for crop growth. *Tillage* is the mechanical manipulation of the soil profile to modify soil conditions, manage crop residues or weeds, or incorporate chemicals for crop production. Tillage can be exhaustive or minimal. Conventional tillage uses multiple tillage operations to bury existing crop residue and prepare a uniform, weed-free seed bed for planting. This method breaks up soil aggregates in the process and destroys soil structure. Consequently, it can result in excessive wind and water erosion.

Conservation tillage, or minimum tillage, involves soil management practices that leave much more crop residue on the soil surface and cause much less soil disruption. As a result, the soil is less susceptible to erosion, and the plant residue acts as a mulch to protect the soil surface from the destructive impact of rainfall as well as to reduce evaporation.

No-tillage, or chemical tillage, is a soil management practice adapted to sloping soils in which herbicides rather than tillage are used to control weeds, while the disruption of soil structure is limited to a narrow slit in the soil surface in which the seeds are planted.

Hillsides and Wetlands

Soil management extends to the way in which soils are manipulated. *Terraces*, for example, are raised horizontal strips of earth constructed along the contour of a hill to slow the movement of downward-flowing water. Tile drains are perforated ceramic or plastic pipes buried in poorly drained soils that act as underground channels to carry water away, lower the water table, and allow a soil to drain faster after rainfall. The benefit of managing potentially erodible soils on hill slopes as permanent pastures is being recognized as another way of managing hillside soils.

Likewise, the value of retaining wet soils as *wetlands* has been acknowledged. Wetlands provide wildlife habitat, assist in flood control, and act as buffers to protect surface waterways from nutrient and soil runoff from cultivated fields.

Chemical Management

Soil management also involves the addition of chemicals to soil: lime to make acid soils more neutral, fertilizers to increase the nutrient level, herbicides and insecticides to control weed and insect pests, soil conditioners to improve soil aggregation, structure, and permeability. A growing technology is the use of mobile global positioning system (GPS) units attached to the equipment that applies these chemicals to soil. Called *site-specific management*, it uses computer technology to regulate chemical addition based on the exact position in a field and previous yield or fertility maps that indicate whether the soil needs to be amended. The goal of site-specific management is to optimize chemical use and profit while minimizing potential chemical loss to other environments by only applying the chemicals to areas where they are needed.

J. Bradshaw-Rouse

See also: Agronomy; Composting; Fertilizers; Hydroponics; Nutrients; Soil; Soil conservation; Soil contamination; Soil degradation; Soil salinization; Sustainable agriculture.

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SOIL SALINIZATION

Categories: Agriculture; environmental issues; pollution

Soil salinization is a process in which water-soluble salts build up in the root zones of plants, blocking the movement of water and nutrients into plant tissues.

Soil salinization rarely occurs naturally. It becomes an environmental problem when it occurs as a result of human activity, denuding once-vegetated areas of all plant life. Rainwater is virtually free of dissolved solids, but surface waters and underground waters (*groundwater*) contain significant quantities of dissolved solids, ultimately produced by the weathering of rocks. *Evaporation* of water at the land surface results in an increase in dissolved solids that may adversely affect the ability of plant roots to absorb water and nutrients.

Arid Climates

In arid regions, evaporation of soil water potentially exceeds rainfall. Shallow wetting of the soil followed by surface evaporation lifts the available dissolved solids to near the surface of the soil. The near-surface soil therefore becomes richer in soluble salts. In natural arid areas, soluble salts in the subsurface are limited in quantity because rock weathering is an extremely slow process. Degrees of soil salinization detrimental to plants are uncommon.

Irrigating arid climate soils with surface or groundwater provides a constant new supply of soluble salt. As the irrigation water evaporates and moves through plants to the atmosphere, the dissolved solid content of the soil water increases. Eventually, the increase in soil salt will inhibit or stop plant growth. It is therefore necessary to apply much more water to the fields than required for plant growth to flush salts away from the plant root zone. If the excess water drains easily to the groundwater zone, the groundwater becomes enriched in dissolved solids, which may be detrimental.

If the groundwater table is near the surface, or if there are impermeable soil zones close to the surface, *overirrigation* will not alleviate the problem of soil salinization. This condition requires the installation of subsurface drains that carry the excess soil water and salts to a surface outlet. The problem with this method is that disposing of the salty drain water is difficult. If the drain water is released into surface streams, it degrades the quality of the stream water, adversely affecting downstream users. If the water is discharged into evaporation ponds, it has the potential to seep into the groundwater zone or produce a dangerously contaminated body of surface water, as occurred at the Kesterson Wildlife Refuge in California, where concentrations of the trace element selenium rose to levels that interfered with the reproduction of resident birds.

Robert E. Carver

See also: Agronomy; Composting; Deserts; Halophytes; Hydroponics; Nutrients; Soil; Soil conservation; Soil contamination; Soil degradation; Soil management.

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SOUTH AMERICAN AGRICULTURE

Categories: Agriculture; economic botany and plant uses; food; world regions

Increasing urbanization in South America raises questions regarding use of both land that is farmed and land that is abandoned.

In South America as elsewhere, landforms, soil, water, climate, and culture interact to produce an arrangement of agricultural production specific to the region. South America can be divided into six general landform regions: the Andes Mountains, the plateaus of the interior of the continent, the river lowlands, the coastal lowlands, the *tierra templada*, and the *tierra fria*.

Andes Mountains

The Andes Cordillera reaches from Venezuela in the north to Tierra del Fuego at the south tip of the continent. Some Andean peaks exceed 20,000 feet (6,100 meters) in height. The mountain soils are rocky and steeply graded. This makes farming difficult but not impossible. Farmers use terrace systems, building up steplike fields carved into the side of a mountain. Because of the limitations of the soils and the difficulty in farming them, the region supports only subsistence agricultural settlements. People in the highlands grow small plots of corn, barley, and especially potatoes on the high-altitude soils.

Highland Growing Regions

In the central eastern region of Brazil are the Brazilian Highlands. To the north of the Amazon basin lies another plateau region called the Guiana Highlands. Both plateaus, which are not much higher than 9,000 feet (2,743 meters), are old geologic structures with relatively rough surfaces to farm. The Brazilian Highlands constitute the world's primary coffee-growing region. More than one-third of the world's coffee is grown there, along with soybeans and oranges. The Guiana Highlands, which stretch through southern Venezuela and Guyana, are covered in savannas (grasslands with trees and shrubs). People there use slash-and-burn agriculture to grow corn and rice.

River Lowlands

Some of the most remote regions in South America are its fastest-developing areas. The northern interior of Brazil in the Amazon basin is covered with the world's largest tropical rain forest, the size of the forty-eight contiguous United States. Within some areas of this rich habitat, gold and huge iron ore deposits have been discovered. Development programs have encouraged mining, hydroelectric projects, ranching, and farming there. This has produced a need for clearing the forests and caused a large migration of people into this otherwise remote, isolated region. It has been estimated that 30,000 square miles (78,000 square kilometers) of tropical rain forest were destroyed annually in the 1990's.

The rain forest is not a highly productive growing region for crops. Soils there are thin and have few nutrients. To grow crops and grasses for cattle, *slash-and-burn agriculture* is practiced. Trees and brush on the land are cut down and burned, and the ashes enrich the soils for a time. This allows for limited production of crops such as corn and rice, but after about three years the nutrients are washed out of the soil by the heavy tropical rains. Farmers and ranchers move on and find new forest area to cut, and the cycle goes on. Rain forests cover only about 5 percent of the total land area of the earth but contain more than half the different types of plants and animals on earth. These forests provide lumber products, medicines, and food.

The Orinoco River drains the Guiana Highlands and the *llanos* region of Venezuela, flowing into the Atlantic Ocean. The *llanos* form a large, expansive plain of grassland between the Andes in Venezuela and the Guiana Highlands. Soils are flooded in this area during the rainy seasons, providing for rich grass development and the support of large cattle ranches.

Selected Agricultural Products of South America

The Amazon River drains the north and western region of Brazil. Although more water moves through the Amazon River than any other river in the world, its location in dense tropical forests under a humid tropical climate makes agriculture there a challenge. Amerindians of the region practice subsistence agriculture, growing yams and bananas and raising some small animals. Cassava, or manioc (a root crop from which tapioca is made) and sugarcane are also grown there in slash-and-burn fashion.

The Paraná, Paraguay, and Uruguay Rivers, south of the Amazon lowlands, dissect a great grassland region known as the Pampas and a forested region known as the Gran Chaco, which extends to northern Argentina. The Pampas is not unlike the Midwest of North America. It is a huge grassy plain nearly 400 miles (640 kilometers) long in the central part of Argentina. Agriculture is the primary industry in Argentina and encompasses 60 percent of the country's land. Large *estancia* (cattle ranches) are common in the region. The soils are well suited to wheat and other grains as well as alfalfa, a grass grown for cattle and horse feed. The level character of the land makes it easy to work, but it is difficult to drain and is prone to flooding.

Paraguay's agricultural zones are divided by the Paraguay River. Tobacco, rice, and sugarcane grow to the east of the river in the more humid climates. To the west, in the drier climates and the Chaco region, is the unique growing area of the Quebracho Forest. Quebracho is a hardwood that grows only in the Chaco. The wood contains tannin, which is used to produce tannic acid, a chemical used for tanning leather. This area is suited for cattle, but because of its rocky and steep topography, the population of goats and sheep rises as one moves farther west toward the Andes. Irrigated with mountain streams from the eastern slopes of the Andes, grapes also grow well and are made into wine.

Coastal Lowlands

The coastal lowlands, up to an altitude of about 2,500 feet (750 meters), encompass an area known as the hot land (*tierra caliente*). Temperatures there average between 75 and 80 degrees Fahrenheit (22 and 24 degrees Celsius), and plantation agriculture abounds. Plantations are huge commercial farming operations that grow large quantities of crops that are usually sold for export. Because of their easy access to port facilities, coastal lowlands historically have been linked with the markets of Europe and North America.

The banana is one of the best-known examples of a plantation crop. It grows well in the wet, hot climate of this zone and has been cultivated there for U.S. and European markets since 1866. In the 1990's, more bananas were traded on the international fruit market than any other commodity. In South America, Ecuador and Brazil are the leading banana producers, with Colombia third. Cacao, the

PhotoDisc

Farmers sell local produce at a market in Ecuador.

bean pods from which cocoa and chocolate are made, is also grown on plantations in this zone. The largest producing area for cacao is Ghana in West Africa, but Brazil and Ecuador are fifth and sixth in world yearly production.

Although sugarcane is grown in almost every country in South America, it does well as a plantation crop in the lowlands of eastern Brazil, the world's largest exporter. There the crop is not used just to produce sugar but also to produce ethanol for gasohol, an alcohol-based gasoline that fuels more than half the automobiles in Brazil. This type of commercial agriculture has made agricultural business the fastest-growing part of the Brazilian economy. Yams, cassava, and other root crops used as staple foods also grow well in this humid, hot climate.

Tierra Templada

Just above the *calienta* zone lies a zone of cooler temperatures, the *tierra templada*, that extends to about 6,000 feet (1,850 meters). Temperatures there range from 65 to 75 degrees (17 to 22 degrees Celsius), and the commercial crop that dominates the landscape is coffee. It is grown on large plantations called *fazendas*. Brazil, the largest South American coffee producer, exports about one-quarter of the world's coffee, producing nearly forty million bags of about 132 pounds each (60 kilograms) annually. Colombia is South America's second-largest coffee producer. Coffee was once the leading export from Colombia, but as a result of a coffee-worm infestation and lower world prices, other products are taking the lead.

Other commercial crops from this zone include fresh fruit. In the central valley of Chile, grape vineyards and apple orchards have emerged. Produce from this region enters stores in the United States and elsewhere as the growing seasons of the domestic products are finishing up. Chilean grapes, apples, peaches, and plums are now sold worldwide. Corn and wheat are also grown in this zone. These staple foods are produced for local consumption and sold only at local markets.

Tierra Fria

A cooler climate, the *tierra fria*, extends from 6,000 feet (1,850 meters) to about 15,000 feet (4,570 meters). Average temperatures there range from 55 to 64 degrees Fahrenheit (12 to 17 degrees Celsius). This zone extends throughout the Andes and can maintain only that plant life that can withstand the limited soils and the cold conditions. In this region of subsistence-type farming, crops and animals are grown and raised mostly for family use.

In the lower reaches of this zone, barley grows well because it requires a short growing season. In the cooler portions of this zone, the potato began. A tuber, the potato can flourish in cold conditions with moderate moisture. The loose soils of this zone are perfect for its production, but it requires a considerable amount of cultivation. Although the potato is used throughout South America, potato production for the continent constitutes only about 5 percent of the world total production. Alpacas, a type of goat, and llamas are also raised there.

M. Mustoe

See also: Central American agriculture; Corn; Ethanol; Grains; Grasslands; Rain-forest biomes; Rain forests and the atmosphere; Rangeland; Rice; Savannas and deciduous tropical forests; South American flora; Wheat.

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SOUTH AMERICAN FLORA

Category: World regions

South America is the most diverse continent in terms of flora, primarily because of its location and geography.

South America's floristic diversity is increased by its high mountains, especially the Andes Mountains, which extend from north to south along the western part of the continent for much of its length. South America has such diverse biomes as tropical *rain forests*, tropical *savannas*, extremely dry deserts, temperate forests, and alpine *tundra*. The largest of these biomes are deserts, savanna, and tropical forest. With the rapid rate of deforestation in places like the Amazon basin, some plants may become extinct before being cataloged, let alone studied.

The *subtropical* desert biome is the driest biome in South America and is considered the driest desert in the world, with an average annual precipitation of less than 0.25 inch (4 millimeters). The desert biome is restricted primarily to the west coast of South America from less than 10 degrees south of the equator to approximately 30 degrees south. Dry conditions prevail from the coast to relatively high elevations in the Andes. The Atacama Desert, in northern Chile, and the Patagonian desert, in central Chile, are the most notable South American deserts. Smaller desert regions also occur in the rain shadow portions of the Andes.

Next on the moisture scale are the *savanna* biomes. Savanna occurs in two distinctly different areas of South America. The largest savanna region includes three distinctive regions: the cerrado; the Pantanal; and farther south, in southern Brazil, Uruguay, and northern Argentina, the grassland called the Pampas. The other savanna region, the *llanos*, is found in lower-elevation areas of Venezuela and Colombia.

Although a few of the forests in South America are dry, most are rain forests, receiving annual precipitation from 79 inches to 118 inches (2,000-3,000 millimeters). The Amazon rain forest, the world's largest, accounts for more than three-fourths of the rain-forest area in South America. One of the most species-rich areas of the world, it is being rapidly destroyed by logging, ranching, and other human activities. Smaller rain forests are located along the southeastern coast of Brazil and in the northern part of Venezuela.

Covering much smaller areas are a small *mediterranean* region in central Chile characterized by cool, wet winters and warm, dry summers. In the far south of Chile and Argentina is a small area of temperate forest, becoming alpine tundra in the far south. Temperatures are relatively cool and mild year-round (except in the far south, where it can be extremely cold in the winter.

Plants of the Subtropical Desert

In the Atacama Desert, one of the world's driest, some moisture is available, but it is limited to certain zones. Coastal regions below 3,280 feet (1,000 meters) receive regular fog (called *camanchacas*). Rainfall is so low in the Atacama Desert that even cacti (which normally store water) can hardly acquire enough water from rainfall alone, so many plants, including *bromeliads*, receive a portion of their water from the fog. At midelevation areas there is no regular fog; thus, there is almost no plant cover. At higher elevations, the rising air has cooled sufficiently to produce moderate amounts of rainfall, although the vegetation is still desertlike. Shrubs typically grow near streambeds, where their roots can reach a permanent source of water.

The Atacama Desert often appears barren, but when a good dose of moisture becomes available *ephemerals* change its appearance, seemingly over-

PhotoDisc

An aerial view of the rain forest in Guyana. In addition to rain forests, South America is home to flora of such diverse biomes as tropical savannas, extremely dry deserts, temperate forests, and alpine tundra.

night. Ephemerals are typically annuals that remain dormant in the dry soil as seeds. When moisture increases, they quickly germinate, grow, flower, and set seed before dry conditions prevail again. In the days and weeks following a good rain, many grasses appear and provide a backdrop for endless varieties of showy flowers, many endemic to (found only in the region of) the Atacama Desert. Among the showier flowers are species of *Alstroemeria* (commonly called irises, although they are actually in the lily family) and *Nolana* (called pansies, although they are members of a family found only in Chile and Peru).

Conditions in the Patagonian desert are less harsh. The vegetation ranges from tussock grasslands near the Andes to more of a shrub-steppe community farther east. Needlegrass is especially abundant throughout Patagonia, and cacti are a common sight. In the shrub-steppe community in the eastern Patagonian desert, the shrubs *quilembai* and the cushionlike *colapiche* are common. Where the soil is salty, saltbush and other salt-tolerant shrubs grow.

Plants of the Tropical Savanna Biome

The cerrado region of east central Brazil and southward is not only the largest savanna biome of South America but also one of the most romanticized of the world's savannas. As in the Old West of North America, the grasslands of Brazil have cowboys who traditionally have used the cerrado for farming and cattle ranching. With ever-increasing pressure from agriculture, the cerrado is now under attack in various ways. Extensive fertilization, associated with modern agriculture, planting of trees for timber production, and the introduction of foreign species, especially African grasses, have all begun to change the cerrado. Frequent fires also have taken their toll. The cerrado contains more than ten thousand species of plants, with 44 percent of them endemic. As much as 75 percent of the cerrado has been lost since 1965, and what remains is fragmented. A number of conservation groups are trying to save as much as possible of what remains.

Two other savanna regions farther south are the Pantanal and the Pampas. Although the Pantanal is a savanna, during the rainy season it becomes a *wetland* and is a haven for aquatic plants. Later, the Pantanal dries out and grasslands appear in place of the water. This unique area is under attack by a variety of human activities, including navigation and artificial drainage projects, mining, agriculture, and urban waste.

The Pampas, like the great prairies that once covered central North America, is composed almost solely of grass. Trees and shrubs grow near bodies of water, but everywhere else grass predominates. Cattle ranching and wheat and corn farming are the primary occupations of the area and are thus the primary threat. Because the area is farther south than the Pantanal, it has a more temperate climate. Pampas grass from this area has been exported as an ornamental plant.

The last major savanna region is the *llanos*, located at lower elevations in the drainage area of the Orinoco River in Venezuela and Colombia. This area has pronounced wet and dry seasons. At the lowest elevations, treeless grasslands persist after the water from the rainy season subsides. On the higher plains is a scattering of smaller trees. The mauritia palm can also be found here in poorly drained areas.

Plants of the Tropical Forest Biome

The Amazon rain forest is the largest contiguous rain forest in the world. It is so large and so lush with tree growth that its *transpiration* is actually responsible, in part, for the wet climate of the region. Plant diversity is so great here that no comprehensive plant guide currently exists for many parts of the Amazon rain forest. Of tens of thousands of plant species, a large number have never been described.

This one-of-a-kind botanical treasure is being destroyed at a rapid pace of between 5,000 and 10,000 square miles (13,000-26,000 square kilometers) per year. The causes for this destruction are primarily logging, agriculture, and cattle ranching. A common practice for preparing an area for cattle ranching or farming has been to simply burn the forest, not even necessarily logging it first, and then to allow the grass and other vegetation or crops grow in its place. The soils of the rain forest are so poor, however, that this practice usually depletes the soil within a few years, and the land becomes a useless wasteland. Mining and oil drilling have also taken their toll.

The Amazon rain forest is an extremely complex biome. The main plant biomass is composed of trees, which form a closed canopy that prevents much of the sunlight from reaching the forest floor. Consequently, the forest floor has little herbaceous growth, and most smaller plants tend to grow as *epiphytes* on the branches and trunks of trees. Common epiphytes in the Amazon rain forest include orchids, bromeliads, and even some cacti. There is a large diversity of bromeliads, ranging from small, inconspicuous species to larger species, such as tank bromeliads that can collect significant amounts of water in their central whorl of leaves. The water in these plants can contain a whole miniature ecosystem, complete with mosquito larvae, aquatic insects, and frogs. Ferns are another significant member of the epiphyte community. Some larger species of ferns, often called tree ferns, also grow in the understory. Lianas, or vines, are a prominent component as well.

The trees that form the canopy are stratified into three fairly discrete levels. The lowest two levels are the most crowded, and the highest level comprises extremely tall trees, often referred to as *emergent trees* because they stand out randomly above the fairly continuous lower two layers. Many of the tallest trees are buttressed at the base, an adaptation that seems to give them greater stability. Beneath the canopy, there are some smaller palms, shrubs, and ferns, but they only occur densely where there is a break in the canopy that allows in greater light.

Some rain-forest species of trees are well known, primarily because of their economic value. A favorite tree for use in furniture is the mahogany. Because its wood is highly prized, many species of mahogany are becoming rare or extinct. The South American rain forests are also the original source of rubber. Brazil had a monopoly on rubber until seeds were smuggled out and planted in Malaysia. Synthetic rubber has now replaced natural rubber for many applications. Another popular tree is the Brazil nut tree, an abundant food source that has been exploited by suppliers of mixed nuts. The native cacao tree produces fruits from which cacao beans are extracted, then processed to make chocolate.

Every year during the rainy season, the lowest elevation areas of the Amazon rain forest are flooded with several feet of water, which recedes after a few months. The trees flourish in this flooding cycle. A few even have unique adaptations, such as producing fruits that are eaten by fish, thus assuring the spread of their seeds. The flooding can be so extensive in some areas that the water reaches the lower parts of the canopy.

Coastal tropical rain forests also occur in northwestern and southeastern South America. There are a high number of endemic species in each of these forests. Some tree species are so rare that they may be found in an area of only a few square miles and nowhere else. Where the tropical rain forest meets the ocean, mangrove trees have become adapted to the tidal environment. Mangroves have prop roots, which make the trees look like they are growing on stilts. They also frequently have special root structures that extend above the water at high tide and allow the roots to breathe. Mangrove trees are also extremely salt-tolerant.

Plants of the Mediterranean and Temperate Forest Biomes

One of the world's five mediterranean climate regions is found in central Chile. This climate is characterized by warm, dry summers and cool, wet winters. The vegetation, called *matorral*, is composed primarily of leathery-leaved, evergreen shrubs that are well adapted to the long summer drought. The matorral is the only mediterranean area that has bromeliads. At lower elevation areas, somewhat inland, many of the shrubs are drought-deciduous; that is, they drop their leaves in the summer. In more inland parts of this biome, the espino tree is common.

Because South America extends so far south, it actually has a small region containing temperate forests. These forests range from temperate rain forest to drier temperate forest, and in all cases are typically dominated by southern beeches. The undergrowth is dominated by small evergreen trees and shrubs. Fuchsias, which are valued the world over for their showy flowers, are common in the undergrowth. Although not rich in species, the temperate rain forests of southern South America can be lush. In the far south, before the extreme climate restricts the vegetation to alpine tundra, a region of elfin woodlands predominates. These woodlands can be nearly impenetrable, with the densest growth often associated with patches of tall bamboo.

Bryan Ness

See also: Deforestation; Deserts; Grasslands; Logging and clear-cutting; Mediterranean scrub; Rainforest biomes; Rain forests and the atmosphere; Rangeland; Rice; Savannas and deciduous tropical forests; South American agriculture; Sustainable forestry.

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SPECIES AND SPECIATION

Categories: Classification and systematics; ecology; evolution

A species is any group of organisms recognized as distinct, with members able to interbreed with one another and produce fertile offspring. Speciation is the evolutionary process whereby a species comes into existence.

Species are distinct kinds of organisms, in that the organism can be recognized as different from other kinds of similar organisms by a combination of characteristic shapes, sizes, behaviors, physiology, or other attributes. For instance, white oaks can be recognized as different from other oak species by growth form and habitat, along with a combination of leaf, fruit, and bark characteristics. To be useful as a diagnostic feature, a characteristic must lend itself to measurement and remain relatively constant generation to generation. Such a hereditary pattern implies that members of a species share a common pool of genetic information.

Although most field guides and keys for species identification are based largely on measurable morphological traits, the *biological species concept*, attributed to Ernst Mayr in the 1940's, defines species as groups of interbreeding populations reproductively isolated from other such groups. Sometimes a greater range of variation can be observed in large, dispersed populations than is found between similar but reproductively isolated species. What, then, determines when a species is formed?

Unfortunately there is no clear-cut answer. Investigators may use different criteria or assign variable levels of importance to characteristics; therefore, a population of plants may be assigned species status by one expert and varietal status by another. While this is confusing to those searching for a name, the problem is indicative of the dynamic and changing nature of life. Because evolution is an ongoing process, some groups of plants are expected to be in transition.

The processes that contribute to variation in large, sexually reproducing populations also are responsible for the origin of species. Isolation and selection of genetically based variation are the only additional requirements. Speciation generally is conceived to involve the separation, isolation, and divergence of a genetic pool of information. Plants that share a common pool of genetic information are split into two pools that remain isolated until identifiable genetic differences accumulate. Classifying a segment of this pool as a species requires recognition of significant genetic differences and the relative isolation of the population.

Allopatric Speciation

The physical separation of a gene pool into populations that are geographically or spatially isolated is termed *allopatric speciation*. The physical separation could be the result of continental drift, uplift or subsidence of landmasses, glaciers, flooding, or radical dispersal of population members. Dispersal of a few fertile population members to an isolated island is a good example. The resulting gene pool, although small, is immediately isolated. For example, if the fruiting inflorescence of a common grass were transported on the struts of an airplane to a small, isolated island, any plants resulting from germination of those seeds would represent a new population, now isolated from the parent population on the distant landmass where the seeds originated. A drastic change in gene frequency could, and likely would, result: A gene present in one out of one thousand in the original population might, in the new, isolated location and within the smaller gene pool, increase in frequency from 0.05 percent to 25 percent if present in one of two plants forming the invading population. This sudden change in frequency is referred to as the *founder's effect*. When such a population is introduced into a new environment, it may rapidly change and give rise to a number of additional new species. The latter process is known as *adaptive radiation* and is credited for the assemblage of unique species often found in isolated areas.

Sympatric Speciation

It is possible for segments of a parent gene pool to diverge without spatial separation, ultimately becoming reproductively isolated. This process is termed *sympatric speciation*. Examples of situations that may lead to sympatric speciation include disruption of pollination that could result from different flowering times among members of a population. Such differences could be caused by variation in soil, moisture, or exposure. One example of this process is associated with the genus *Achillea*, or milfoil. In the late 1940's, investigators separated clumps of two species of milfoil to produce genetically identical clones that were subsequently transplanted to different elevations in the Sierra Nevada. Plants grown during this process exhibited a wide range of morphological variation. Not only did they look different; they flowered at different times. Thus, even genetically identical individuals of one species can be reproductively isolated if the timing of flowering precludes visitation by a common pollinator.

Polyploidy

Genetic variation can occur rapidly through an increase in chromosome number. Although recombination of genes brought about by sexual reproduction provides the greatest amount of the observable variation in a population, abrupt and large-scale change is also associated with a process called *polyploidy*. Through polyploidy, a plant can have its entire set of chromosomes multiplied. If the increase in chromosome number is brought about when chromosomes fail to separate after they duplicate during meiosis, an individual's number of chromosomes may double. That process is known as *autopolyploidy*. An increase in chromosome number associated with hybridization resulting from combination of two separate sets of chromosomes is termed *allopolyploidy*. Although typically sterile, an allopolyploid may duplicate its combined set of chromosomes, resulting in a fertile autoallopolyploid.

Although polyploidy occurs naturally in many plants, the results so frequently are associated with desirable changes in the bloom of ornamentals that polyploidy is often deliberately induced by chemical treatment. It is estimated that one-half or more of all flowering plant species may have arisen through some form of polyploidy.

Hybridization

Offspring produced from the interbreeding of related species, *hybridization*, may be either sterile or fertile. If the offspring are sterile, the genetic pools of parental species are not altered, because genes are not able to flow between the two. If the offspring are fertile, as are hybrids of crosses between North American and European species of sycamores, interbreeding among fertile hybrids and parent populations can provide a bridge for the merging of genetic information. With time, the flow of such genetic material can lead to an increase in variation, a decrease in interspecific differences, and an interesting taxonomic problem as to when the two parent species should be reclassified as one. Currently geographic isolation maintains the genetic integrity of these parental species.

Recombination Speciation

Although the original source of variation is permanent change in DNA (mutation), *recombination* of genetic material through sexual reproduction accounts for the vast majority of variation between generations. The result of this variation, acted upon by natural selection, leads to changes in the frequencies of genes within a population. The latter is often stated as a definition of evolution. Rapid selection of recombinants has been proposed as the method of speciation by which the anomalous sunflower, *Helianthus anomalus*, was produced from hybrids of two other species of sunflower, *Helianthus annulus* and *Helianthus petiolaris*. Studies, in fact, have duplicated the proposed process. After several generations of natural selective pressure, experimentally produced hybrids of *Helianthus annulus* and *Helianthus petiolaris* were demonstrated to be the genetic equivalents of naturally occurring *Helianthus anomalus*.

Sterile Hybrids

Plant hybrids often are sterile because newly combined hereditary material is so different that chromosomes will not pair during meiosis. Viable gametes, therefore, are not produced. This apparent genetic blind alley does not always translate into a lack of evolutionary success, however. Many sterile hybrids demonstrate an ability to reproduce *apomictically*, meaning they reproduce vegetatively rather than sexually. Species of blackberry, aspen, and many grasses reproduce by apomictic methods. Some, like dandelion, may have populations that are fertile and populations of infertile hybrids that produce seed with embryos that were produced asexually. Apomixis obviously does not promote variation, but it may permit expansion of populations where there is little chance for cross-pollination, as in areas of high disturbance or environmental stress.

Reproductive Isolation

Once a gene pool has separated and diverged into populations identifiable as separate species by genetic or morphological traits, the resulting segments of the pool must remain separated. As long as they are separate and distinct, populations can be labeled as separate species.

Barriers that prevent the flow of hereditary material may be classed as prezygotic or postzygotic. *Prezygotic mechanisms* prevent successful fertilization and include geographic isolation, temporal isolation (flowering at different times), mechanical isolation (flowers structurally different), and incompatible gametes. *Postzygotic mechanisms* prevent production of fertile adults and include hybrid inviability (offspring that do not live to sexual maturity), hybrid sterility, and offspring of hybrids that are weak.

John F. Logue

See also: Adaptations; Angiosperm evolution; Coevolution; Evolution: convergent and divergent; Evolution: gradualism vs. punctuated equilibrium; Evolution of plants; Gene flow; Genetic drift; Genetics: mutations; Hybrid zones; Hybridization; Nonrandom mating; Population genetics; Reproductive isolating mechanisms; Selection; Systematics and taxonomy; Systematics: overview.

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SPERMATOPHYTA

Categories: *Plantae*; taxonomic groups

The Spermatophyta *are those members of the* Tracheobionta *that produce seeds. At one time this category was considered to be natural, composed only of closely related groups with homologous seeds. It is now known that seeds evolved many different times during evolutionary history and that different groups of extant seed plants may or may not be closely related to other groups of extinct or extant spermatophytes.*

Scientists once thought that the seed plants were monophyletic, derived from a single common ancestor. It is now known they are polyphyletic, derived from more than one ancestral group. The distinctions can be seen in the variations among seed structures and functions.

Seed Structure

A seed is a complex reproductive structure composed of multiple generations of tissue that develop from an *ovule*. The outer layer of the seed is usually composed of thick-walled cells of the parental sporophyte that form a *seed coat*. Internal to the seed coat is typically a layer of stored food, which may consist of *megagametophyte* tissue or of a unique tissue of a new generation called *endosperm*. At the center of the seed is a new embryonic plant that emerges to become the seedling when the seed germinates. Scientists recognize two basic types of seed plants: gymnosperms and angiosperms. Gymnosperms are plants with "naked seeds." That is, the ovule is exposed to the environment and is not covered by a protective layer. In angiosperms, by contrast, the ovule is contained within a specialized structure, the *carpel*.

The outer layer of a seed, the seed coat, develops from the outer layers of the ovary, the *integument*. The integument is composed of sporophyte tissue of the parent plant. As the integument develops, it forms an enlarging sheath around the central ovule tissue, the *nucellus*. The integument does not completely enclose the nucellus but leaves a small pore, the *micropyle*, through which pollen grains or the pollen tube will move prior to fertilization. A *megaspore mother cell* within the nucellus undergoes meiosis to produce four megaspores. In gymnosperms, only one megaspore is functional, and it develops into a female gametophyte containing archegonia. In angiosperms, one, two, or all four of the megaspore nuclei may contribute to the female gametophyte.

In gymnosperms, a single egg forms within each archegonium. Pollen grains are drawn into the micropyle, and the pollen germinates to form a *pollen tube*. In most gymnosperms, the pollen tube grows through the nucellus until it reaches the archegonium, where the sperm are released to fertilize the egg. The fertilized egg, or *zygote*, grows into an *embryo*, a new sporophyte generation. Meanwhile, the integument enlarges to close the micropyle and hardens to form the seed coat. The remaining tissue of the female gametophyte functions as a store of food to nourish the embryo until the seed germinates. Because multiple archegonia are formed in the female gametophyte, more than one egg may be fertilized within a single ovule, but usually only a single embryo grows to full size.

In angiosperms the entire female gametophyte usually consists of a seven-celled *embryo sac*. Three cells, the egg and two *synergids*, lie near the micropyle. Three cells, the *antipodals*, form on the end opposite the micropyle. The remaining central cell contains two nuclei, the *polar nuclei*. Pollen germinates on the outside of the carpel in a specialized region called the *stigma*. The pollen tube grows down through the carpel tissue toward the ovules and eventually grows into the micropyle and through the nucellus of one ovule until it reaches a synergid. The sperm nuclei are discharged into the synergid cell, which subsequently degenerates. One sperm goes on to fertilize the egg, while the second fertilizes both polar nuclei. The fertilized egg develops into a diploid embryo in a manner similar to that of gymnosperms. The product of the other sperm and the two polar nuclei is a triploid cell, the primary endosperm. The endosperm cell also undergoes mitosis to form a multicellular triploid endosperm tissue, which functions directly as a stored food reserve in monocots. In dicots, the endosperm typically degenerates, and the nutrients are absorbed by the cotyledons of the embryo, which then serve as a food reserve.

Seed Function

Reproduction by means of seeds confers a number of advantages to seed plants for colonizing terrestrial habitats. First, the seed coat provides physical protection from predators and from dehydration. In many cases seeds, protected by the seed coat, pass unharmed through the digestive tracts of animals who have eaten them. In fact, the physical abrasion of chewing and stomach acid action associated with passage through an animal's digestive tract may be necessary to soften the coat and permit seed germination. The seed coat may also promote *dormancy* through chemical inhibition or by limiting water uptake. In this way the seed coat helps the seed survive periods of environmental stress, such as dry or cold seasons during which plant growth cannot occur. During the period of dormancy, seeds can be dispersed to new areas by a number of means, such as lofting through the air, floating on water, or being transported in an animal's digestive tract or on its body.

The seed will *germinate* only when conditions are suitable for growth. Stored food provides a nutrient supply to support early growth of the seedling. Most seeds germinate belowground, where the environment is moister and the temperature more uniform than on the soil surface. Thus early growth occurs before the seedling is exposed to light and is able to photosynthesize. Finally, the typical embryo in the seed has already formed root and shoot primordia, which are ready to function as soon as they absorb water and begin to grow.

Marshall D. Sundberg

See also: Angiosperm evolution; Angiosperm life cycle; Angiosperm plant formation; Angiosperms; Conifers; Cycads and palms; Dormancy; Flower structure; Flower types; Germination and seedling development; Ginkgos; Gnetophytes; Gymnosperms; Plant life spans; Pollination; Reproduction in plants; Roots; Seeds; Stems; *Tracheobionta*.

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SPICES

Categories: Economic botany and plant uses; food

Spices are a group of plant products used to impart flavor to foods. Unlike herbs, spices are generally derived not from the leafy and other green portions of the plant, but rather from the seeds, fruits, flower parts, bark, or rhizomes. Spices are also generally distinguished from herbs by the greater strength, intensity, or pungency of their flavors.

For thousands of years, humans have added spices and herbs to their foods in order to improve taste. Before modern refrigeration and canning, the first signs of spoiling could be masked by adding parts of aromatic plants—spices and herbs. In modern times, spices and herbs are added only to enhance the flavor of foods.

Spices are distinguished from herbs based upon what part of a plant is used and the way it is prepared. Generally spices are flavorings from dried seeds, fruits, or flower parts. A few spices are from dried bark and rhizomes. Spices can be used as intact dried fruits or seeds, but most often they are ground into a powder used in food preparation. Herbs, by contrast, are typically flavorings from leaves or other green parts of plants. Spices are used in a wide variety of dishes, from sweet to savory: desserts, breads, pickles, fruits, meats, and vegetables. Different spices are characteristic of different ethnic and regional cuisines.

In the late twentieth century, with the rise in global communications and travel as well as mass movement of migrant populations, the "typical" spices of North American cuisine increased and became more diverse, particularly in regions where many different cultures came together.

Allspice, from the myrtle family, is prepared from the dried fruit of a West Indian tree, *Pimenta dioica*. Whole allspice is used in preparing pickles and relishes and to flavor meats such as pot roast; the powder is used in cakes, cookies, pies, and mincemeat.

Anise seeds, from the celery family, come from the herbaceous plant anise, *Pimpinella anisum*, from the Mediterranean region. Whole anise seeds are used as flavorings in stews, pot roasts, and some Chinese meat dishes. Crushed or powdered anise seeds are used as flavorings in Italian cookies, cakes, and liqueurs, as well as German breads.

Cardamom, from the ginger family, is prepared from the seed pods of large herbaceous cardamom plants, *Elettaria cardamonum*, native to India. The dried pods are crushed and used in many Indian and African meat and vegetable dishes, in rice dishes, and in Scandinavian breads.

Cinnamon, from the laurel family, is made from the dried bark of several species of small tropical trees in the genus *Cinnamomum*. The bark is cut into 3- or 4-inch lengths and is permitted to curl. These dried "cinnamon sticks" often flavor hot cider and other beverages as well as meat stocks. Ground cinnamon is widely used to flavor cookies, pies, cakes, sweet rolls, and candies and is added to Mexican meat dishes.

Cloves, from the myrtle family, are the dried, unopened flower buds of a tropical tree, *Eugenia caryophyllata*, possibly native to the Moluccas Islands. The dried buds are ground for use in cookies, gingerbread, pies, and cakes. They are used whole in pickle brines or to flavor ham and other meats.

Coriander, from the celery family, comes from the dried seeds of the herbaceous plant *Coriandrum sativum*, a Mediterranean native. The seeds are used either whole in pickles and preserves or ground in cookies and puddings.

Cumin, from the celery family, comes from the dried seeds of the herbaceous plant *Cuminum cynimum*, also native to the Mediterranean region. Powdered cumin is widely used to flavor stews, fish and meat dishes, curries, and Mexican dishes, and it is one of the main ingredients of commercial chili powder.

Ginger, from the ginger family, is prepared from the thick, underground rhizomes (often called ginger root) of a large perennial, herbaceous plant, *Zingiber officinale*, native to islands of the Pacific. Powdered ginger, from the dried rhizome, is widely used in cookies, gingerbread, and other baked goods. Fresh ginger rhizome is used in many Asian dishes, and sweetened crystallized ginger is used in pickles or is eaten as candy.

Mace and nutmeg, from the *Myristicaceae* family, are two spices that come from the seeds of the nutmeg tree, *Myristica fragrans*, native to the Moluccas Islands. The hard seed has a covering of strips of reddish material; dried and ground, that material is called mace. The rest of the seed becomes nutmeg. Both mace and nutmeg are used in cakes, cookies, pies, and puddings.

Mustard, from the mustard family, comes from the dried seeds of herbaceous mustard plants. *Brassica sinapis* is the most widely used species. Mustard has been used in cooking for a very long time; its native origins are unknown. Ground to a powder, mustard is used in sauces and meat dishes, and whole mustard seeds are used in pickles.

Paprika, from the nightshade family, is a spice prepared from the dried fruits of a sweet pepper, *Capsicum annuum*, a native of Central America. Paprika is used to flavor a variety of meat, vegetable, egg, and cheese dishes.

Black and white pepper, from the pepper tree family, are both produced from the dried fruits (peppercorns) of *Piper nigrum* shrubs, native to India. Black pepper is made by picking and drying the unripe fruits. White pepper is prepared from riper fruits that are soaked in water. After the outer fruit wall is rubbed off, a smooth white seed remains. The dried peppercorns are either ground or shipped whole to be ground at the time of use. Pepper is used in all sorts of meat, cheese, vegetable, and salad dishes.

Red pepper, from the nightshade family, is made into a spice by grinding the dried fruits of any of several species of the genus Capsicum*, native to tropical regions of the Americas. Peppers are used to flavor meat and vegetable dishes characteristic of Mexican, Caribbean, Indian, Chinese, Thai, and many other cuisines.*

Red pepper, from the nightshade family, is a spice made by grinding the dried fruits of any of several species of hot peppers or chilies of the genus *Capsicum*, native to tropical regions of the Americas. *Capsicum frutescens* produces cayenne pepper. Ground or crushed, the peppers are used to flavor meat and vegetable dishes characteristic of Mexican, Caribbean, Indian, Chinese, Thai, and many other cuisines.

Saffron, from the iris family, is the most expensive spice, made from the stigmas of the flowers of a crocus plant, *Crocus saturis*, native to southern Europe and Asia. On top of the female part of the flower, the stigmas consist of three slender filaments; it takes about seventy-five thousand dried stigmas to make one pound of saffron, and each must be picked by hand. Used intact or ground, saffron adds a deep yellow color and a slightly bitter taste to breads, sauces, soups, meat, and rice dishes. Turmeric (Ginger family) is prepared from the dried rhizome of a perennial herbaceous plant, *Curcuma longa*, native to the East Indies. Turmeric gives color and a slightly sweet flavor to pickles, cakes, cookies, salad dressings, sauces and meat dishes.

John P. Shontz

See also: Herbs.

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STEMS

Category: Anatomy

The stem is the part of a vascular plant that supports the leaves and reproductive structures, often at some distance above the ground.

Stems have two chief functions: to support various plant structures and to transport water and nutrients. Most stems support the leaves and reproductive organs at some distance above the ground. Such elevation is important to both leaves, whose function is to trap light energy for *photosynthesis*, and flowers, because being positioned above the ground helps attract *pollinators*. Fruits also benefit from being held aloft because height improves the chances of long-distance seed dispersal.

While being off the ground has advantages for shoot-borne organs, it also has one big disadvantage. These organs are far from their source of water, the soil, and therefore run the risk of drying out unless adequate water can be supplied. Therein lies the second function of stems: to conduct a supply of water from the roots to the organs. Stems also conduct nutrients in both directions between the roots and organs of the plant.

Structure

Unlike roots, which branch at irregular intervals and do not bear organs such as leaves or reproductive structures, stems have a definite pattern of organization that consists of alternating *nodes* and *internodes*. Each node is a point on a stem at which an organ is attached. Adjacent nodes are separated by an internode, a zone that lacks any attached organs. The part of the stem closest to the ground is called the *proximal end*, while the part farthest away is called the *distal end*. In many plants, internodes at the proximal end are the longest. Toward the distal end, the internodes tend to be progressively shorter.

An actively growing stem has an *apical meristem* at its extreme distal end. In this region, new stem tissue is produced. In the apical meristem, cells actively divide and elongate, causing the stem to become longer. That elongation process is called *primary growth*. Immature leaves are also produced at the apical meristem. Immediately after the new cells enlarge, they undergo differentiation to form primary tissue.

Newly formed stems tend to be soft, because the walls of the young cells are thin. Moreover, the stems are typically green because of the presence of photosynthesizing cells on the periphery. Such soft, green stems are termed *herbaceous*. These herbaceous stems often turn hard and woody through time.

At each node, the angle that is formed when a leaf attaches to the stem is called an *axil*. At that juncture is found an embryonic shoot, called an *axillary bud*. Normally, axillary buds remain dormant for some time. Eventually, however, many buds break dormancy and elongate to form a lateral shoot, called a *branch*.

Different species of plants have different patterns of *leaf arrangement*. Most plants display an alternate arrangement, in which only one leaf is inserted at a node. Plants with alternate leaves include oak trees, goldenrod, geraniums, and lilies. Plants with two leaves at a node, in what is called an opposite arrangement, include maples, lilacs, phlox, and mints. Finally, many plants, such as trillium, catalpa, and bedstraw, have three or more leaves at a node, in what is called a whorled arrangement.

Some plants exhibit very little internodal development. The result is that the plant consists of a cluster of leaves right at the soil surface. These are called rosette plants and are represented by dandelion, hawkweed, and plantain.

Woody Plants

Some plants produce an herbaceous stem that will develop a secondary growth of hard, woody tissue. These *woody plants* can be categorized as *trees*, which have only a single main stem emerging from the ground, or as *shrubs*, which have several stems coming from the ground. The development of woody tissue from herbaceous tissue results from a process called *lignification*, in which the walls of cells inside the stem become thick and hard because of the presence of a material called lignin.

The lignified inner cells of the stem are collectively called wood. Lignification causes the stem to become more rigid, allowing it to support more weight. In temperate climates with pronounced cold winters, an herbaceous stem becomes lignified during its first winter. In more moderate climates, stems become lignified gradually. In either case, the outside of the stem becomes covered with water-impermeable bark.

Woody plants that grow in temperate areas vary in their rates of growth from one season to another. Stems grow most rapidly during the spring and summer. The rate of growth declines markedly at the end of summer and during fall. Little, if any, growth occurs during winter.

Woody plants, especially *deciduous* ones, have a few features that are lacking in herbaceous plants, which have unprotected stems. First, when a leaf drops off a woody plant at the end of the growing season, it leaves a scar on the stem. The shapes of leaf scars vary from one species to another; some are circular, others are triangular, still others look like small lines. A second feature found on a woody plant is a *terminal bud*. That structure usually forms when the apical meristem stops actively growing at the end of the summer. The terminal bud is typically dormant during the winter and is often enclosed by one or more hard, modified leaves called *terminal bud scales*. Those scales protect the bud against injury by cold and predators.

When warm weather or abundant rainfall returns, the bud breaks its dormancy, and a new stem is produced. As the young shoots begin to elongate, the bud scales fall off, resulting in scars that encircle the stem. Thus, the bud scales mark the juncture between the growth that occurs in two successive years. Because a new set of bud scale scars is produced at the beginning of every growing season, one can tell the age of a stem by counting the number of sets of bud-scale scars from the base to the extreme distal end.

Finally, the bark that encircles woody stems does not allow air to pass between the inside of the stem and the outside. That poses a problem for the cells immediately under the bark, which need oxygen to survive. To help overcome this problem, many woody stems contain raised corky dots called *lenticels* scattered over the surface. The cells of the lenticels are spongy and allow air to diffuse to the living cells beneath.

Modified Stems

Many plants have stems that are horizontal instead of erect. *Stolons*, also called *runners*, are horizontal stems that lie above the soil surface. Stolons are found on strawberry plants, for example. *Rhizomes* are horizontal stems that lie below the soil surface. Ferns, irises, milkweeds, and goldenrods produce rhizomes. Both stolons and rhizomes often produce *adventitious roots*, which are roots that form along a stem or anywhere else roots typically do not grow. *Tubers* are thickened rhizomes that store starch. The potato is probably the best-known tuber. Interestingly, plants such as kohlrabi have thickened tuberlike stems that are borne above ground.

A *bulb* is a budlike modified stem that has sets of thick leaves closely overlapping one another (as an onion does). A *corm* is similar to a bulb except that the leaves are thin and papery, and they surround a stem that is short and fleshy. Gladiolus and crocus both produce corms.

Some plants, especially those that grow in desert regions, have thick, succulent stems that serve to store and conserve water. The stem is either padlike (such as that of a prickly-pear cactus) or barrel-shaped (such as that of a saguaro cactus) and is typically covered by a thick layer of green photosynthesizing cells and sharp spines. Asparagus and a few other plants produce stems called *cladophylls*, which are flattened, highly branched, and capable of photosynthesis.

Some branch stems, such as those of hawthorn, are modified to form sharp structures called *thorns*. In contrast, the sharp structures on the surfaces of rose and blackberry stems, commonly referred to as thorns, are actually *prickles*, while sharpened leaves such as those of holly are called *spines*. Finally, some woody plants, such as birches, produce stubby side branches called *spur shoots* that grow only a few millimeters each year.

Growth

Three types of primary tissue form the stem's interior: *dermal tissue*, *vascular tissue*, and *ground tissue*. Dermal tissue forms a thin layer surrounding the herbaceous stem and protects it from drying out. Vascular tissue is composed of *xylem* and *phloem* and serves to conduct water, minerals, and organic substances throughout the plant. In most plants, it forms a ring within the stem. Woody plants have a ring of cells called the *vascular cambium* located within the vascular tissue. The vascular cambium actively divides during the growing season, producing wood to the inside and bark to the outside, and causes the stem to increase in width. Finally, ground tissue has two main functions: photosynthesis and storage. It is found both at the extreme core of the stem and in a ring immediately inside the dermal tissue but outside the vascular tissue.

Many plants vary from these basic patterns. For example, in plants such as lilies and grasses, the cells of the vascular tissue occur in small clusters that are interspersed with the ground tissue. In woody plants, the vascular tissue makes up the bulk of the stem.

Many internal (hormonal) and external (environmental) factors affect stem growth. At least two classes of hormones appear to increase the growth of stems when applied to the plant: *auxins* and *gibberellins*. Auxins cause individual cells to become longer, whereas gibberellins stimulate both cell division and elongation. Gibberellins appear to be important in the life cycles of *biennials*, which are plants that typically spend their first year as a rosette and then flower in their second year. Before flowering, the second-year plant must produce an erect flowering stem, a process called *bolting*. When a biennial bolts, the new internodes are long rather than short, and gibberellins appear to cause this elongation.

Many environmental factors can influence stem growth, but light and physical damage to the apical meristem are perhaps the most dramatic. Plants that grow in light that comes from one side (instead of from the top) tend to bend toward the light, a process called *phototropism*. Plants that grow in complete darkness tend to have stems that are abnormally long and thin and are yellow in color. Such stems are said to be *etiolated*.

Finally, when the apical meristem is intact, lateral buds typically remain dormant. When, however, the meristem is removed by herbivory or clipping, at least one of the lateral buds is released from dormancy, producing a branch that then becomes the new meristem. The process by which an intact apical meristem inhibits the growth of the laterals is termed *apical dominance*. Research has shown that phototropism, etiolation, and apical dominance are mediated through the hormone auxin.

Kenneth M. Klemow

See also: Bulbs and rhizomes; Cacti and succulents; Dormancy; Flowering regulation; Garden plants: shrubs; Growth and growth control; Growth habits; Hormones; Leaf anatomy; Leaf arrangements; Plant tissues; Roots; Shoots; Wood.

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STRIP FARMING

Categories: Agriculture; economic botany and plant uses

Strip farming is the growing of crops in narrow, systematic strips or bands to reduce soil erosion from wind and water and otherwise improve agricultural production.

The origins of strip farming can be traced to the *enclosure movement* of postmedieval Great Britain. Landlords consolidated the small, fragmented strips of land farmed by tenant peasants into large block fields in an effort to increase agricultural production. Peasant plots were typically 1 acre in size: 220 yards, or one furlong in length (the distance a team of oxen can plow before resting) and 22 yards in width (the amount one team of oxen can plow in one day). After enclosure, fields were 100 or more acres in size. Larger fields were more productive but were also more exposed to wind and water erosion and nutritional exhaustion.

As agricultural production gradually shifted to new lands in the Americas and colonial Africa, farmers continued to use large-field farming techniques and developed large-field plantations. By the early twentieth century, all readily tilled lands had been opened by the plow and were suffering the effects of water and wind erosion. Strip farming, also known as strip cropping, was developed as a *soil conservation* measure during the 1930's. During the 1960's strip farming became an important tool to prevent water and air pollution and improve wildlife habitat.

Agricultural Hazards

Wind erosion begins when wind velocity at 1 foot (0.3 meter) above soil level increases beyond 13 miles (21 kilometers) per hour. *Saltation* and *surface creep* also allow soil to move. In saltation, small particles are lifted off the surface. These articles travel ten to fifteen times the height to which they are lifted, then spin downward with sufficient force to dislodge other soil particles and break earth clods into smaller particles. Surface creep occurs when particles too small to be lifted move along the surface in a rolling motion. The wider the field, the greater the cumulative effect of saltation and surface creep. These factors can lead to an avalanche of soil particles across the widest fields even during moderate wind gusts.

Water erosion begins when raindrops or flowing water suspends soil particles above the surface and transports them downslope by splash or *runoff*. Ice crystals expand, then contract when melted, dislodging soil particles and making them available for both water and wind erosion. Water also *leaches* nutrients and chemicals from the soil, causing the soil to experience both nutrient loss and an increase in salts and acids.

The U.S. Department of Agriculture computes annual soil loss from agricultural and developed land using the formula A = RKLSCP. In this formula, *A* equals annual soil loss, *R* equals the amount of rainfall on the plot, *K* equals the erosion factor for the type of soil on the plot, *L* equals the length of the slope on which the plot is located, *S* equals the angle of the slope, *C* equals the type of crop or soil cover on the plot, and *P* equals the presence of management conservation practices such as buffers, terraces, and strip farming. Soil loss tolerances are calculated for each plot. The tolerance is the amount of soil that can be lost without reducing productivity. Loss tolerances range from 1 to 5 tons per acre per year. Farmers and developers reduce soil losses to tolerance levels by reducing soil exposure to wind and rain and by utilizing conservation practices, such as strip farming.

Alleviating Hazards

Strip farming reduces field width, thus reducing erosion. Large fields are subdivided into narrow, cultivated strips. Planting crops along the contour lines around hills is called *contour strip cropping*. Planting crops in strips across the top of predominant slopes is called *field stripping*. Crops are arranged so that a strip of hay or sod (such as grass, clover, or alfalfa) or a strip of close-growing small grain (such as wheat or oats) is alternated with a strip of cultivated row crop (such as tobacco, cotton, or corn). Rainwater runoff or blown dust from the row-crop strip is trapped in this way as it passes through the subsequent strip of hay or grain, thus reducing soil erosion and pollution of waterways. Contour or field strip cropping can reduce soil erosion by 65 to 75 percent on a 3 to 8 percent slope.

Cropping in each strip is usually *rotated* each year. In a typical four-strip field, each strip will be cultivated with a cover crop for one or two years, grain for one year, and row-crop planting for one year. Each strip benefits from one or two years of nitrogen replenishment from *nitrogen-fixing* cover crops, such as alfalfa, and each strip benefits from one year of absorbing nutrient and fertilizer runoff from the adjacent row-crop strip.

Strip widths are determined by the slope of the land: the greater the slope, the narrower the strips. In areas of high wind, the greater the average wind velocity, the narrower the strips. The number of grass or small-grain strips must be equal to or greater than the number of row-cropped strips.

Terraces are often constructed to reduce the slope of agricultural land. At least one-half of the land between each terrace wall is cultivated with grass or a close-growing crop. Diversion ditches are often used to redirect water from its downhill course across agricultural land. These ditches usually run through permanently grassed strips, through downhill grass waterways constructed across the width of the strips, and through grassed field borders surrounding each field.

Gordon Neal Diem

See also: Agriculture: modern problems; Erosion and erosion control; Slash-and-burn agriculture; Soil conservation; Soil management; Soil salinization; Sustainable agriculture.

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STROMATOLITES

Categories: Algae; bacteria; evolution; paleobotany

Stromatolites are laminated, sedimentary fossils formed from layers of blue-green algae (also known as blue-green bacteria or cyanobacteria). Located throughout the world, these ancient remnants of early life have revealed much about the "age of algae."

Stromatolites are the most common megascopic fossils, contained within ancient rocks dating to 3.5 billion years in age. In both the living and fossil form, they are created by the trapping and binding of sediment particles and the precipitation of calcium carbonate to the sticky surface of matlike filaments grown on a daily cycle by blue-green algae (also known as cyanobacteria). Modern stromatolites are found throughout the world; they are of particular use in the creation of hydrocarbon reservoirs, in geologic mapping, and as indicators of paleoenvironments.

Distribution of Stromatolites

In the geologic record, stromatolites are the most abundant of fossils found in rocks dating to the Precambrian era, that period of time from the origin of Earth (approximately 4.6 billion years ago) up to 544 million years ago. The oldest fossil stromatolites are contained in the 3.3-billion- to 3.5-billion-year-old Warrawoona group of rocks in Australia. Close in age are the 3.4-billion-year-old stromatolites of the Swaziland group of South Africa. Somewhat more removed are those associated with the 2.5-billion- to 2.8-billion-year-old Bulawayan Limestone, also in Africa.

All these examples originated in the Archean eon, the first recorded period of geologic history, extending from approximately 4 billion to 2.5 billion years ago. During the Proterozoic eon, immediately following the Archean eon and extending to 544 million years ago, stromatolites became prolific. This Proterozoic expansion is probably reflective of the initial development of continental landmasses and associated warm, photic continental shelf regions, as plate tectonics became a controlling process in the early development of the earth's crust.

Throughout the Archean and Proterozoic eons, blue-green algae underwent a steady and progressive state of biologic evolution, recognized today as the singular, common megascopic fossil of the Precambrian time period. For this reason, the Precambrian is often referred to as the "age of algae," or, more specifically, the "age of blue-green algae." Throughout the Phanerozoic eon, defined as 544 million years ago to the present, blue-green algae underwent minimal evolution, probably because their evolutionary state had become adapted to a variety of environments, reducing the need for further diversification.

Stromatolitic-building algae maintained their dominance of the aquatic world during the Early Phanerozoic eon (544 million to about 460 million years ago). With the rather abrupt appearance, however, of shelled, grazing, and cropping invertebrates in the early Phanerozoic eon, blue-green algae began to decline in significance. Today, as compared to their Precambrian domination, they have, on a relative scale, become endangered.

Geographically, fossil stromatolites are ubiquitous on every continent, especially within sedimentary carbonate rock sequences older than 460 million years. On southeastern Newfoundland, stromatolites built by blue-green algae of the genus *Girvanella* are found in conglomerate and limestone strata of the Bonavista Formation (approximately 550 million years in age). In the Transvaal region of South Africa, delicately banded stromatolitic structures compose one of the most widespread of early Proterozoic shallow-water carbonate deposits in the world, extending over an area exceeding 100,000 square kilometers.

In nearby Zambia, algal stromatolites are closely associated with rock sequences containing economic levels of copper and cobalt. Upper Permian

(250 million years ago) stromatolite horizons can be traced over an area of northern Poland exceeding 15,000 square kilometers. Miocene age (15 million years old) algae of the species *Halimeda* compose the limestone-forming rocks of the island of Saipan in the Mariana Islands of the Pacific Ocean. In North America, fossil algal-bearing rocks include the 2-billion-year-old Gunflint (Iron) Formation of Ontario, Canada, and the well-developed stromatolitic horizons of Early Paleozoic era (450 million years ago) composing the Ellenberger Formation of Oklahoma and Texas.

Classification and Identification

The classification and identification of stromatolites are often concluded on the basis of overall morphology, particularly the size, shape, and internal construction of the specimen. The relevant literature makes use of a variety of morphological terms, including the adjectives "frondose" (leaflike), "encrusting," "massive," "undulatory" (wavelike), "columnar," "laminar," "domed," "elliptical," and "digitigrade" (divided into fingerlike parts). Through the study of modern blue-green algae, it is suggested that three environmental criteria are of importance in stromatolite geometry development. These are direction and intensity of sunlight, direction and magnitude of water current, and direction of sediment transport. As an example, the extant elliptical stromatolites of Shark Bay, western Australia, are oriented at right angles to the shoreline as the result of strong current-driven wave and scour action. Under certain environmental conditions, cyanobacteria growth surfaces are not preserved, producing fossil algal structures characterized by a lack of laminae (leaf blades). These structures are termed *thrombolites*, in contrast to laminar-constructed stromatolites.

NOAA/National Undersea Research Program Collection

Stromatolites are formed by a slow buildup of microbial mats trapping sediment particles and the precipitation of calcium carbonate. Modern stromatolites are found throughout the world.

While stromatolites are generally described as megascopic in size, discussion of specific dimensions relates both to laminae thickness and to overall size. Stromatolite laminae of the Precambrian-aged Pethei Formation, an outcropping along the shores of Great Slave Lake in the Northwest Territories of Canada, are both fine and coarse in dimension. The coarse-grained layers, formed of lime-mud pellets and calcium and magnesium carbonate rhombs, are principally less than 5.0 millimeters in thickness. The fine-grained laminae, composed of calcium carbonate clay and silt-sized particles, are, on average, only 0.5 millimeter thick.

In size, individual stromatolites can range from centimeters up to several meters. Fossils of the common Precambrian genus *Conophyton* occur in a range of sizes, from pencil-sized shapes to columns up to 10 meters in diameter. Subspherical varieties of stromatolite-like structures, formed by the accretion of successive gelatinous mats of blue-green algae and generally less than 10 centimeters in diameter, are termed *oncolites*. Stromatolitic complexes in the Great Slave Lake district measure 80 meters long by 45 meters wide by 20 meters in thickness and can be continuously traced for distances exceeding 160 kilometers.

Albert B. Dickas

See also: Algae; Cyanobacteria; Evolution of cells; Fossil plants; Paleoecology.

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SUCCESSION

Categories: Ecology; ecosystems; genetics; reproduction and life cycles

Succession is the progressive and orderly replacement of one biological community by another until a relatively stable, self-maintaining community is achieved.

Succession is an important ecological phenomenon because it allows the maximum variety and number of species to occupy a given area through time and leads to the establishment of an ecologically stable *climax community* that represents the most complex and diverse biological system possible, given existing environmental conditions and available energy input. As succession proceeds, significant changes occur in species composition, nutrient cycling, energy flow, productivity, and stratification. Changes also occur within the climax community; however, these changes act to maintain the climax, not alter it.

Immature communities tend to have high populations of a few species that are relatively small and simple. *Biomass* (weight of living material) is low, and nutrient conservation and retention are poor. *Food chains* are short, and available energy is shared by few species. Community structure is simple and easily disrupted by external forces. As communities mature, larger and more complex organisms appear, and there is a higher *species diversity* (number of different species). Biomass increases, and nutrients are retained and cycled within the community. The greater number of species results in more species interactions and the development of complex *food webs*. Community productivity (conversion of solar energy to chemical energy), initially high in immature communities, becomes balanced by community respiration as more energy is expended in maintenance activities.

Stages of Succession

The entire sequence of communities is called a sere, and each step or community in the sequence is a *seral stage*. The climax community is in balance, or *equilibrium*, with the environment and displays greater stability, more efficient nutrient and energy recycling, a greater number of species, and a more complex community structure than that of each preceding seral stage.

Each seral stage is characterized by its own distinctive forms of plant and animal life, which are adapted to a unique set of chemical, physical, and biological conditions. Excepting the climax community, change is the one constant shared by all seral stages. Changes can be induced by abiotic factors, such as erosion or deposition, and by biotic factors, modification of the environment caused by the activities of living organisms within the community.

These self-induced factors bring about environmental changes detrimental to the existing community but conducive to invasion and replacement by more suitably adapted species. For example, lichens are one of the first colonizers of barren rock outcrops. Their presence acts to trap and hold windblown and water-carried debris, thereby building up a thin soil. As soil depth increases, soil moisture and nutrient content become optimal for supporting mosses, herbs, and grasses, which replace the lichens. These species continue the process of soil-building and create an environment suitable for woody shrubs and trees.

In time, the trees overtop the shrubs and establish a young forest. These first trees are usually shade-intolerant species. Beneath them, the seeds of the shade-tolerant trees germinate and grow up, eventually replacing the shade-tolerant species. Finally, a climax forest community develops on what once was bare rock, and succession ends.

Primary and Secondary Succession

The sere just described—from barren rock to climax forest—is an example of *primary succession*. In primary succession, the initial seral stage, or pioneer community, begins on a substrate devoid of life or unaltered by living organisms. Succession that starts in areas where an established community has been disturbed or destroyed by natural forces or by human activities (such as floods, windstorms, fire, logging, and farming) is called *secondary succession*.

An example of secondary succession occurs on abandoned cropland. This is referred to as old-field succession and begins with the invasion of the abandoned field by annual herbs such as ragweed and crabgrass. These are replaced after one or two years by a mixture of biennial and perennial herbs, and by the third year the perennials dominate. Woody shrubs and trees normally replace the perennials within ten years. After another ten or twenty years have passed, a forest is established, and ultimately, after one or two additional seral stages in which one tree community replaces another, a climax forest emerges.

Both primary and secondary succession begin on sites typically low in nutrients and exposed to extremes in moisture, light intensity, temperature, and other environmental factors. Plants colonizing such sites are tolerant of harsh conditions, are characteristically low-growing and relatively small, and have short life cycles. By moderating the environmental conditions, these species make the area less favorable for themselves and more favorable for plants that are better adapted to the new environment. Such plants are normally long-lived and relatively large. Secondary succession usually proceeds at a faster rate than primary succession, because a well-developed soil and some life are already present.

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Aquatic Environments

Succession can also take place in aquatic environments, such as a newly formed pond. The pioneer community consists of microscopic organisms that live in the open water. Upon death, their remains settle on the bottom and join with sediment and organic matter washed into the pond. An accumulation of sediment provides anchorage and nutrients for rooted, submerged aquatic plants such as pondweeds and waterweeds. These add to the buildup of sediment, and as water depth decreases, rooted, floating-leaved species such as water lilies prevent light from reaching the submerged aquatics and eliminate them.

At the water's edge, emergent plants rooted in the bottom and extending their stems and leaves above water (cattails, rushes, and sedges) trap sediment, add organic matter, and continue the filling-in process. The shallow margins fill first, and eventually the open water disappears and a marsh or bog forms. A soil rich in partially decomposed organic matter and saturated with water accumulates. As drainage improves and the soil becomes raised above the water level, trees and shrubs tolerant of wet soils invade the marsh. These act to lower the water table and improve soil aeration. Trees suited to drier conditions move in, and once again a climax community characteristic of the surrounding area develops.

Influence of Climate

The American ecologist Frederic E. Clements (1874-1945) believed that the characteristics of a climax community were determined solely by regional climate. According to Clements, all communities within a given climatic region, despite initial differences, eventually develop into the same climax community. Some seral stages might be abbreviated or skipped entirely, while others could be lengthened or otherwise modified; however, the end result would always be a single climax community suited to the regional climate. This phenomenon is called *convergence*, and Clements's single-climax concept is known as the *monoclimax theory*.

Some ecologists have found the monoclimax theory to be simplistic and have offered other theories. One of these, the *polyclimax theory*, holds that, within a given climatic region, there could be many climaxes. It was noted that in any single climatic region, there were often many indefinitely maintained communities that could be considered separate and distinct climaxes. These developed as a result of differences caused by soil type, soil moisture, nutrients, slope, fire, animal activity (grazing and browsing), and other factors. Clements countered that these would eventually reach true climax status if given enough time and proposed terms such as *subclimax* (a long-lasting seral stage preceding the climax) and *disclimax* (a nonclimax maintained by continual disturbance) to describe such situations.

A third theory, the *climax pattern concept*, views the climax as a single large community composed of a mosaic or pattern of climax vegetation instead of many separate climaxes or subclimaxes. Numerous habitat and environmental differences account for the patterns of populations within the climax; no single factor such as climate is responsible.

While there is little doubt about the reality of succession, it is apparently not a universal phenomenon. For example, disturbed areas within tropical rain forests do not undergo a series of seral stages leading to reestablishment of the climax community. Instead, the climax is established directly by the existing species. Nevertheless, in most regions succession is the mechanism by which highly organized, self-maintained, and ecologically efficient communities are established.

Steven D. Carey

See also: Community-ecosystem interactions; Ecology: concept; Ecosystems: overview; Genetic drift; Reforestation; Reproductive isolating mechanisms; Selection; Species and speciation.

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SUGARS

Categories: Economic botany and plant uses; food; nutrients and nutrition; photosynthesis and respiration

Refined from sugarcane, sugar beets, and corn, sugars are a major and vital part of nutrition and provide the basic molecular structure for most living matter.

Sugars, through the process called cellular respiration, are the primary power sources used to produce adenosine triphosphate (ATP), the energy exchange molecule that sustains all life. Energy is stored in organisms as starch or fat but is burned as sugar. Sugars include some of the simplest carbohydrates, and they are building blocks of more complicated molecules. Common sugars include glucose, fructose, sucrose, maltose, and lactose. Alcohol (ethanol) derived from sugar fermentation is an important product to the food and beverage, fuel, and drug manufacturing industries. The primary sugar derived from plants is sucrose, a disaccharide composed of two simpler sugars, glucose and fructose, joined together.

History of Use in Food

Demand for sugar and other food flavorings was particularly strong before canning and refrigeration. People often had to eat partially spoiled food, and they eagerly sought ways to improve its flavor. Items with high sugar levels, such as berries and grapes, were especially prized.

Sugarcane (*Saccharum officinarum y officinarum*) has a stem that can be squeezed to deliver a sucrose-rich syrup, and the leftover woody material (*bagasse*) can be dried and burned to boil off water. Molasses syrup or solid sugar can be made in this way. Arab traders brought sugarcane to Europe in the 1100's. By the 1500's European colonization in Brazil and the Caribbean provided rich growing fields. So important and valuable were sugar crops that in 1800 the new countries of Haiti and the United States had similar gross national products.

However, the cravings and rivalries that created sugar empires caused their decline. England and its allies fought a series of wars with France in the late 1700's and early 1800's, and British blockades kept molasses out of Europe. France's Napoleon responded by offering a prize for a process to produce sugar from a European-grown plant. A sugar beet process won, and cane sugar was never again as centrally important.

Yearly, sucrose production from sugarcane and sugar beets is more than 100 million metric tons. Both crops are excellent soil conditioners. Sugarcane is a tall, periodically harvested grass, so it limits soil erosion that would occur in bare ground. Meanwhile, cane roots steadily grow and increase humus in the soil. Sugar beets require plowing and

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are dug from the ground during harvesting, but they, too, leave extensive roots.

When sucrose prices rose in the 1950's, high-fructose sweeteners were developed as alternatives. Enzymes are used to break starches into fructose. Corn syrup, one fructose sweetener, is cheaper than sucrose and has displaced much U.S. sucrose use. Elsewhere, fructose syrups are made from wheat, rice, tapioca, and cassava.

Sugar and Alcohol

The fermentation of alcohol has been a major aspect of sugar use since antiquity. Fungi called *yeasts* convert sugars into ethyl alcohol (ethanol); the yeasts can produce only mild alcohol levels. Alcohol, although medically classified as a depressant, can provide a short-term energy boost. It also acts as a mild poison that desensitizes the central nervous system, allowing drinkers to feel relaxed. Ancient Egyptians and Mesopotamians fermented grains into beer, while Greeks and Phoenicians traded wine from grapes. In the Middle Ages, alchemists experimented with distillation, a process in which a substance boiled out of one substance is cooled back into liquid elsewhere. Distillation transformed beers and wines into whiskeys and brandies, alcoholic drinks several times more potent.

Caribbean sugar and alcohol formed one leg of the "triangle trade" from the 1600's through the early 1800's. New Englanders sold fish for Caribbean molasses, fermented it, and distilled it into rum. They traded rum in Africa for slaves, sold largely in the Caribbean.

Fuel and Other Uses

Ethyl alcohol can burn more efficiently than gasoline in the internal combustion engines used in automobiles. However, because gasoline has historically been cheaper, research and development work on ethanol as a fuel was minimal until the 1970's. The energy crisis of 1973 involved oil shortages and soaring prices, and it stimulated many experimental ethanol programs. Most experiments were abandoned when oil prices dropped in the mid-1980's, but Brazil persevered in a national program of sugar-cane alcohol fuel.

Even Brazilian ethanol is only barely economically competitive with fossil fuels. The major problem is that energy expenditures in the manufacture of ethanol include fuel for tending the fields and gathering cane, energy lost to yeasts (about half, although the yeasts do yield high-protein byproduct), and another half of the remainder expended for distilling the material to 95 percent alcohol. Suggested improvements include developing more efficient yeasts and performing the distillation process under partial vacuum, which would allow continuous processing rather than batch processing.

Theoretically, the most efficient way to use sugar energy would be the development of electrical fuel cells that would take energy from sugar, just as living organisms do. Losses from yeast digestion and distillation would be eliminated, and a fuel cell might achieve 50 percent efficiency, rather than the 25 percent efficiency of internal combustion engines, yielding eight times more energy. This approach could create an energy revolution if the technical problems could be overcome. (Energy-efficient processes must be developed for *saccharification*, or hydrolysis, of cellulose from wood and garbage.)

Sugars can also be nutrients for generating other products. Specialized groups of other cells, such as juice-producing cells from oranges or fiber-producing cells from cotton, can be cultured with sugar nutrients, for example, and genetic engineering has developed yeasts that produce specialty chemicals such as catalysts.

Roger V. Carlson

See also: ATP and other energetic molecules; Carbohydrates; Ethanol; Grasses and bamboos; Microbial nutrition and metabolism; Respiration; Yeasts.

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SUSTAINABLE AGRICULTURE

Categories: Agriculture; disciplines; economic botany and plant uses; environmental issues

Sustainable agriculture is the practice of growing and harvesting crops in a manner that will allow the land to return to its precultivation state. It seeks to maintain the quality of air, soil, and water resources for future human use and for wildlife.

Most twentieth century agricultural practices were based upon continued economic growth. This practice demonstrated dramatic increases in production but had negative impacts on the environment through the losses of plant and animal *habitats*, depletion of soil nutrients, and increases in pollution of water supplies. The concept of sustainable development is based on using renewable resources and working in harmony with ecosystems. The World Commission on Environment and Development described the concept of sustainable development as being able "to meet the needs of the present without compromising the ability of future generations to meet their own needs." Sustainable agriculture strives to manage agricultural activities in such a way as to protect air, soil, and water quality as well as conserve wildlife habitats and *biodiversity*.

Problems Caused by Agriculture

Water pollution is one of the most damaging and widespread effects of modern agriculture. Runoff from farms accounts for more than 50 percent of sediment damage to natural waterways. Cleanup of the chemicals and nutrients associated with this runoff in the United States costs an estimated $2 billion to $16 billion per year. Heavy application of nitrogen fertilizers and pesticides has raised the potential for groundwater contamination. Feedlots that concentrate manure production lead to further groundwater contamination. Several of the most commonly used pesticides have been detected in the groundwater of at least one-half of the states in the United States. In addition, growing highly specialized *monoculture* crops, which requires a heavy reliance on agricultural chemicals, has depleted the natural organic nutrients that were formerly rich in North American *topsoils*.

Research has shown that many of the farm-based chemical agents, pesticides, fertilizers, plant-growth regulators, and antibiotics are now found in the food supply. These chemicals can be harmful to humans at moderate doses, and chronic effects can develop with prolonged exposure at lower doses. Further, widespread pesticide use has been shown to severely stress animals other than the target pest, including bee populations. Pesticides have often led to resurgences of pests after treatment, occurrences of secondary pest outbreaks, and resistance to pesticides in the target pest.

Because of these growing problems, many American farmers are turning to sustainable agriculture. The U.S. federal government has offered guidance for this transition through the Sustainable Agriculture Farm Bill, passed by Congress in 1990. The bill provides that sustainable agriculture, through an integrated system of plant and animal production practices, can, over the long run, meet human food and fiber needs, enhance environmental quality and natural resources, make the most efficient use of nonrenewable resources, maintain economic viability of farm operations, and enhance the quality of life for farmers and consumers.

Water Conservation

Water is one of the most important resources for agriculture and for society as a whole. In the western United States, it allows arid lands to produce crops through irrigation. In California, limited surface water supplies have caused overdraft of groundwater and the consequent intrusion of salt water, which causes a permanent collapse of aquifers. In order to counteract these negative effects, sustainable farmers in California are improving water conservation and storage methods, selecting drought-resistant crop species, using reduced-volume irrigation systems, and managing crops to reduce water loss. Drip and trickle irrigation can also be used to dramatically reduce water usage and water loss while helping to avoid such problems as soil salinization.

Salinization and contamination of groundwater by pesticides, nitrates, and selenium can be temporarily managed by using tile drainage to remove water and salt. However, this often has adverse affects on the environment. Long-term solutions include conversion of row crops to production of drought-tolerant forages and the restoration of wildlife habitats.

Contour Plowing and Terracing

One of the most important aspects of sustainable agriculture is soil conservation. Water runoff from a field having a 5 percent slope has three times the water volume and eight times the soil erosion rate as a field with a 1 percent slope. In order to prevent excessive erosion, farmers can leave grass strips in the waterways to capture soil that begins to erode. *Contour plowing*, which involves plowing across the hill rather than up and down the hill, helps capture overland flow and reduce water runoff. Contour plowing is often combined with strip farming, where different kinds of crops are planted in alternating strips along the contours of the land. As one crop is harvested, another is still growing and helps recapture the soil and prevent water from running straight down the hill. In areas of heavy rainfall, tiered ridges are constructed to trap water and prevent runoff. This involves a series of ridges constructed at right angles to one another. Such construction blocks direct runoff and allows water to soak into the soil.

Another method of soil conservation is *terracing*, in which the land is shaped into level shelves of earth to hold in the water and soil. To provide further stability to soil, soil-anchoring plants are grown on the edges of the terraces. Terracing, although costly, can make it possible to farm on steep hillsides. Some soils that are fairly unstable on sloping sites or waterways can require that perennial species of grasses be planted to protect the fragile soil from cultivation every year.

Green Manure

Farmers also use *green manure*—crops that are raised specifically to be plowed under—to introduce organic matter and nutrients into the soil. Green manure crops help protect against erosion, cycle nutrients from lower levels of the soil into the upper layers, suppress weeds, and keep nutrients in the soil rather than allowing them to leach out. Legumes such as sweet clover, ladino clover, and alfalfa are excellent green-manure crops. They are able to extract nitrogen from the air into the soil and leave a supply of nitrogen for the next crop that is grown. Some crops, such as beans and corn, can cause high soil erosion rates because they leave the ground bare most of the year. In sustainable farming, crop residues are left on the ground after harvest. Residues help reduce soil evaporation and even excessive soil temperatures in hot climates. Many farmers choose to use cover crops rather than residue crops. Which cover crop to use depends on which geographical area farmers live in and if they wish to control erosion, capture nitrogen in the fall, release nitrogen to the crop, or improve soil structure and suppress weeds.

Cover Crops

When planting crops with high nitrogen requirements, such as tomatoes or sweet corn, farmers can use cover crops such as hairy vetch or clover. Both these cover crops decompose and release nutrients into the soil within one month. To fight erosion, a farmer might choose a rapid-growing cover crop, such as rye. Rye provides abundant ground cover and an extensive root system below the soil to stop erosion and capture nutrients. Alfalfa, rye, or clover can be planted after harvest to protect the soil and add nutrients and can then be plowed under at planting time to provide a green manure for the crop. Cover crops can also be flattened with rollers, and seeds can be planted in their residue. This gives the new plants a protective cover and discourages weeds from overtaking the young plants. Use of natural nitrogen also reduces the risk of water contamination by agricultural chemicals.

Reduced Tillage

Sustainable agriculture emphasizes the use of reduced tillage systems. There are three reduced tilling systems that sustainable farmers use to disturb the soil as little as possible. Minimum till involves using the disc of a chisel plow to make a trench in the soil where seeds are planted. Plant debris is left on the surface of the ground between the rows, which helps further prevent erosion. Several sustainable planting techniques help prevent soil erosion. Conser-till farming uses a coulter to open a slot just wide enough to insert seeds without disturbing the soil. No-till planting involves drilling seeds into the ground directly through the ground cover or mulch. When mulch is still in place, a narrow slit can be cut through the cover or crop residues in order to plant the new crops.

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Crop Rotation vs. Monoculture

Planting the same crop every year on the same field can result in depleted soils. In order to keep the soil fertile, nitrogen-depleting crops (such as sweet corn, tomatoes, and cotton) should be rotated every year with legumes, which add nitrogen to the soil. Planting a winter cover crop, such as rye grass, protects the land from erosion. Such cover crops will, when plowed under, provide a nutrient-rich soil for the planting of a cash crop. *Crop rotations* improve the physical condition of the soil because of variations in root depth and cultivation differences.

In nature, plants grow in mixed meadows, which allow for them to avoid insect infestations. Agricultural practices that use monoculture place a great quantity of the food of choice in easy proximity of the insect predator. Insects can multiply out of proportion when the same crop is grown in the field year after year. Since most insects are instinctively drawn to the same home area every year, they will not be able to proliferate and thrive if crops are rotated and their crop of choice in not in the same field the second year.

Crop rotation not only helps farmers use fewer pesticides but also helps to control weeds naturally. Some crops and cultivation methods inadvertently allow certain weeds to thrive. Crop rotations can incorporate a successor crop that eradicates the weeds. Some crops, such as potatoes and winter squash, work as cleaning crops because of the different style of cultivation that is used on them. Pumpkins planted between rows of corn will help keep weeds at bay.

Integrated Pest Management

Most sustainable farmers use *integrated pest management* (IPM) to control insect pests. Using IPM techniques, each crop and its pest is evaluated as an ecological system. A plan is developed for using cultivation, biological methods, and chemical methods at different timed intervals. Although effective, profitable, and safe, the IPM techniques have been widely adopted only for a few crops, such as tomatoes, citrus, and apples.

The goal of IPM is to keep pest populations below the size where they can cause damage to crops. Fields are monitored to gauge the level of pest damage. If farmers begin to see crop damage, they put cultivation and biological methods into effect to control the pests. Techniques such as vacuuming bugs off crops are used in IPM. IPM encourages growth and diversity of beneficial organisms that enhance plant defenses and vigor. Small amounts of pesticides are used only if all other methods fail to control pests. It has been found that integrated pest management, when done properly, can reduce inputs of fertilizer, lower the use of irrigation water, and reduce preharvest crop losses by 50 percent. Reduced pesticide use can cut pest-control costs by 50 to 90 percent and increases crop yield without increasing production costs.

Toby R. Stewart and Dion Stewart

See also: Agriculture: modern problems; Biofertilizers; Biopesticides; Composting; Erosion and erosion control; Hydroponics; Integrated pest management; Monoculture; Organic gardening and farming; Soil conservation; Soil management; Strip farming; Sustainable forestry.

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MAGILL'S ENCYCLOPEDIA OF SCIENCE

PLANT LIFE

Volume 4

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Sustainable Forestry–Zygomycetes
Indexes

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PUBLISHER'S NOTE

Magill's Encyclopedia of Science: Plant Life is designed to meet the needs of college and high school students as well as nonspecialists seeking general information about botany and related sciences. The definition of "plant life" is quite broad, covering the range from molecular to macro topics: the basics of cell structure and function, genetic and photosynthetic processes, evolution, systematics and classification, ecology and environmental issues, and those forms of life—archaea, bacteria, algae, and fungi—that, in addition to plants, are traditionally studied in introductory botany courses. A number of practical and issue-oriented topics are covered as well, from agricultural, economic, medicinal, and cultural uses of plants to biomes, plant-related environmental issues, and the flora of major regions of the world. (Readers should note that, although cultural and medicinal uses of plants are occasionally addressed, this encyclopedia is intended for broad information and educational purposes. Those interested in the use of plants to achieve nutritive or medicinal benefits should consult a physician.)

Altogether, the four volumes of *Plant Life* survey 379 topics, alphabetically arranged from *Acid precipitation* to *Zygomycetes*. For this publication, 196 essays have been newly acquired, and 183 essays are previously published essays whose contents were reviewed and deemed important to include as core topics. The latter group originally appeared in the following Salem publications: *Magill's Survey of Science: Life Science* (1991), *Magill's Survey of Science: Life Science, Supplement* (1998), *Natural Resources* (1998), *Encyclopedia of Genetics* (1999), *Encyclopedia of Environmental Issues* (2000), *World Geography* (2001), and *Earth Science* (2001). All of these previously published essays have been thoroughly scrutinized and updated by the set's editors. In addition to updating the text, the editors have added new bibliographies at the ends of all articles.

New appendices, providing essential research tools for students, have been acquired as well:

- a "Biographical List of Botanists" with brief descriptions of the contributions of 134 famous naturalists, botanists, and other plant scientists
- a Plant Classification table
- a Plant Names appendix, alphabetized by common name with scientific equivalents
- another Plant Names appendix, alphabetized by scientific name with common equivalents
- a "Time Line" of advancements in plant science (a discursive textual history is also provided in the encyclopedia-proper)
- a Glossary of 1,160 terms
- a Bibliography, organized by category of research
- a list of authoritative Web sites with their sponsors, URLs, and descriptions

Every essay is signed by the botanist, biologist, or other expert who wrote it; where essays have been revised or updated, the name of the updater appears as well. In the tradition of Magill reference, each essay is offered in a standard format that allows readers to predict the location of core information and to skim for topics of interest: The title of each article lists the topic as it is most likely to be looked up by students; the "Category" line indicates pertinent scientific subdiscipline(s) or area(s) of research; and a capsule "Definition" of the topic follows. Numerous subheads guide the reader

through the text; moreover, key concepts are italicized throughout. These features are designed to help students navigate the text and identify passages of interest in context. At the end of each essay is an annotated list of "Sources for Further Study": print resources, accessible through most libraries, for additional information. (Web sites are reserved for their own appendix at the end of volume 4.) A "See also" section closes every essay and refers readers to related essays in the set, thereby linking topics that, together, form a larger picture. For example, since all components of the plant cell are covered in detail in separate entries (from the *Cell wall* through *Vacuoles*), the "See also" sections for these dozen or so essays list all other essays covering parts of the cell as well as any other topics of interest.

Approximately 150 charts, sidebars, maps, tables, diagrams, graphs, and labeled line drawings offer the essential visual content so important to students of the sciences, illustrating such core concepts as the parts of a plant cell, the replication of DNA, the phases of mitosis and meiosis, the world's most important crops by region, the parts of a flower, major types of inflorescence, or different classifications of fruits and their characteristics. In addition, nearly 200 black-and-white photographs appear throughout the text and are captioned to offer examples of the important phyla of plants, parts of plants, biomes of plants, and processes of plants: from bromeliads to horsetails to wheat; from Arctic tundra to rain forests; from anthers to stems to roots; from carnivorous plants to tropisms.

Reference aids are carefully designed to allow easy access to the information in a variety of modes: The front matter to each of the four volumes includes the volume's contents, followed by a full "Alphabetical List of Contents" (of all the volumes). All four volumes include a "List of Illustrations, Charts, and Tables," alphabetized by key term, to allow readers to locate pages with (for example) a picture of the apparatus used in the *Miller-Urey Experiment*, a chart demonstrating the genetic offspring of *Mendel's Pea Plants*, a map showing the world's major zones of *Desertification*, a cross-section of *Flower Parts*, or a sampling of the many types of *Leaf Margins*. At the end of volume 4 is a "Categorized Index" of the essays, organized by scientific subdiscipline; a "Biographical Index," which provides both a list of famous personages and access to discussions in which they figure prominently; and a comprehensive "Subject Index" including not only the personages but also the core concepts, topics, and terms discussed throughout these volumes.

Reference works such as *Magill's Encyclopedia of Science: Plant Life* would not be possible without the help of experts in botany, ecology, environmental, cellular, biological, and other life sciences; the names of these individuals, along with their academic affiliations, appear in the front matter to volume 1. We are particularly grateful to the project's editor, Bryan Ness, Ph.D., Professor of Biology at Pacific Union College in Angwin, California. Dr. Ness was tireless in helping to ensure thorough, accurate, and up-to-date coverage of the content, which reflects the most current scientific knowledge. He guided the use of commonly accepted terminology when describing plant life processes, helping to make *Magill's Encyclopedia of Science: Plant Life* easy for readers to use for reference to complement the standard biology texts.

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SUSTAINABLE FORESTRY

Categories: Disciplines; economic botany and plant uses; environmental issues; forests and forestry

Sustainable forestry is a system of forest management that relies on natural processes to maintain a forest's continuing capacity to produce a stable and perpetual yield of harvested timber and other benefits, including recreation, wildlife habitat, and forest-related commodities.

Forest management in the United States first became an issue in 1827 when the Department of the Navy and President John Quincy Adams saw the need for a continuous supply of mature timber for ship construction. In the 1860's, the American Association for the Advancement of Science first discussed the need for *sustained-yield* forestry. In 1878, the Cosmos Club, a Washington, D.C., club of intellectuals, proposed the wise use of natural resources for the greatest good, for the greatest number, and for the longest time, establishing the foundation for the *conservation movement*. The first national forest reserves were established by the U.S. government in 1891, and the first selective logging and marketing of U.S. government timber reserves occurred in 1897. *Clear-cutting* was the general method of timber harvesting. Continued clear-cutting during the twentieth century accelerated the deforestation of private and Forest Service lands, leading to concerns about soil erosion, water pollution, wildlife habitat loss, and the sustained availability of forest resources.

Management Systems

Forest science developed the high-yield forestry *plantation tree farming* system in the 1930's. By the 1960's, ecological concerns had led to *restoration forestry*, which emphasized human intervention to reconstruct forest ecosystems and return forests to baseline conditions that existed before clear-cutting or plantation planting. By the 1980's, new understandings concerning the complexity of forest ecosystems led to an emphasis on perpetually sustaining existing forest resources rather than relying on human efforts to reconstruct forests.

Sustainable Alternatives

Sustainable forestry is an alternative to clear-cutting, the standard logging practice. Clear-cutting removes all timber in one harvest that usually occurs no more than once every sixty to one hundred years. Both mature and immature trees are removed in one process. Logging roads are cut into the forest so heavy machinery can remove all trees from a large area, often about 100 acres at a time. Road construction and clear-cutting lead to soil erosion, topsoil and nutrient loss, silting and pollution of waterways, the loss of wildlife habitat, and the loss of recreational benefits. Repeated cycles of growth and clear-cutting erode soil nutrition, destroy plants, animals, and microorganisms in the ecosystem necessary for healthy forest growth, and reduce the value of future harvests.

Sustainable forestry is also an alternative to *monoculture* plantation forestry. Plantation forestry requires active human intervention to plant tree seedlings, control disease and pests, and nurture the timber stand to maturity. Plantations usually feature a grid planting of a single tree species, with all trees maturing simultaneously. The lack of species and age diversity makes tree plantations unsuitable for wildlife habitat or recreation and makes trees susceptible to disease and pests. Monoculture plantations also deplete species-specific minerals and other nutrients in the soil, reducing its future productivity.

Goals

Sustainable forest management techniques seek a perpetual high yield of timber and pulpwood while maintaining *biodiversity* and natural forest ecosystems and permitting forests to restore their vitality through natural processes, such as foliage decomposition and fire.

Sustainable forestry maintains a balance between natural environmental stresses and the human needs for timber, pulpwood, recreation, and a

PhotoDisc

In sustainable forestry, natural tree stands are thinned to sustain a mixed-age, mixed-species forest. This is an alternative to clear-cutting, a standard logging practice, which removes all timber in one harvest; as shown, both mature and immature trees are removed in one process.

variety of harvested forest products. In spite of the effort to maintain this balance, various sustainable forestry methods often tend to favor either ecosystem maintenance or high timber yields.

Sustainable forestry with an ecosystem emphasis is the discipline of repeated thinning of natural tree stands to sustain a mixed-age, mixed-species forest that is naturally perpetuated by seeds from the mature trees. The forest is periodically thinned, usually every twenty years, to provide a steady income to the forest owners, permit the remaining trees to reach their full maturity, and provide space for new seedlings to grow. When the timber stand reaches full sustainable maturity, immature trees are continuously harvested for pulpwood, and mature trees over one hundred years of age are continuously harvested for high-quality lumber. Natural processes promote the health of the forest and revitalize the forest soil. Diversity in both age and species makes the forest a suitable habitat for a variety of forest-dwelling species and human recreation. The forest is able to recover quickly from natural disasters, fires, or drought.

Sustainable forestry with an emphasis on timber yield divides the forest into subplots, then manages each subplot to produce two sequential high-yield plantation crop cycles of eighty years each before permitting the plot to grow to maturity in a third four-hundred-year cycle. The third cycle permits the forest soil to restore its vitality and produces an old-growth forest suitable for wildlife and eventual timber harvesting. Once fully implemented, this system ensures that each forest has subplots at each stage of growth and harvesting, from newly planted plots to old-growth plots with trees at or near four hundred years of age.

Gordon Neal Diem

See also: Deforestation; Forest and range policy; Forest management; Forests; Logging and clear-cutting; Monoculture; Rangeland; Reforestation; Sustainable agriculture; Timber industry; Wood and timber.

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SYSTEMATICS AND TAXONOMY

Categories: Classification and systematics; disciplines

Systematics deals with evolutionary, or phylogenetic, relationships among organisms, whereas taxonomy is more involved with the classification, naming, and description of organisms. In practice, the two terms are often used interchangeably to refer to the study of relationships among organisms, which in turn often derives from their description and drives their naming.

The history of the disciplines of systematics and taxonomy has shifted with the evolution over the years of the state of knowledge about living organisms, their origins, and their relationships. There has been a historical shift from an emphasis on classification (simply naming and identifying organisms) to the study of phylogenetic (evolutionary) relationships. Classification traditionally focused on defining the relationships among organisms based primarily on their overall similarity in morphology and appearance. *Phylogenetics* is now the more common approach in studying the relationships among organisms and involves constructing phylogenies, or *evolutionary trees*, using evidence from evolutionary relationships. In addition, the advent of genetics and DNA research has significantly changed the way many biologists approach classification, leading in some cases to reconsideration of former taxonomic relationships.

Ancient World and Middle Ages

The roots of taxonomy go back to Greeks, most notably the philosopher Theophrastus in the third century B.C.E., who wrote two treatises on plants, *Peri phyton historias* (also known as *Historia plantarum*; "Enquiry into Plants," 1916) and *Peri phyton aition* (also known as *De causis plantarum*; English translation, 1976-1990). Theophrastus's system and many other early classification systems grouped plants into herbs, undershrubs, shrubs, and trees. Classification of plants, beyond this more or less simplistic approach, was not attempted until the latter part of the sixteenth century, when Andrea Cesalpino published *De plantis libri* (1583). Between the time of the Greeks and Cesalpino, most botanical work was done in the name of medicine, and numerous plants were described because of their usefulness as herbs.

Naming of plants was haphazard, at best. Colloquial names were used by some, and Latin phrases not only were used to describe a plant but also served as official names. There was no accepted length for Latin phrase names, and the names carried little information about how a particular plant might be related to others.

Linnaeus and the Birth of Modern Taxonomy

In 1753 Carolus Linnaeus published his *Species plantarum*, which quickly brought simplicity and order to the naming of organisms, including plants. Linnaeus introduced *binomial nomenclature*, which standardized the naming of all organisms by using two Latin words, which together were referred to as the *species* name. The first word in the species name was the *genus*, which immediately identified how an organism fit into the classification system.

In addition to improving the system of naming, Linnaeus revolutionized the classification system by introducing a hierarchical approach. Similar species were grouped together into genera. Similar genera were grouped into *families*. In turn, families were grouped into *orders*, orders into *classes*, classes into *phyla*, and phyla into *kingdoms*, the most inclusive of the categories. Although his classification of organisms implied no evolutionary relationships, it was useful for bringing some order to taxonomy. All of these hierarchical categories are used for all types of organisms, including plants, although in plants the name *division* is sometimes used instead of the phylum.

According to Linnaeus, the turnip, *Brassica rapa*, which is the name Linnaeus gave to this species, is in the same genus as black mustard, *Brassica nigra*. The genus *Brassica* is in the mustard family, *Brassicaceae*, along with related genera such as *Raphanus* and *Arabis*. The family *Brassicaceae* is in the order *Capparales*, along with related families like *Capparaceae* and *Resedaceae*. *Capparales* is a member of the class *Eudicotyledones*, which includes all the other orders commonly referred to as dicots or dicotyledons. Class *Eudicotyledones* belongs to the division *Anthophyta*, along with class *Monocotyledones*. *Anthophyta*, along with all other green plants in divisions like *Coniferophyta* (the gymnopserms) and *Pteridophyta* (the ferns), belongs in kingdom *Plantae*. Each of these categories has a standard suffix, such as *-phyta* for divisions, *-opsida* for classes, *-ales* for orders, and *-aceae* for families, so that the rank of a name is immediately apparent. Rare exceptions to these rules exist.

In addition to the main categories in the hierarchy, many subdivisions are used. For example, between the levels of kingdom and division, there is subkingdom, which would contain within it one or more divisions. The *sub-* prefix can be used before any of the categories, so that there are subclasses, subfamilies, and even subspecies. The prefix *super-* can also be used to define additional ranks. For example, a superfamily contains one or more related families, and a superorder contains one or more related orders.

Classification Since Linnaeus

Linneaus's binomial nomenclature and hierarchical classification system have been used ever since, but when particular taxa have been added, the classification system has undergone great change. The placement of taxa by Linnaeus was done in what is called an artificial manner. He grouped taxa into categories based on the organisms' overall similarities and the possession of particular physical characteristics. Linnaeus's system is called an *artificial classification system* because he made no attempt to group taxa based on evolutionary relationships. Although other plant taxonomists since Linnaeus have also produced artificial classifications, after evolution became more generally accepted in science, many attempts were made to produce a "natural," or phylogenetically based, classification that would reflect, as much as possible, the evolutionary relationships of the taxa.

One of the first, and still highly respected, phylogenetic classifications of plants was published in 1892 by Adolf Engler. It was actually a revision of an earlier classification by August Wilhelm Eichler. With the help of Karl Prantl and others, the system continued to be elaborated until 1911 and became a twenty-volume work called *Die natürlichen Pflanzenfamilien* (1887-1911; the natural families of plants). The families and genera, instead of being ordered alphabetically, were ordered within their taxonomic ranks, from most evolutionarily primitive to most advanced. It was so influential that plant specimens stored in many herbaria are still organized by what is now referred to as the Engler and Prantl system.

As more and more sophisticated phylogenetic studies have been done, many other plant taxonomists have attempted to improve on Engler and Prantl's system. Some of the more notable plant taxonomists of the twentieth century have included John Hutchinson, Armen Takhtajan, Arthur Cronquist, Robert F. Thorne, and Rolf M. T. Dahlgren. The differences among the systems proposed by these various taxonomists are mainly due to different opinions about which plant taxa should be considered most primitive and which most advanced. The identification of what the first land plants, first seed plants, and first flowering plants were like is still uncertain, leaving ample room for speculation. Consequently, a number of competing classification systems exist today. Modern information from DNA analysis and cladistics continues to sharpen taxonomists' understanding of how plants should be classified, but more work remains to be done.

Naming Rules: The Genus and Below

The rules for naming plants are very specific. The International Code of Botanical Nomenclature (ICBN) contains authoritative rules on the correct way to name plants, as well as groups such as algae and fungi, which have traditionally been considered plants in a broad sense. Rules for naming fossil plants are also covered. Revisions to the code take place on a regular basis.

For a plant name to be accepted, it must be validly published. For any new species (or genus) described before 1953, "validly published" could mean anything from publication in a newspaper or catalog to publication in a respected scientific journal or other professional work. Since 1953, all new names must be published in accepted scientific publications. In addition, all new species (or genus) descriptions must include a complete description in Latin, often called the *Latin diagnosis*.

Sometimes two or more plant taxonomists inadvertently describe the same species, giving it different names. When this happens, the earliest validly published name is given priority and is considered the correct name; any other names are called *synonyms*. May 1, 1753, the date Linnaeus published *Species plantarum*, is considered the starting date for determining priority, and any names published before this date are not considered.

In addition to being validly published, a *type specimen* must be identified. A type specimen is a preserved plant specimen that is designated by the author as the best representative of the new species. An author can define more then one type, in which case the first designated specimen is the holotype and duplicates are called *isotypes*. Each of these is placed in an established herbarium so other plant taxonomists can examine it.

All names of taxonomic groups are treated as Latin, regardless of their source. Proper names and non-Latin words must be Latinized, following specific rules in the ICBN. Species names always comprise the genus name, with the first letter capitalized, followed by the species epithet, which is not capitalized. Both names must be either italicized or underlined to denote the name as a species name. A complete species name is also followed by the name of the author who named it. Author names are often abbreviated, and many author names have official abbreviated forms. An example of a species named by Linnaeus is *Brassica rapa* L. (the L. stands for Linnaeus). The author's name should not be italicized or underlined. Once a genus has been referred to in a scientific paper, later references to species within the genus can then be written with the genus abbreviated to just the first letter and the author's name is left off: for example, *Brassica rapa* L. becomes *B. rapa*.

In a species with a lot of variability, subspecies and varieties can also be described. Some plant taxonomists consider subspecies to be of higher taxonomic rank than varieties, whereas others treat them as equivalent. Often particular taxonomists will use only one of these ranks to describe taxa below the species rank. Any species can be split into two or more varieties or subspecies. The variety or subspecies that contains the type specimen is always considered the typical variety or subspecies. For example, the species *Abies magnifica* Andr. Murray (California red fir) has been divided into two varieties. The typical variety is *A. magnifica* var. *magnifica*, and the other variety is *A. magnifica* var. *shastensis* Lemmon. Notice that the word "variety" is abbreviated as "var." and is not italicized or underlined and that the name of the author of the variety follows the variety name (except for the typical variety, where the author is assumed to be the author of the species). The word "subspecies" is abbreviated as "ssp." and is also not italicized or underlined.

For the sake of simplicity, italics are now often used for taxonomic groups higher than the genus, all the way up to the phylum. However, strictly speaking, only the genus and species names are italicized.

How Names Are Chosen

Names can be chosen for a variety of reasons and can be derived from anything, as long as the source word is Latinized, if it is not already in Latin. One of the most common name choices is one that describers some obvious characteristic of the plant. For example, the genus name *Trillium* nicely describes the fact that essentially all the plant parts are in three's (*tri-* meaning "three"), and the species epithet for *T. albidum* nicely describes the striking white petals of this species.

Names can also be derived from the geographic location where the plant is found. These kinds of names are most commonly found in species epithets, such as *Juniperus californica* (California juniper) or *Carex norvegica* (Scandinavian sedge). In rare cases, a genus will be named after a place, as in *Idahoa*, a mustard genus found in Idaho and elsewhere in the western United States.

Another popular approach is to name a plant after someone famous, as in the genera *Darwinia* (after Charles Darwin) and *Linnaea* (after Carolus Linnaeus). Species epithets are often given the name of the person who collected the plant. Examples of this type include *Pseudotsuga menziesii* and *Iris douglasii*.

Some species are named with less originality, using very common Latin epithets. For example, *Juncus ambiguus*, meaning ambiguous, not only is nondescriptive but also leaves some doubt about what the author intended. Then there is *Fritillaria affinis*, where the epithet *affinis* simply means "like." Like what? In cases like these, it may be necessary to refer to the original publication where the species is described to understand why the name was given.

Naming Rules: Above the Genus

Above the genus the type concept is used to determine correct names. All family names must be derived from a genus name within the family. For example, the rose family is called *Rosaceae*, which is derived from the genus *Rosa*, and the lily family is called *Liliaceae*, which is derived from the genus *Lilium*. Exceptions to this rule are only allowed when acted upon by the International Botanical Congress. In 2001, there were only eight exceptions to the family naming rules. These are referred to as conserved family names and are of long-standing usage. These *conserved names* can be used, but each also has a name derived according to the rules, and the names can be used interchangeably. The eight conserved names, and their alternatives (in parentheses) are *Palmae* (*Arecaceae*); *Gramineae* (*Poaceae*); *Cruciferae* (*Brassicaceae*); *Leguminosae* (*Fabaceae*); *Guttiferae* (*Clusiaceae*); *Umbelliferae* (*Apiaceae*); *Labiatae* (*Lamiaceae*); *Compositae* (*Asteraceae*).

Two common ranks between the family and genus are subfamily and tribe. Names for these should also follow the type concept, with their name being derived from a genus within them. The proper suffixes for subfamilies and tribes are *-oideae* and *-inae*, respectively.

Ranks above the family level can be chosen either by the type concept or by using a common characteristic of members of the taxon. Standard suffixes for these higher ranks are mentioned above. Using the type concept, the flowering plants, or angiosperms, are phylum *Magnoliophyta* (based on the genus *Magnolia*), but a common alternative name is *Anthophyta*. Likewise, the gymnosperms are phylum *Pinophyta* (after the genus *Pinus*), but are also commonly called *Coniferophyta*. In each of these cases, both names are valid and are used preferentially by different plant taxonomists.

Sometimes, not only the names will differ, but even the suffixes may not follow the standards. For example, using the type concept, the class names for the monocots and dicots (the two major groups of flowering plants) are *Liliopsida* and *Magnoliopsida*, respectively. Alternative names, in common use, are *Monocotyledones* and *Eudicotyledones*, respectively.

Why Names Change

Some common reasons that names change are the result of changes in taxonomic opinion, the discovery that the current name is not the oldest published name, or the discovery that it has some other technical problem. Although such name changes can be annoying and unpopular to some people, they are essential if the ICBN is to be followed. If plant taxonomists and others were to be free to ignore the rules, then confusion would result.

Plant taxonomists are continually studying relationships among plants, and as new discoveries are made, they are incorporated into the classification system. Sometimes it is discovered that a species needs to be split into two species, in which case the plants that include the holotype retain the original name, and the remaining plants are given a new name. On the other hand, separate species are sometimes found to be so similar that they are reclassified as belonging to the same species, in which case all the plants from both original species are given the name that was published first. These same rules must be applied to all taxonomic levels whenever taxonomic conclusions warrant splitting or joining of taxa.

Changes in classification at the genus level can also affect species names. For example, if two genera are found to be so similar that they end up being combined into one genus, or some of the species from one genus are found to be more related to members of another genus and are therefore moved into it, species names will be affected. When this happens, the new species name will carry two authors' names after it (the original author of the old species name and the author of the new species name), and it is considered a new combination. The species does not have to be redescribed, but the change must be validly published. Thus, the species *Castilleja exserta* (A. A. Heller) Chuang & Heckard used to be in the genus *Orthocarpus* and was called *Orthocarpus exsertus* A. A. Heller. Note that the author of the original species name appears in parentheses. Also note, in this case, that the ending of the species epithet had to be changed slightly to follow proper rules of Latin grammar. Similar rules are followed when a taxon changes from a species to a variety (or some other lower rank) or vice versa. For example, *Potentilla breweri* S. Watson was later determined to be so closely related to the *P. drummondii* Lehm. that it was changed to a variety of this species, *P. drummondii* var. *breweri* (S. Watson) B. Ertter.

Sometimes a simple study of the published names of taxa in a particular plant group reveals that a currently used name is invalid according to ICBN rules. For example, it may be discovered that the same species name has been published twice, by different authors who have also identified different holotypes. In this case the current name is considered illegitimate and cannot be used, and the name must be changed to the next oldest validly published name. Alternatively, it may be discovered that a currently used species name is not actually the oldest validly published name, in which case the name must be changed to the older name. Such changes can be controversial, especially when the species is very common and is used by many people who are not plant taxonomists themselves. Nontaxonomists do not often understand the reasons for such changes. A notable example of this problem is for the species *Pseudotsuga menziesii* (Mirb.) Franco. The name *P. douglasii* Carr. was used for many years and led to the use of the common name Douglas fir. This species is extremely important to foresters, and when the name had to be changed, many resisted the name *P. menziesii*. With the change in scientific name, the common name should probably be Menzies fir, but it remains Douglas fir.

Future of Plant Taxonomy

Plant taxonomy is a field that has completely embraced modern methods and uses data from molecular genetics, biochemistry, and electron microscopy to gain greater insights into plant evolutionary relationships. The use of computers to perform detailed phylogenetic and cladistic analyses has also revolutionized the field. A greater emphasis on evolutionary relationships and processes has led to a much better understanding of species concepts and relationships but has led others to consider doing away with the species concept as currently used. Continuing studies using modern approaches should lead to ever better classification systems that better reflect the evolutionary history of plants.

Bryan Ness

See also: Angiosperm evolution; Biochemical coevolution in angiosperms; Cladistics; Coevolution; Competition; Evolution: convergent and divergent; Evolution: gradualism vs. punctuated equilibrium; Evolution of plants; Fossil plants; Molecular systematics; Reproductive isolating mechanisms; Selection; Species and speciation; Systematics: overview.

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SYSTEMATICS: OVERVIEW

Categories: Classification and systematics; disciplines

Systematics is the description and study of the diversity exhibited by living organisms. The goal of systematics is classification, or assigning an organism to a particular category within a logical scheme that accurately reflects underlying patterns of evolutionary relationships. The evolutionary history of an organism—its patterns of ancestry and descent through time, on which systematics and classification are largely based—is the organism's phylogeny.

In a formal scientific sense, *systematics* is the study of the diversity exhibited by living organisms and their evolutionary history. It involves the accurate and precise description of organisms and their *diagnostic* (distinguishing) features, the use of a uniform system for assigning names to organisms, and the development of an appropriate classification scheme to reflect the evolutionary relationships among the organisms being considered.

Systematics itself can be subdivided into several phases. The first phase of systematics, *identification*, involves the determination of whether an unknown plant belongs to a known, previously named group of plants. This is often achieved by examination of a diagnostic manual for plant identification, consultation with reference collections of plants (termed *herbaria*), and collaboration with an authority who possesses expertise with a particular group. The uniform system for naming organisms is referred to as *nomenclature* and typically involves using a Latin binomial (a genus name followed by a species name) to designate a particular organism's species name. The use of a uniform nomenclature is arrived at through consensus and greatly facilitates communication among scientists when discussing organisms.

The final, and perhaps most elusive goal of systematics, *classification*, entails assigning an organism or group of organisms to a particular category in a logical hierarchical scheme that accurately reflects underlying patterns of natural (that is, evolutionary) relationships. This hierarchical scheme typically consists of large inclusive groupings (such as classes and orders) containing less inclusive, progressively nested groups (such as families, genera, and species). A group of organisms at any hierarchical level can be abstractly referred to as a *taxon*.

In a strict sense, *taxonomy* can be defined as the science of assigning names to groups of organisms. The major difference between systematics and taxonomy is evolutionary, in that systematics encompasses all that taxonomy strives for and also attempts to re-create or elucidate the evolutionary history of the organisms under investigation. In essence, the ultimate goal of systematics is the accurate description of the evolutionary history of organisms.

Homologous Versus Analogous Characters

Those diagnostic features of an organism that are used in its identification and subsequent classification are termed *characters*. The different manifestations of the characters are *character states*. Characters can involve any aspect of morphology, anatomy, biochemistry, and the genetic composition of an organism. The more reliable characters used for systematics must have a genetic basis; that is, they must be inherited in a predictable and reliable fashion and be subject to a minimal amount of variation by nongenetic factors. *Superficial characters*, which should be excluded from consideration, are subject to environmental modification or lack a predictable genetic basis. For example, the height of a plant or overall size of leaves typically are not good characters, as a number of environmental factors, such as nutrients, water availability, or soil depth and texture, readily influence these traits.

One difficulty faced by systematists is in determining the true nature of character similarities among different groups of organisms. *Homologous characters* have a direct evolutionary relationship (that is, a common origin). An example of such characters is the placentation of the ovaries in different taxa of the superorder *Caryophyllales*. Placentation is the arrangement of the placentas (the structures to which the ovules are attached) in the ovary. All *Caryophyllales* have free central placentation, basal placentation, or some form in between. It is presumed this kind of placentation arose first in the common ancestor to all members of this superorder.

In contrast, *analogous characters* have different origins but are similar due to convergent evolution. An example is the presence of the succulent habit (fleshy stems and highly reduced, absent, or modified leaves) in members of two families of different evolutionary origins, the *Euphorbiaceae* of the Old World and the *Cactaceae* (cactus family) of the New World. For an evolutionarily sound classification scheme, one needs to emphasize homologous characters and be extremely cautious in using analogous characters.

Evolution and Classification

Some previous classification schemes were highly *artificial*, in that they did not reflect true evolutionary relationships but rather grouped different organisms together on the basis of superficial similarities. One example of this is the classification of plants based on their growth form, such as grouping all woody plants together, all herbaceous plants in a separate group, and shrubs in yet a third group. The publication of Charles Darwin's *On the Origin of Species by Means of Natural Selection* in 1859 prompted systematists to revise their thinking and cast their efforts at classification in an evolutionary context. This has been manifest in the efforts of systematists to elucidate the *phylogeny* of related groups of organisms.

In its essence, phylogeny refers to the evolutionary history of a group of organisms. This evolutionary history entails an understanding of the genealogy of a group or groups of organisms, their patterns of ancestry and descent through time. This conceptual approach is analogous to reconstructing a person's family tree or genealogy from often fragmentary and indirect evidence.

Phylogenetic Systematics

Phylogenetic systematics focuses on evolutionary processes and speciation events as core components of classification. The objective is to describe the results of speciation events (the species themselves) and to document the events and processes that have led to the present state of biological diversity. Classification is an attempt to reflect the evolutionary history of the living organisms and their *lineages*. A group of organisms that resemble one another and have a common evolutionary origin is termed a lineage. This concept often includes the ancestral population that first gave rise to this group of organisms and all individuals, both extant and extinct, that are members of that particular group. To achieve this goal, systematists rely on observable features and traits of the organisms and distinguish between the different means by which these characters might arise in different groups of organisms.

Most systematists use character similarities as a basis for grouping organisms together, but this can cause some difficulty in terms of homologous versus analogous characters. However, not all homologous characters are of an identical nature in terms of origin and persistence through time. This problem of distinguishing the true nature of character similarities has been taken to a higher level by phylogenetic systematists through a methodology termed *cladistics*. In this framework, the nature of homologous characters is further distinguished. Character states that are present in the evolutionary ancestor or ancestral population of a particular organism or set of organisms are referred to as *ancestral*. Character states that are absent in the ancestor but present in descendants are referred to as *derived*. Ancestral states that are shared by both ancestral and descendant, or derived, organisms are termed *symplesiomorphic*. Derived character states not present in the ancestral organisms but shared by two or more lineages are termed *synapomorphic*. A novel character state that is present in only one lineage, and therefore has little use in classification outside that lineage, is termed *autapomorphic*.

A key tenet of phylogenetic systematics is that only *monophyletic* taxa should be formally recognized. A monophyletic group consists of an ancestral taxon and all its descendant taxa. A *polyphyletic* group is composed of two or more ancestral taxa and their descendant taxa and is not an evolutionarily appropriate grouping. Some traditional classifications use polyphyletic groups, and there is much discussion regarding the scientific validity and utility of such schemes.

Phylogenetic Trees

A common way of communicating phylogenetic relationships or patterns is through *phylogentic trees*, which are diagrammatic representations of the genealogy of taxa or patterns of relationships. Typically, a decision is made as to which taxa or character states are of recent origin and which occurred in the past. The origin of the tree is referred to as the *root*, and the character changes across the tree (from ancestral to derived taxa) are given a directionality (ancestral versus derived) that is termed *polarity*. In general, phylogenetic trees are rooted (and therefore the directionality of evolutionary change determined) using a near-relative taxon, termed the *outgroup*, of the group under consideration.

Ideally, all aspects of the phylogenetic tree should be testable, as with any sound scientific hypothesis. Great progress has been made in evaluating the evolutionary relationships of the flowering plants through phylogenetic systematics. Undoubtedly, with the use of new characters and the development of improved methods of data analysis, further progress in this rapidly changing field is certain.

Pat Calie

See also: Angiosperm evolution; Biochemical coevolution in angiosperms; Cladistics; Coevolution; Evolution: convergent and divergent; Evolution: gradualism vs. punctuated equilibrium; Evolution: historical perspective; Evolution of plants; Flower types; Fossil plants; Molecular systematics; Systematics and taxonomy.

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TAIGA

Categories: Biomes; ecosystems; forests and forestry

"Taiga" derives from a Russian word for the forests of cone-bearing, needle-leaved, generally evergreen trees of northern Eurasia and North America. "Coniferous forest" and "boreal forest" are other names given to this biome. Some botanists include the temperate rain forests along the Pacific Coast of North America and the coniferous forests in the western mountains in the taiga.

While the term "coniferous forest" can be applied to temperate rain forest and coniferous forest biomes in the western mountains, the terms "taiga" and "boreal forest" should be restricted to the northern forests. "Taiga" is also sometimes used in a more restricted way, to mean a subdivision of the boreal forest.

Components

The dominant plants in the taiga are cone-bearing, needle-leaved, evergreen trees, such as pines, spruces, and firs. North American taiga is dominated by two species of spruce: black spruce (*Picea mariana*) and white spruce (*Picea glauca*). Jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), and eastern larch (*Larix laricina*, a deciduous conifer) are also important in parts of the taiga. A few deciduous flowering trees are also important components. Quaking aspen (*Populus tremuloides*, the most widespread tree species in North America) and paper birch (*Betula papyrifera*) are two examples. Eurasian taiga is dominated by related species of spruce and pine and has the same character.

Determinants and Adaptations

Taiga occurs in a broad band across Canada, Alaska, Siberia, and Europe; essentially, this band is interrupted only by oceans. This pattern suggests that climate plays a major role in determining the distribution of the taiga. Average temperatures are cool, and precipitation is intermediate, but evaporation is low because of the cool temperatures. Hence, moisture is generally available to plants during the growing season. The growing season is short, and winters are long. *Permafrost* is present in the northern part of the taiga, and wetlands are common because drainage is often deficient. These physical conditions are primarily determined by the high latitude at which taiga occurs, but why taiga develops under these conditions is not entirely clear.

The length of the growing season may help explain why the dominant taiga trees are evergreen. Because they retain their leaves through the winter, these trees can carry out some photosynthesis on mild winter days. More important, they avoid the energetic expense of replacing all their leaves at one time. Deciduous trees put tremendous amounts of energy into leaf replacement each spring and must replace those energy stores as well as produce energy for growth during the growing season. Deciduous forests generally occur south of the taiga, where the growing season is longer. However, some deciduous trees are successful in the taiga, so other adaptations must also be important.

Asexual reproduction probably contributes to the success of taiga trees, especially in severe environments. Black and white spruce reproduce by *layering*, the growth of a new tree from a lower branch which makes contact with the ground. Most deciduous trees of the taiga can sprout from the roots or other underground parts if the aboveground part of the tree is damaged or killed. Both strategies allow new trees to develop using the resources of the parent tree. In contrast, some plants growing from seed do not have sufficient resources to survive.

Fire is an important environmental factor in the taiga. Many of the conifers produce at least some cones which open and release their seeds only after they have been heated intensely, as in a forest fire. Jack pine responds to fire this way, as does black spruce to a lesser extent. Most deciduous trees send up new stems from undamaged underground parts after a taiga fire. White spruce does not employ ei-

The dominant plants in the taiga are cone-bearing, evergreen trees. A few deciduous, flowering trees are also important components, such as these aspens, the most widespread tree species in the North American taiga.

ther of these strategies but does have efficient seed dispersal and so can move into a burned area fairly quickly. Similar adaptations make Eurasian taiga species fit for life in northern environments. Apparently, no single suite of adaptations suits a tree species for taiga life; instead various combinations of characteristics are employed by the different species.

Adjacent Zones

The taiga is bordered by tundra to the north, and the meeting place between the two biomes is a broad transition zone often called the "taiga-tundra," or forest-tundra. This *ecotone* is composed of a mixture of forest and tundra plants, with trees becoming fewer and smaller from south to north until conditions become so harsh that trees can no longer grow.

The southern boundary of the taiga is often adjacent to deciduous forest, grassland, or parkland. These are also broad, transitional ecotones. In eastern North America, the northern hardwood forest region is such a transition zone and is composed primarily of a mixture of trees from the deciduous forests and the taiga. The aspen parklands in the west are also transitional. Quaking aspen from the taiga and grasses from western grasslands mix in this zone between the taiga and grassland biomes.

Environmental Concerns

Human activities may have less impact on the taiga than on many other biomes, primarily because the taiga occurs in a harsh environment less accessible to humans than many other biomes. Still, there are serious concerns. Acid rain became a problem for the taiga in eastern Canada in the late twentieth century. These forests are northeast of the industrial centers in the United States, and the prevailing southwesterly winds move nitrogen and sulfur oxides into eastern Canada, where they precipitate on plants and soil. Both oxides interact with water to produce acids, thus acidifying the soil and plant leaves. Many ecologists believe that acid precipitation has seriously damaged the taiga of both North America and Eurasia.

Global warming is a second and perhaps more insidious threat to the taiga. The taiga will almost certainly be negatively impacted by changes in temperature, the length of the growing season, fire frequency and intensity, and precipitation patterns. Taiga itself may play a role in carbon storage and mitigation of the greenhouse effect. This possibility, its role as a source of timber, and the inherent value of the biome and its component species make it imperative that the taiga be conserved.

Carl W. Hoagstrom

See also: Acid precipitation; Arctic tundra; Biomes: definitions and determinants; Biomes: types; Community-ecosystem interactions; Conifers; European flora; Forest fires; Forest management; Forests; Greenhouse effect; Gymnosperms; North American flora; Old-growth forests; Sustainable forestry; Timber industry; Tundra and high-altitude biomes.

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TEXTILES AND FABRICS

Categories: Agriculture; economic botany and plant uses

Cotton, flax, ramie, hemp, jute, and other cellulosic fiber plants are all sources capable of producing textiles and fabrics that can be used to create knitted, woven, or nonwoven cloth material or fiber and yarn intended for fabric production.

All textiles are made through the use of *fibers*, thin strands of natural or artificial material. A fiber is a threadlike strand, usually flexible and capable of being spun into *yarn*. About forty different fibers are of commercial importance. While textiles are primarily made from yarn, they are also made by felting, which is the process of pressing steamed fibers together to make cloth. All knitted and woven textiles are made from yarn, while fibers alone are used to produce nonwoven cloth. The invention of the spinning machines and weaving machines during the Industrial Revolution greatly increased production and boosted the demand for fibers.

The textile industry has created a tremendous diversity of products available for use in clothes, home furnishings, and industrial and special applications. These products are fabricated from natural resources such as animals, plants, and minerals, as well as from synthetic compounds. The major classifications of fibers by source are natural and artificial. *Natural fibers* are those fibers found in nature such as those from animals and plants.

About 5000 B.C.E., in Egypt's Nile Valley, the flax plant was grown and processed into a cloth which was used to wrap mummies of Egyptian rulers. By about 3000 B.C.E., people in Switzerland, India, and Peru were using cotton. The trade in textiles as an international commodity began around 1700 B.C.E. as cotton manufacture became more developed in China, Egypt, India, Iraq, and Africa. In more recent history, the Industrial Revolution had a profound effect on the making of textiles, and textile manufacturing was established by the early 1900's as an industry in many countries of the world.

Plant Fibers

A major plant fiber source is the cellulose from plants. Cellulosic fiber can be found in a plant's leaves, stems or stalks, seed pods, or fruit, as applicable. Pina, from the pineapple plant, is an example of a leaf fiber. Flax, jute, ramie, and hemp are fibers taken from a plant's stem or stalk, also known as *bast fibers*. Cotton and kapok are examples of seed pod and fruit fibers. Azlon fibers are produced from proteins found in soybeans and corn. Cotton and flax are the major plant fibers. One plant source which is not cellulosic is sap from the rubber tree, which can be processed into yarn.

Fiber Makeup

The textile fabric that one can see and touch is composed of many individual fibers. The differences between fibers is determined by their chemical composition and individual unique structure. Molecular combinations of different elements are called compounds. Any particular (molecular) compound always contains the same type and number of elements and their atoms. This gives each compound unique characteristics that determine its particular end use as a textile. When many molecules making up a compound are connected to one another in a line, they form a *linear molecule*. If this linear molecule is very long, it is called a *polymer*. Animal hair, the living matter of plants, and some synthetic compounds all contain polymers. These long-string linear molecular compounds are the building blocks of fibers, which can then be made into fabrics. When polymers are formed synthetically, the process is called *polymerization*.

Only a few elements, in different combinations, make up all the natural and artificial fibers in textiles. For example, carbon, hydrogen, and oxygen, in various combinations, make up all the plant cellulosic fibers. The protein fibers contain nitrogen as well. Chlorine, fluorine, silicon, and sulfur are other elements found in some fibers. Artificial fibers may be constructed from natural polymers that have been reshaped or from synthesized polymers made through chemical processes.

All fabric fibers have a characteristic length; these range from less than 0.375 inch to more than 40 yards (1 centimeter to 36 meters). A relatively short fiber ranging from fractions of an inch to a few inches is known as a *staple fiber*. A relatively long fiber measured in yards is known as a *filament fiber*. A natural fiber is always used in the length in which it has grown. Artificial fibers, on the other hand, can be made in any length, regardless of whether they are reshaped or synthesized. The end use application of the artificial fiber will determine what its optimum length should be.

Artificial Fibers from Plant Sources

After their early beginnings in the late 1800's, there was wide-ranging development of artificial fibers in the 1900's. There are two subgroups of artificial fibers: reconstituted or altered fibers made from natural sources, and fibers made from chemical compounds. Artificial fibers are produced from compounds having a wide range of chemical composition and internal structure. However, this range of products can be broken down into groups of fibers that have similar composition and structure. A generic name is given to each of these groups. For naturally occurring materials there are six generic families: acetate/triacetate, azlon, glass fiber, metallics, rayon, and rubber. All these families are legally defined and identified. Manufacturers making any of these products register a trademark name (or trade name) for their particular fiber.

Developed as a substitute for silk, the first artificial fiber was named rayon around 1925. *Wood pulp* is the major cellulose source of raw material used to produce rayon fiber. Cotton linters (a byproduct of cotton production) is another source. These sources are chemically processed to extract and purify the cellulose. In regenerating cellulose into rayon, the purified cellulose undergoes several chemical and mechanical treatments before being forced through a spinneret machine. Acetate and triacetate are two other artificial fibers that are based on cellulose as a raw material.

PhotoDisc

Cotton, one of the major plant fibers worldwide, is an example of a seed pod fiber.

Yarn

Yarn is generally defined as a continuous strand of fibers spun together as a group which can then be used to make fabrics. In practice, the majority of yarns are made in one of four ways: twisting a number of (short) fibers together, twisting a number of (long) filaments together, laying a number of (long) filaments together without twist, or twisting or not twisting a single (long) filament to produce a *monofilament* (thread).

Yarn should be strong, flexible, and elastic so that it can be braided, knotted, interlaced, or looped as it is processed by various methods into a fabric. A system of producing tightly twisted yarns results in worsted yarn that is firmer and smoother than regular yarn. Yarns are often made by blending two or more different fibers to combine the strong points of each. When a manufactured yarn is texturized the long, plain, uniform yarn is changed to exhibit bulk, loft, and three-dimensional appearance. Stretchability may also be included. Yarns are curled, crimped, and twisted when texturized.

Textile Production

The major textile production methods are *weaving* and *knitting*. Minor methods produce braids, nets, lace, tufted carpets, and other products. The only fabrics made which do not use yarn are those nonwoven fabrics made directly from fibers before they are processed into yarn. Felt is the traditional nonwoven product. Textiles can be classified by their weave or structure. The value of a textile depends on many factors, primarily the quality of the raw material; the characteristics of the fiber/yarn; smoothness, hardness, and texture; fine, medium, or coarse fibers/yarn; density of yarn twist and density of weave; dyes/colors and pattern; and finishing processes.

A major method for producing fabrics is weaving, in which yarns are interlaced at right angles to each other. This method was used by the ancient Egyptians. Weaving continued to be done by hand as a manual labor task until machines were developed during the Industrial Revolution. The invention of the flying shuttle and the steam-powered loom in the 1700's were major contributors to automating the weaving process.

Three basic types of weaves are plain, twill, and satin. There can be variations within each of these three weaves. Besides the type of weave and the yarn types used, another variation of the weaving process is how close together the yarns are interlaced.

Knitted fabrics are formed by continuously interlooping one or more yarns. The knitting process may have been used to make fabrics as early as the first century. Knitting remained a hand labor skill until the eighteenth century, when powered knitting machines were developed.

Various knitting processes within the basic weft knit type include plain knit, purl knit, rib knit, and interlock stitch. Weft knits are produced by machine and by hand. For another basic method, the warp knitting process uses a machine in which many parallel yarns are interconnected simultaneously to form loops in the lengthwise direction. Within the basic warp type process, tricot knitting and raschel knitting are two methods used. Special processes that are variations of the two basic methods, sometimes in combination with special yarns, produce double knits, high pile knits, Jacquard knits, full-fashioned knits, textured knits, stretch knits, and bonded knits.

Finishes

Finishes are the treatments given to fibers, yarns, or fabrics to improve their basic characteristics. The three types of finishes employed are mechanical treatments, heat treatments, and chemical treatments. It is common for one or more of these treatments to be applied to practically every fabric produced. They change the appearance of the product, as in its look or feel, or add a functional characteristic such as waterproofing or flameproofing. Brushes, rollers, and hammers may be used in mechanical treatments. Heat-setting of thermoplastic material is a common heat treatment. Chemicals such as acids, bases, bleaches, polymers, and reactive resins are used to chemically change the characteristics of a material.

The aesthetic finishes, by process name, include bleaching, brushing and shearing, calendering, carbonizing, crabbing, decating, fulling, glazing, mercerizing, napping and shearing, scouring, singeing or gassing, sizing, and tentering. The functional type finishes make textiles abrasion-resistant, antibacterial, antisoil and antistain, antistatic, durable press (permanent press), flame/fire retardant/resistant, moth repellent, permanently crisp, shrink resistant, waterproof, water repellent, or wrinkle resistant.

Fabric Design

The major elements of fabric design are the *visual* (how it looks) and the *tactile* (how it feels). Solid colors or shades of black, white, and all colors can be applied in an unending combination of patterns and designs. The feel of the fabric can be varied by the types of yarn used, the fabrication method, how the color pattern is applied, and the types of finishes used. Dyeing and printing are two major methods of applying a pattern, color, or both, to a fabric. Dyes can be applied to fiber, yarn, or fabric. Color can be applied by at least three methods: directly, the discharge method, and the resist or reserve method. Printing is typically done by methods such as roller printing, block printing, toiles de Jouy, stencil, screen printing, spray printing, electroplating, and by hand.

The Textile Industry

The textile industry is dynamic, with new processes, techniques, and methods constantly being developed. Sometimes they add to, and sometimes they replace, previous ways of operating. The idea of evolution and change can be applied to all parts of the industry, such as raw material and fiber development, yarn production technique, fabrication method, finishing technology, and the printing, dyeing, and design processes. The primary goal of all research and development is to sell a product attractive to consumers. Consumer research is an important factor in determining what the public wants, thereby helping to drive and focus the technology in particular directions. Federal laws govern textile labeling and product advertising, and the industry has developed voluntary self-regulating product quality and testing standards.

Robert J. Wells

See also: Agriculture: history and overview; Australian agriculture; Biopesticides; *Bromeliaceae*; Cacti and succulents; Cycads and palms; Farmland; Fertilizers; High-yield crops; North American agriculture; Plant domestication and breeding; Plants with potential; Soil degradation; Timber industry.

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THIGMOMORPHOGENESIS

Categories: Movement; physiology

Thigmomorphogenesis refers to the influence of mechanical stimuli on plant growth and development. Many plants respond to stimuli such as wind or touch, intentionally by human beings or unintentionally by farm machineries and animals.

Plants subjected to thigmomorphogenesis, or physical disturbances such as wind and touch, generally respond through reduction in the rate of stem elongation and shoot height, and they increase in stem diameter. All of these features result in the formation of short, stocky plants. This response is purely adaptive and allows individual plants to compensate for the different levels of stress that occur in their natural environment. The advantage of this is that shorter and stronger plants are less easily damaged by natural mechanical stresses (especially wind) than their taller, more slender counterparts. Inhibitory effects of mechanical stress on flowering of a few species have also been observed. Thigmomorphogenesis is common and may be as important to plants as their responses to light, temperature, water, and gravity.

Response Indoors

The indoor plant environment (greenhouses, sheds, and homes) influences the plants' hardiness with regard to mechanical stimuli. Unless deliberately altered, the indoor space is typically a calm, windless environment. Moving air causes a plant to lose moisture faster; in contrast, a windless environment encourages the development of a thin *cuticle* (waxy layer on outer epidermal walls, such as leaf surfaces). The absence of physical disturbance also promotes formation of long cells with thin *cell walls*. These modifications result in the development of slender stems, which are not adapted to the buffeting provided by the wind outside.

Tall plants usually occur under indoor conditions where there is a relatively low light level and few physical disturbances. These morphologies are simply a response to the environment in which the plants are grown and, unless conditions change, these plants are well adapted to such an environment. Problems occur once the plants are transplanted outside because of the dramatic change in environment. On the other hand, plants in the wild are hardened by the wind, bright sunlight, lack of nutrients, and fluctuations in soil moisture and therefore show little further response to mechanical stress.

Response in Nature

Wind-tolerant and wind-intolerant genotypes exist within any population of plants. The plants that are capable of withstanding high levels of physical disturbances will respond by modifying their structures. They respond by growing more slowly and changing the way they build their cells. The cells that are produced are short and thick-walled, thereby making for short, sturdy plants. The decrease in elasticity also provides plants with a means of absorbing the strain within their structures. In trees, the response is usually increased *taper*, which is the result of a reduction in height or increase in radial growth. Increased radial growth confers bending stiffness and maintains a tree's vertical orientation in windy environments.

Location of Response

It has been shown that plants' response to mechanical stimuli is localized and not whole-plant-based, as was previously thought. The more highly stressed areas of the plants, such as the base of the stem, are the areas that exhibit the greatest response. Most information available deals with the effects on aerial components of plants. Knowledge of the effects on roots is quite limited. To examine this, researchers have compared corn and sunflower plants that have been flexed with still ones. It was found that both species were able to change the morphologies and mechanical properties of their roots in response to wind. Furthermore, mechanically stimulated plants were found to have more numerous, thicker, and stiffer roots than still plants.

Perception of Stimuli

How do plants perceive mechanical stimuli? Calcium ions have been implicated in mediating various growth responses including thigmotropism and thigmonasty (discussed below). Calcium may also be involved in thigmomorphogenesis. Differentially expressed genes have been isolated and are being identified to increase knowledge of the molecular and physiological responses of plants to increased mechanical stimuli. In *Arabidopsis*, mechanical stimuli appear to induce the expression of certain genes that encode proteins related to *calmodulin*, a calcium-binding protein. Calcium levels have also been reported to increase in stressed cells. Deformation of stressed cells may result in the opening of calcium channels in the cell membrane. Ethylene, a gaseous plant growth regulator, has also been implicated because mechanical stimulation results in increased ethylene production.

Commercial Application

Thigmomorphogenesis is especially important for vegetable producers who use automated crop transplanters in the field and where robustness of the seedlings is important. Scientists are aware that plants grown in greenhouses tend to be thin and limp as a result of high temperatures, low light levels, abundance of nutrients, and low wind speeds. Automated machinery easily damages these kinds of plants. To counter this problem, commercial agriculturists often resort to the use of chemical growth regulators, high concentrations of fertilizers, salts, and water-absorbent gels. They also reduce the amounts of nitrogen and phosphorus available to the seedlings.

By a simple technique of brushing or stroking plants several times a day, these problems may not only be overcome, but crop quality may also be significantly improved. Several kinds of plants have been shown to respond very well to mechanical stimulation. The technique of brushing or stroking seedlings has been shown to work on a variety of vegetable plants, such as cabbage, lettuce, tomatoes, cucumbers, and bedding plants including petunias, fuchsias, marigolds, and salvia. The effect of thigmomorphogenesis can also be used when planting trees. When short stakes are used instead of a long ones, the unsupported part of the stem can flex, making it stronger and tougher.

Other Plant Responses

Thigmomorphogenesis may be confused with *thigmotropism* and *thigmonasty*. In thigmotropism, the plant responds directly to the direction of the source of the stimulus. For example, contact of tendrils stimulates the coiling response caused by differential growth of cells on opposite sides of the tendril. In thigmonasty, the response is unrelated to the direction of the source of stimulus. An example of thigmonasty is the movement of the leaves of sensitive plants due to the rapid change in turgor pressure in specific cells at the base of leaflets. Thigmomorphogenesis is related to thigmonasty because the response is also not in the direction of the stimulus. However, thigmomorphogenesis involves alteration of growth pattern and is irreversible.

Danilo D. Fernando

See also: Heliotropism; Nastic movements; Tropisms.

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TIMBER INDUSTRY

Categories: Economic botany and plant uses; environmental issues; forests and forestry

The timber industry comprises a diverse group of companies and organizations using wood and fiber harvested from forests in the production of solid wood products (such as furniture and lumber), reconstituted wood products (such as particle board), pulp and paper, and chemicals.

Globally, about 3.8 billion cubic meters of wood were used for human consumption in 1995. The rate was increasing by 2.3 percent per year, faster than the rate of population growth. More than fifty thousand establishments in the United States are involved in the manufacture of *forest products*, and this industry contributed approximately 8 percent of the United States' gross national product in 1980. In addition, many other commercial products are derived from forest resources, including types of fuel, medicine, and food, and specialty items such as Christmas trees. Globally, the Food and Agriculture Organization of the United Nations (FAO) estimated in 1992 that more than one-half of all harvested wood is used for fuel and that the majority of energy needs in many developing countries is met by fuel wood. The FAO found in 1995 that the global demand for wood was about 3.8 billion cubic meters per year and that this demand was increasing by about 86 million cubic meters per year.

Historical Significance

The development of the forest products industry parallels the development of Western civilization. From Robin Hood to Paul Bunyan, the utilization of forest products is ingrained in Western mythology and culture. Development of the first *forest management* techniques in the Middle Ages was motivated by security interests related to the continued availability of wood for shipbuilding. In North America, the westward movement of European culture was accompanied by, and in some cases motivated by, the development of the forest products industry. Eventually, first in Europe and then in North America, it was realized that natural forests could indeed be depleted and that it was necessary to develop techniques for regenerating and managing forest ecosystems to ensure a continued supply of wood products to meet human needs. This process is still occurring in many developing countries.

Old-Growth Forests

All ecosystems develop within the context of natural *disturbance cycles*. Whether the natural agent is fire, flooding, or windstorms, every hectare on the earth is subject to periodic disturbance even without the influence of human activity. The disturbance intervals may be very long in some systems; forests consisting of *late-successional* species that have not been disturbed in an extended interval are commonly referred to as *old-growth forests*.

The forest products industry developed through the utilization of these natural forests. As they became scarcer, forest management techniques were developed to ensure the restoration of forests following utilization. As old-growth forests containing large trees were depleted, manufacturing technology had to change to use smaller-sized material that could be harvested from *second-growth forests*. This led to the development of composite wood products such as oriented strand board, particle board, and laminated beams.

Sustained Yield

Humans obtained goods and services from natural forests for millennia before increasing population, the development of agriculture, and utilization technology begin to lead to the depletion of natural forests. Fear of the depletion of natural forests and an impending timber famine led to development of the *sustained yield* concept, which holds that forests should be managed to produce wood products at a rate approximately equal to the natural rate of biological growth. The development of the sustained yield concept was associated with the belief that properly managed forests could produce a continuous, never-ending flow of wood and fiber. This concept is still evolving to include recognition that the continued survival of all species and the maintenance of ecosystem structure and function, as well as the production of goods and services, are of vital interest to human society.

Effects of Timber Harvesting

It is possible to harvest forest products in such a way as to mimic natural disturbance and to ensure the continued functioning and survival of all ecosystem components. Unfortunately, there are many examples of harvesting that have led to long-term disruption and alteration of ecological processes. Nutrient loss, erosion, and species loss following poorly designed or implemented harvesting operations can result in the loss of biodiversity and a reduction in long-term productive capacity.

The removal of forest *canopy* trees, whether through harvesting or natural disturbance, leads to increased soil temperature, increased decomposition, increased leaching of nutrients and soil carbon, and, if extreme, a reversion to an *early-successional plant* community. Removal of the canopy trees will usually lead to increased erosion, which, if harvesting is not properly implemented, can be severe and result in degradation of water quality and aquatic habitat. Programs promoting fire protection in the twentieth century resulted in the interruption of natural disturbance cycles in many ecosystems. In these cases, artificial disturbance through harvesting may be the only way to ensure the continued presence of early-successional species in the landscape. In many cases, these early-successional tree species are fast growing, straight, and relatively easy to artificially plant and regenerate. These early-successional forests are ideally suited for the production of pulp and paper, fuel wood, and such products as posts and poles. The challenge to industrial and public land managers is to develop the appropriate mix of all successional stages in the

PhotoDisc

In North America, the westward movement of European culture was accompanied by, and in some cases motivated by, the development of forest products and timber industries.

landscape in order to ensure the continued survival of all species and the maintenance of ecosystem structure and function, while allowing for utilization to meet the needs of the globally expanding human population.

David D. Reed

See also: Coal; Erosion and erosion control; Forest fires; Forest management; Forests; Logging and clear-cutting; Old-growth forests; Rain-forest biomes; Succession; Sustainable forestry; Taiga; Wood and charcoal as fuel resources.

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TRACHEOBIONTA

Categories: *Plantae*; seedless vascular plants; taxonomic groups

Tracheobionta *is the subkingdom of plants that contain vascular tissues, xylem and phloem. They are commonly known as the vascular plants.*

Vascular plants are plants that have tissues called xylem and phloem as conducting tissues. *Xylem* is tissue composed of vessels, fibers, and tracheids responsible for upward conduction of water and dissolved minerals; it also functions as the supporting tissue of stems. *Phloem* is conducting tissue that is responsible for moving food manufactured in the leaves to other parts of the plant, including the roots. The botanical name for the vascular plants is *Tracheobionta*. This group of plants includes both seedless and seed plants, including the flowering plants (angiosperms).

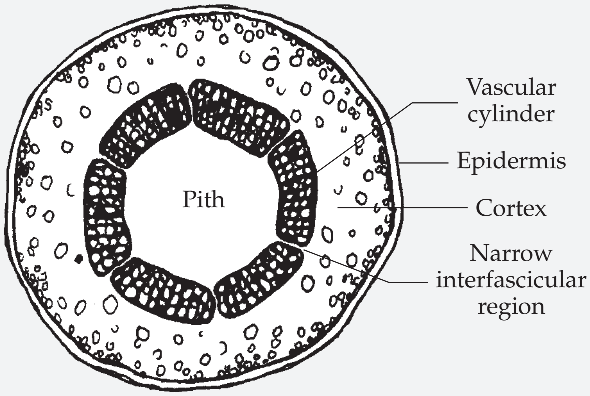
Fossil forms of *Tracheobionta* are well represented, because the tough, lignified cell walls of xylem preserve well. Most vascular plants produce seeds and are classified as *Spermatophyta*, but the ferns and related groups are seedless. Tracheobionts are primarily terrestrial, although some are epiphytic or aquatic.

Life Cycle

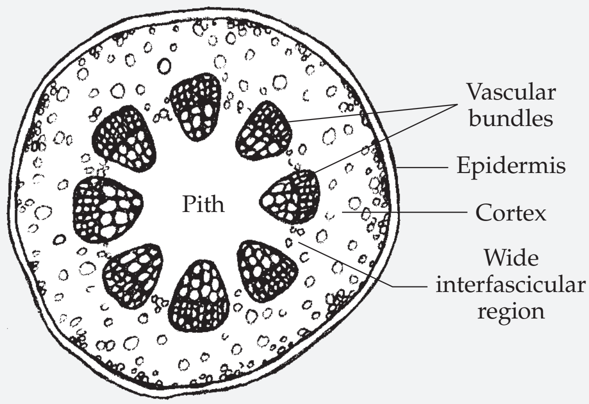
The life cycle of vascular plants is characterized by alternation of a conspicuous diploid sporophyte generation with a reduced haploid gametophyte generation, termed *alternation of generations*. The sporophyte exists independently of the gametophyte and typically exhibits indeterminate growth. That is, a single sporophyte plant can live and continue to grow for many years due to the activity of its apical and lateral meristems. The gametophyte, although free-living and independent in the more primitive vascular plants, is dependent on the sporophyte in seed plants.

The spores produced by the sporophyte fre-

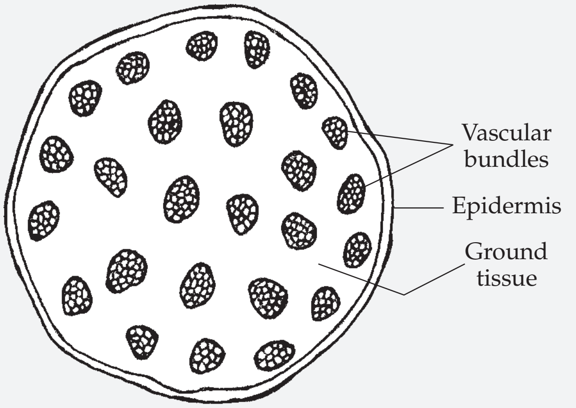
**Stem Structure
(transverse sections)**



Hollow cylinders surrounding the pith



Vascular bundles ringing the pith



Vascular bundles throughout the pith

Kimberly L. Dawson Kurnizki

quently have a tough, well-defined wall hardened by the wall material sporopollenin. Some seedless vascular plants, including most ferns, are homosporous; they produce a single type of spore. The spore germinates and grows out of the spore wall to form an exosporic gametophyte. This free-living haploid plant produces both antheridia and archegonia. *Antheridia* are saclike sex organs with a thin jacket layer of cells surrounding a mass of sperm cells. In seedless plants, and even in some of the seed plants, the sperm are flagellated and motile. *Archegonia* are typically flask-shaped sex organs with a thin jacket layer of cells surrounding a large egg cell. Part of the jacket is an elongate neck that provides a passage through which the sperm can swim to fertilize the egg.

All of the seed plants, and some ferns and fern allies, are *heterosporous*; that is, they produce both small microspores and large megaspores. Microspores form male gametophytes that produce sperm, whereas megaspores form female gametophytes that produce eggs. In seedless plants, the microgametophytes produce typical antheridia; in seed plants, the microgametophytes are pollen grains. In all but flowering plants, the megagametophyte produces archegonia. In flowering plants, the megagametophyte is an embryo sac. Both the mega- and microgametophytes are endosporic; that is, they develop within the original spore wall.

Vegetative Structure

The sporophyte of vascular plants typically has three distinctive vegetative organs: roots, stems, and leaves. Each contains xylem and phloem in a specific, predictable pattern characteristic of the division. The vascular tissues of stems and roots are called a *stele*. All roots have a simple stele with xylem forming a core in the center of the root, surrounded by phloem, either in a single sheath or in separate strands. In woody plants, multiple layers of xylem form in succession, pushing phloem and any external tissues outward. These layers of xylem are wood. Members of all divisions of vascular plants except psilotophytes form roots.

The *stems* of the simplest vascular plants have a stele similar to that of roots with a solid core of xylem in the center surrounded by phloem. In more specialized seedless plants, the pattern of xylem may be divided into separate bands surrounded by phloem. In stems of the most complex seedless plants, discrete vascular bundles form a ring around a core of parenchyma, the *pith*. In each bundle a core of xylem is surrounded by phloem; such stems are termed amphiphloic. Seed plants and horsetails have a similar arrangement, except that phloem is found only to the outside of xylem in each bundle; the stems are ectophloic. In woody plants, the ring of vascular bundles become connected by a vascular cambium that produces a succession of layers of new xylem, the wood. In monocot stems, the vascular bundles are distributed throughout the stem, rather than in a single ring surrounding a pith.

Leaves are characteristic of all divisions of vascular plants except some psilotophytes. The simplest leaves are small and scale-like and have a single vascular bundle forming a midrib. The vascular bundle in the leaf is a direct offshoot of the single vascular bundle in the stem. Such leaves are called *microphylls*. In plants with stems containing a pith, the leaves are supplied by one or more vascular bundles, which branch within the broadened blade of the leaf to form many veins. A gap is left in the stele where a leaf trace exits to supply the leaf. With a more extensive network of vascular tissue, these leaves are typically large and are termed *megaphylls*.

Sporangia

Sporangia are specific regions of the sporophyte body where meiosis occurs to produce spores. A single sporophyte can produce tens of millions of spores per year. The position, structure, and development of sporangia provide useful criteria for distinguishing the major groups of vascular plants.

In psilotophytes, two or three fused sporangia are located in the axils of leaves or leaflike appendages. In horsetails (*Sphenophyta*), sporangia terminate the main stem axis, forming a cone or strobilus. Lycophytes typically produce sporangia on the upper surface of leaves near their attachment to the stem. Depending on the group, these sporophylls may resemble vegetative leaves or may be concentrated into terminal *cones*. In ferns, sporangia also are typically localized on sporophylls. Frequently these sporangia are clustered in groups, called *sori* (singular "sorus"), on the edge or underside of the leaf. In gymnosperms, sporangia are concentrated in *strobili*, which can be quite large. Both the megasporangiate and microsporangiate cones of some cycads may approach a meter in length. In flowering plants, sporangia are localized in the flowers.

Among seedless vascular plants, two distinct sporangium types can be recognized based on structure and development. In the more primitive groups, a superficial layer of cells divides to form two layers. The outer layer forms the sporangium wall or jacket, while the inner layer becomes sporogenous tissue that undergoes meiosis to form spores. *Eusporangia* formed in this way have multiple-layered walls and frequently are at least partially embedded in vegetative tissue. In contrast, *leptosporangia* begin development from a single superficial cell. Following cell division, the inner of the two daughter cells forms a stalk that raises the sporangium above the vegetative tissue. The outer daughter cell eventually forms a single-layered jacket or capsule around a mass of sporogenous cells. Certain cells of the jacket layer differentiate to form an *annulus*, a specialized structure to open the sporangium and aid in spore dispersal.

Gametangia

Antheridia and archegonia are *gametangia* produced by the gametophyte. In vascular plants they are complex structures consisting of a sterile jacket layer of cells surrounding and protecting the gametes. Antheridia produce as few as four sperm (in *Isoetes*) to several thousand sperm in some eusporangiate ferns. All archegonia produce a single egg within a *venter*, the swollen base of the organ, which is usually embedded in gametophyte tissue. Extending out from the venter is an elongate *neck*, which becomes tubular when the neck canal cells degenerate to form an opening through which sperm can swim. At the base of the neck canal, adjacent to the egg, is a *ventral canal cell*.

The gametangia of seed plants are much reduced. The microgametophyte is a pollen grain, consisting of only two to four cells when it is released from the microsporangium. Depending on the group, zero, one, or two *prothallial cells* form, which represent the vegetative male gametophyte. The *tube cell* and *generative cell* may be interpreted as an antheridium. The generative cell divides to form two sperm. The megagametophyte of gymnosperms consists of a few thousand cells that typically form several archegonia, each consisting of four neck cells, a ventral canal cell, and a large egg. In flowering plants the entire megagametophyte, the embryo sac, typically contains only seven cells, one of which is the egg.

Embryogeny

In all plants with an archegonium, fertilization and the early stages of embryo development occur within the venter. This helps to establish a polarity with the first cell division. In all but the leptosporangiate ferns, the first cell division forms a new cell wall parallel to the surface of the gametophyte; one daughter cell faces inward, while the second faces out through the neck canal. In the horsetails and a few ferns, the *apical cell*, which will form the new sporophyte body, faces outward, a condition known as exoscopic. However, in most plants the apical cell faces inward (is endoscopic), and initially the embryo grows into the gametophyte tissue. As the embryo continues to grow, a *shoot apex* with leaf primordia forms at the apical end, and a *root apex* forms at the opposite pole.

Phylogenetic Trends

Some general evolutionary trends within the *Tracheobionta* are a reduction in the size and independence of the gametophyte generation and increasing dominance of the sporophyte. In the ferns and fern allies, the gametophyte may be photosynthetic and free-living, often resembling a very small liverwort in size and general shape. These are inconspicuous, however, compared to the large, leafy sporophytes. In seed plants, the larger megagametophyte is reduced to a countable number of cells, from a few thousand in gymnosperms to as few as seven in flowering plants. This gametophyte is retained within the sporangium and derives water and nutrients from the supporting sporophyte. This reduction is most dramatic in the microgametophyte, where the pollen grain consists of fewer than a handful of cells. Although the pollen of a few seed plants produces swimming sperm, in most cases a pollen tube grows to deliver sperm to the egg and free water is no longer required for fertilization.

In contrast to the reduction of the gametophyte, the sporophyte becomes increasingly larger and complex with development of the vascular tissues. Specialized organs, roots, stems, and leaves evolved for absorption of water and nutrients, to provide aerial support, and to increase photosynthetic surface area in a terrestrial environment. Development of vascular tissue provided the physical and physiological support required for the evolution of these structures.

Marshall D. Sundberg

See also: Angiosperms; Conifers; Cycads and palms; Evolution of plants; Ferns; Ginkgos; Gnetophytes; Gymnosperms; Horsetails; Lycophytes; Psilotophytes; Reproduction in plants; Seedless vascular plants; *Spermatophyta*.

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TRIMEROPHYTOPHYTA

Categories: Evolution; paleobotany; seedless vascular plants; taxonomic groups

As first proposed by Harlan Banks in 1968, the trimerophytes evolved from the rhyniophytes and then gave rise, either directly or indirectly, to all other groups of vascular land plants except the zosterophyllophytes and lycopods.

The trimerophytes appeared and diversified between 406 million and 401 million years ago, during the Devonian period. They evolved from the rhyniophytes (*Rhyniophyta*), and they share a number of characteristics with that group. Both groups branched by having an axis fork into two branches of equal size. Viewed from the side, the point of branching would appear like a capital Y. Both groups also bore elongate sporangia at the ends of some of these branches.

The chief feature that distinguished the two groups was size. The rhyniophytes were small plants, approximately 25 centimeters (10 inches) or less in height. The trimerophytes could reach heights in excess of 1 meter (1 yard). Because the trimerophytes were larger than the rhyniophytes, some species had a single main axis from which the lateral branches arose. Establishing a taxonomic group just because some of its members were bigger than other contemporary plants is unusual. Some researchers believe that the group is too broadly defined to be taxonomically useful. The two best-known genera, *Psilophyton* and *Pertica*, are more similar to early ferns and gymnosperms than they are to each other, supporting the belief than the trimerophytes are not a valid taxonomic group.

The smaller, herbaceous trimerophytes, such as *Psilophyton*, branched by forking into two branches of equal or unequal size and bore sporangia at the ends of some of these branches. Other trimerophytes, such as *Pertica*, were robust plants that probably reached the size of small shrubs. They had a large, central axis that gave rise to smaller lateral branches. In *Pertica quadrifaria* and *P. dalhousii*, the lateral branches forked synchronously from four to six times before ending in either sterile tips or elongate sporangia. The sporangia opened (dehisced) along one side by means of a longitudinal slit. Where known, the vascular tissue of the trimerophytes consisted entirely of primary phloem and xylem and seemed insufficient to support a plant more than a meter tall. The plants grew in dense clonal stands (a growth pattern called turfing), where the aerial axes could provide mutual support for each other.

At any site, about half of the trimerophytes present were fertile. The high proportion of fertile axes suggests plants that grew rapidly and reached reproductive maturity quickly. Since the sporangia all appear to be at the same stage of development, the aerial stems of the trimerophytes probably terminated their lives with a burst of reproduction. New growth would then arise from the perennial rhizomes or root systems when favorable conditions returned. The trimerophytes preferred to live near fresh water in habitats that were susceptible to flooding. At this time in earth history, size was more important for spore dispersal than for light interception to power photosynthesis.

Trimerophyton robustius

The trimerophytes are named for *Trimerophyton robustius*, a Canadian plant originally described as *Psilophyton robustius* by J. W. Dawson. The genus is based on a single specimen about 12 centimeters (5 inches) long. *Trimerophyton*'s central axis gave rise to spirally arranged lateral branches. Initially, the lateral branches were believed to fork twice to produce a total of nine axes. The first forking produced three new axes. The second forking of each new axis produced three more axes for a total of nine. When viewed from the side, the point of branching appeared similar to a tripod. Each of these nine branches forked into two branches from two to three more times. The ends of the branches were terminated by elongate sporangia that were all at the same stage of development. Reinterpretation of Dawson's specimen indicates that the first divisions in the lateral branches resulted in two rather than three new axes. If this interpretation is correct, *Trimerophyton* no longer possesses the diagnostic trait that names and identifies the trimerophytes. The stem of *Trimerophyton* was naked (lacked leaves or enations). Enations resemble leaves, but they lack vascular tissue and, therefore, have no veins. Both roots and rhizomes are unknown for *Trimerophyton*.

Psilophyton

At least nine species of *Psilophyton* are known. They range in size from small plants (*P. dapsile*) that lacked a central main axis to larger plants that had prominent central axes. The stems could be naked (*P. dapsile*, *P. dawsonii*, and *P. forbesii*) or variously cloaked with spiny or peglike enations (*P. crenulatum*, *P. princeps*, and *P. charientos*). The short species and the lateral branch systems of the larger species branched by forking to produce two new axes. The sterile branches end in blunt tips and the fertile ones in paired sporangia. The sporangia occur in dense clusters of thirty-two or more.

Psilophyton princeps was the first valid species described. Dawson named his Canadian fossils in 1859 but did not publish a reconstruction of the plant until 1870. As reconstructed by Dawson, the naked aerial stems arose from a rhizome (a stem that runs horizontally along the ground) and branched by forking. Sporangia were borne at the ends of the branches and hung down toward the ground (that is, the sporangia were pendant). Dawson also figured a spiny axis that he named *P. princeps* var. *ornatum*. This variety was subsequently found to have lateral sporangia and was redescribed as *Sawdonia ornata*. *Sawdonia* is classified as a zosterophyllophyte.

None of the parts (aerial stem, sporangia, or rhizome) of Dawson's original *Psilophyton princeps* were found attached to each other. They were ultimately found to represent parts of three distinct plants. *Psilophyton princeps* itself was covered with short, peglike enations and bore clusters of terminal sporangia at the ends of some of its lateral branches. The naked axis bearing the pendant sporangia was named *Dawsonites arcuatus*. *Dawsonites* has remained in the *Trimerophytophyta* for convenience because scientists are not sure of its exact affinities. The rhizome was renamed *Taeniocrada dubia* and may belong in the *Rhyniophyta* (possibly in the genus *Stockmansella*). *Taeniocrada* is simply a long, naked axis that lacks any unique structural features.

Pertica

Plants of this genus (*P. quadrifolia*, *P. dalhousii*, and *P. varia*) are the largest trimerophytes, reaching heights of a meter or more. The stem appears naked but is actually covered with small (0.4-millimeter) bumps call papillae. The strongly developed main axis gave rise to short lateral branches in groups of four. The lateral branches could fork into two or three new axes of equal size. These axes could be either sterile or fertile. The fertile branches were mixed in with the sterile branches. The fertile branches end in dense, spherical clusters of round to elongate sporangia, which opened by a slit down the side. If Dawson's specimen of *Trimerophyton* did produce some lateral branches by forking into three axes, the specimen may actually represent a short segment of *P. varia* that branched in this fashion.

Progeny

The great majority of both fossil and living plants can trace their lineages back to the trimerophytes, specifically to the *Psilophyton-Pertica* complex. Derived groups include the ferns, horsetails, gymnosperms, and angiosperms. The trimerophytes are very similar to the early ferns and gymnosperms, most notably to the extinct progymnosperm *Tetraxylopteris*. The resemblance is so great that some researchers feel that the *Trimerophytophyta* is not a valid group. The trimerophytes are very different in appearance from the ferns, gymnosperms, and angiosperms that are alive today.

The groups that evolved from the trimerophytes had far greater impact on the global environment than their predecessors, the rhyniophytes, zosterophyllophytes, and trimerophytes, did together. These latter groups had a very narrow habitat range, had shallow rooting systems or rhizomes, and were not seed producers. Their successors had well-developed root systems, as seen in the increased thickness and horizontal zonation of fossil soils (paleosols). The development of seeds allowed the gymnosperms and angiosperms to escape from a dependence on moist, lowland habitats to ensure reproductive success and to colonize drier, upland habitats. The development of seeds allowed the spread of forests from 377 million to 362 million years ago. The spread of forests was followed by a worldwide increase in the deposition of black shale and the formation of coal. The organic material represented by these deposits reflected a significant loss of carbon dioxide from the atmosphere. The decrease in atmospheric carbon dioxide brought on a period of continental glaciation and caused a mass extinction of tropical marine invertebrates due to decreased water temperature. The tropical sea's surface temperate cooled from 40 degrees Celsius (104 degrees Fahrenheit) about 345 million years ago to between 24 and 26 degrees Celsius (77 degrees Fahrenheit) about 280 million years ago.

Gary E. Dolph

See also: Cladistics; Evolution of plants; Ferns; Fossil plants; Lycophytes; Paleobotany; Plant tissues; *Rhyniophyta*; Seedless vascular plants; Shoots; Species and speciation; Stems; *Zosterophyllophyta*.

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TROPHIC LEVELS AND ECOLOGICAL NICHES

Categories: Classification and systematics; ecology; ecosystems

To be meaningful, classification of organisms based on divisions within the food pyramid, called trophic levels, often must be considered alongside the particular space, or place niche, occupied by an organism and its functional role in the community, the totality of the organism's interactions and relationships with other organisms and the environment, or ecological niche.

For many years, ecologists referred to niche in terms of an organism's place in the *food pyramid*. The food pyramid is a simplified scheme showing organisms' interactions with one another while obtaining nourishment. The food pyramid is represented visually as a triangle, often with four horizontal divisions, each division being a different trophic level.

The base of the food pyramid is the first trophic level and contains the primary *producers*, photosynthetic plants. At the second trophic level are the primary *consumers*; these are the *herbivores*, such as deer and rabbits, which feed directly on the primary producers. At the third trophic level are the secondary consumers are the *omnivores*, which eat both plants and animals. The fourth trophic level contains the tertiary consumers, animals that eat only meat—*carnivores* such as the mountain lion. The members of the uppermost trophic level are the *scavengers*, such as hyenas and buzzards, and the *decomposers*, including fungi and bacteria. The organisms in this trophic level break down all the nutrients in the bodies of plants and animals and return them to the soil to be absorbed and used by plants.

All living things are dependent on the first trophic level, because plants alone have the capability to convert solar energy to energy found in, for example, glucose and starch. The food pyramid takes the geometric form of a triangle to show the flow of energy through a system. Because organisms lose a percentage of the energy they absorb

At the second trophic level of the food pyramid are the primary consumers; herbivores, such as this moose, feed directly on plants, the primary producers.

from the sun or consume by eating, less energy is found at each higher level of the pyramid. Because of this reduced energy, fewer organisms can be supported by each higher trophic level. Consequently, the sections of the pyramid get smaller at each higher trophic level.

Through the years, two concepts of *niche* have evolved in ecology. The first is the *place niche*, the physical space in which an organism lives. The second is the *ecological niche*, which encompasses the particular location occupied by an organism and its functional role in the community. The functional role of a species is not limited to its position within a food pyramid; it also includes its interactions with other organisms while obtaining food. Specific methods of tolerating climate, water or nutrient conditions, soil conditions, parasites, and other factors of the environment are part of its functional role. In other words, the ecological niche of an organism is its natural history: all the interactions and interrelationships of the species with other organisms and the environment.

Niche Overlap

The study of relationships among organisms has been the focus of ecological science since the 1960's. Before that time, researchers had focused on the food pyramid and the effects of population changes of a single species upon predator-prey relationships. The goal of understanding how species interact with one another can be better accomplished by defining the degree of *niche overlap*, the sharing of resources among species. When two species use one or more of the same elements of an ecological niche, they exhibit *interspecific competition*. It was once believed that interspecific competition would always lead to survival of only the better competitor of the two species—that no two species can utilize the same ecological niche. It was conjectured that the weaker competitor would migrate, begin using another resource not used by the stronger competitor, or become extinct. It is now believed that the end result of two species sharing elements of ecological niches is not always exclusion.

Ecologists theorize that similar species do, in fact, coexist, despite the sharing of elements of their ecological niches. *Character displacement* leads to a decrease in niche overlap and involves a change in the morphological, behavioral, or physiological state of a species without geographical isolation. The more specialized a species, the more rigid it will be in terms of its ecological niche. A species that is general in terms of its ecological niche needs will be better able to find and use an alternative for the common element of the niche. Because a highly specialized species cannot substitute whatever is being used, it cannot compete as well as the other species. Therefore, a specialized species is more likely to become extinct.

For example, some species of tropical orchids are so specialized that they rely on a single species of bee for pollination. The flowers so closely resemble female bees that male bees attempt to copulate with them, and in the process transfer pollen from flower to flower. If one of these species of bees were to become extinct, the associated orchid species, unable to reproduce, would soon follow. On the other hand, many species of daisies are freely pollinated by bees, flies, beetles, and a number of other insects. Even if a few of these pollinator species were to become extinct, daisies would be able to continue to reproduce using the remaining pollinator species.

Hence, species with specialized ecological niche demands (*specialists*) are more in danger of extinction than those with generalized needs (*generalists*). Although this fundamental difference in survival can be seen between specialists and generalists, it must be noted again that exclusion is not an inevitable result of competition. There are many cases of ecologically similar species that coexist.

When individuals of the same species compete for the same elements of the ecological niche, it is referred to as intraspecific competition. Intraspecific competition results in *niche generalization*, the opposite result from that of interspecific competition. In increasing populations, the first inhabitants will have access to optimal resources. The opportunity for optimal resources decreases as the population grows; hence, intraspecific competition increases. Deviant individuals may begin using marginal resources that are in less demand; those individuals will slowly come to use fewer optimal resources. That can lead to an increase in the diversity of ecological niches used by the species as a whole. In other words, the species may become more generalized and exploit wider varieties of niche elements.

Why Study Niches?

The shift in meaning and study from mere space and trophic level placement in the food pyramid to ecological niche has been beneficial for the field of ecology and for human activities. This focus on community ecology is much more productive for the goal of ecology, the understanding of how living organisms interact with one another and with the nonliving elements in the environment.

Perhaps more important is the attempt to describe niches in terms of community ecology, which can be essential for some of humankind's confrontations with nature. One relevant function of community-oriented studies of ecological niches involves endangered species. In addition to having aesthetic and potential medicinal values, an endangered organism may be a keystone species, a species on which the entire community depends. A keystone species is so integral to keeping a community healthy and functioning that if it is obliterated the community no longer operates properly and is not productive.

Habitat destruction has become the most common cause of drastic population declines of species. To enhance the habitat of the endangered species, it is undeniably beneficial to know what conditions cause a species to favor its particular preferred habitat. This knowledge involves details of many of the dimensions of an ecological niche integral to specific population distribution. Danger to the survival of a species also occurs when an introduced organism competes for the same resources and displaces the native species. Solving such competition between native and introduced species would first involve determining niche overlap.

Researching and understanding all the dimensions of ecological niches can prevent environmental manipulations by humankind that might lead to species extinction. Many science authorities have agreed that future research in ecology and related fields should focus on solving three main problems: species endangerment, soil erosion, and solid waste management.

This focus on research in ecology often means that studies of pristine, undisturbed communities is the most helpful for future restoration projects. Although quantitative and qualitative descriptions of pristine areas seem to be unscientific at the time they are made, because there is no control or experimental group, they are often the most helpful for later investigations. For example, after a species has shown a drastic decline in its population, the information from the observations of the once-pristine area may help to uncover what niche dimension was altered, causing the significant population decrease.

Jessica O. Ellison

See also: Animal-plant interactions; Competition; Community-ecosystem interactions; Ecology: concept; Ecosystems: overview; Ecosystems: studies; Endangered species; Food chain; Species and speciation; Succession.

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TROPISMS

Categories: Movement; physiology

Tropisms are the means by which plants grow toward or away from environmental stimuli such as light, gravity, objects to climb, moisture in soil, or the position of the sun.

Although plants appear not to move, they have evolved adaptations to allow movement in response to various environmental stimuli; such mechanisms are called tropisms. There are several kinds of tropism, each of which is named for the stimulus that causes the response. For example, gravitropism is a growth response to gravity, and phototropism is a growth response to unidirectional light. Tropisms are caused by *differential growth*, meaning that one side of the responding organ grows faster than the other side of the organ. This differential growth curves the organ toward or away from the stimulus. Growth of an organ toward an environmental stimulus is called a positive tropism; for example, stems growing toward light are positively phototropic. Conversely, curvature of an organ away from a stimulus is called a negative tropism. Roots, which usually grow away from light, are negatively phototropic. Tropisms begin within thirty minutes after a plant is exposed to the stimulus and are usually completed within approximately five hours.

Phototropism

Phototropism is a growth response of plants to light coming from one direction. Positive phototropism of stems results from cells on the shaded side of a stem growing faster than cells along the illuminated side; as a result, the stem curves toward the light. The rapid elongation of cells along the shaded side of a stem is controlled by a plant hormone called *auxin* that is synthesized at the stem's apex. Unidirectional light causes the auxin to move to the shaded side of stems. The increased amount of auxin on the shaded side of stems causes cells there to elongate more rapidly than cells on the lighted side of the stem. This, in turn, causes curvature toward the light.

Only blue light having a wavelength of less than 500 nanometers can induce phototropism. The photoreceptors in this system are called *cryprochromes* and may alter the transport of auxin across cellular membranes, thereby facilitating its transport to the shaded side of the stem. Phototropism is important for two main reasons: It increases the probability of stems and leaves intercepting light for photosynthesis and of roots obtaining water and dissolved minerals that they need.

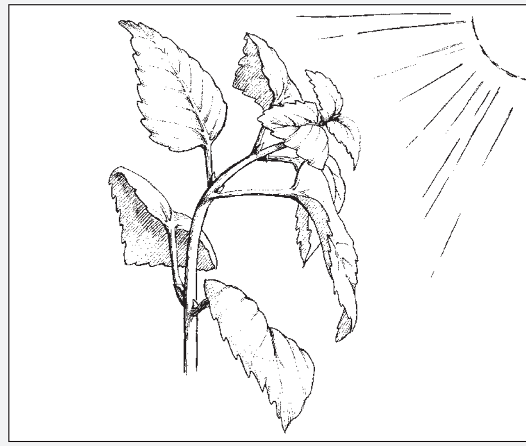
Gravitropism

Gravitropism is a growth response to gravity. The positive gravitropism of roots involves the root cap, a tiny, thimble-shaped organ approximately 0.5 millimeter long that covers the tip of roots. Decapped roots grow but do not respond to gravity, indicating that the root cap is necessary for root gravitropism. Gravity-perceiving cells, called *columella cells*, are located in the center of the root cap. Each columella cell contains fifteen to twenty-five amyloplasts (starch-filled plastids) which, under the influence of gravity, sediment to the lower side of columella cells. This gravity-dependent sedimentation of amyloplasts is the means whereby roots sense gravity, possibly by generating electrical currents across the root tip. These gravity-induced changes are then transmitted to the root's elongating zone, located 3 to 6 millimeters behind the root cap. The differential growth that causes curvature occurs in the elongating zone.

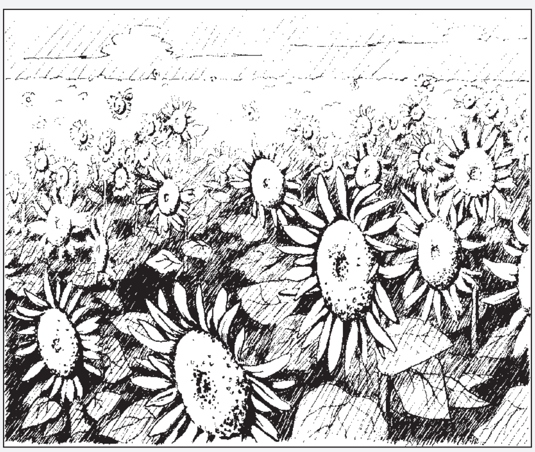
When roots are oriented horizontally, growth along the lower side of the elongating zone is inhibited, thereby causing the root to curve downward. Among the first events that produce this differential growth is the accumulation of calcium ions along the lower side of the root tip. Calcium ions move to the lower side of the cap and elongating zone of horizontally oriented roots. This movement may be aided by electrical currents in the root. The accumulation of calcium along the lower side of the root causes the auxin to accumulate there as well.

Tropisms

Gravitropism (geotropism)



Phototropism



Heliotropism (solar tracking)

Thigmotropism

Kimberly L. Dawson Kurnizki

Because auxin inhibits cellular elongation in roots, the lower side of the root grows slower than the upper side of the root, and the root curves downward. When the root becomes vertical, the lateral asymmetries of calcium and auxin disappear, and the root grows straight down.

Gravity-sensing cells in stems are located throughout the length of the stem. As in roots, the auxin and calcium ions in stem cells direct the negative gravitropism (in this case, upward curvature) of shoots. As auxin accumulates along the lower side, calcium ions gather along the upper side of horizontally oriented stems. The accumulation of auxin along the stem's lower side stimulates cellular elongation there. Gravitropism increases the probability of two important results: Roots will be more likely to encounter water and minerals, and stems and leaves will be better able to intercept light for photosynthesis.

Thigmotropism

Thigmotropism is a growth response of plants to touch. The most common example of thigmotropism is the coiling exhibited by specialized organs called *tendrils*. Tendrils are common on twining plants such as morning glory and bindweed. Prior to touching an object, tendrils often grow in a spiral. This type of growth is called *circumnutation*, and it increases the tendril's chances of touching an object to which it can cling. Contact with an object is perceived by specialized epidermal cells on the tendril. When the tendril touches an object, these epidermal cells control the differential growth of the tendril. This differential growth can result in the tendril completely circling the object within five to ten minutes. Thigmotropism is often long-lasting. For example, stroking one side of a tendril of garden pea for only a few minutes can induce a curling response that lasts for several days. Thigmotropism is probably controlled by auxins and ethylene, as these regulate thigmotropic-like curvature of tendrils even in the absence of touch.

Growing tendrils touched in the dark do not respond until they are illuminated. This light-induced expression of thigmotropism may indicate a requirement for adenosine triphosphate (ATP), as ATP will substitute for light in inducing thigmotropism of dark-stimulated tendrils. Tendrils can store the sensory information received in the dark, but light is required for the coiling growth response to occur. Thigmotropism by tendrils allows plants to "climb" objects and thereby increases their chances of intercepting light for photosynthesis.

Hydrotropism and Heliotropism

Roots also grow toward wet areas of soil. Growth of roots toward soil moisture is called *hydrotropism*. Roots whose caps have been removed do not grow toward wet soil, suggesting that the root cap is the site of moisture perception by roots. Hydrotropism is probably controlled by interactions of calcium ions and hormones such as the auxins.

Heliotropism, or "solar tracking," is the process by which plants' organs track the relative position of the sun across the sky, much like a radio telescope tracks stars or satellites. Different plants have different types of heliotropism. The "compass" plants (*Lactuca serriola* and *Silphium laciniatum*) that grow in deserts orient their leaves parallel to the sun's rays, thereby decreasing leaf temperature and minimizing desiccation. Plants that grow in wetter regions often orient their leaves perpendicular to the sun's rays, thereby increasing the amount of light intercepted by the leaf. Heliotropism occurs in many plants, including cotton, alfalfa, and beans. Sunflowers get their name from the fact that the flowers follow the sun across the sky.

On cloudy days, leaves of many heliotropic plants become oriented horizontally in a resting position. If the sun appears from behind the clouds late in the day, leaves rapidly reorient themselves—they can move up to 60 degrees in an hour, which is four times more rapid than the movement of the sun across the sky. Heliotropism is controlled by many factors, including auxins.

Growth, Survival, and Beyond

Plants, like animals, are finely tuned to their environment; their growth and development are influenced strongly by that environment. Tropisms are rapid, while other responses such as flowering are long-term and are associated with changes of season. Regardless of their duration, most responses of plants to environmental stimuli are the result of growth and are controlled, at least in part, by hormones.

Tropisms account for many common examples of plant growth, including curvature of stems toward a window and the "climbing" of many plants up posts and fences. More important, tropisms help a plant to survive in its particular habitat, making use of separate systems for detecting and responding to environmental stimuli. Biologists are studying these systems in hopes of being able to mimic these detection and "guidance" systems. Scientists at the National Aeronautics and Space Administration (NASA) study how plants perceive and respond to gravity in hopes that this knowledge will help in the understanding of how to grow plants in deep space. NASA scientists also hope that understanding the gravity detection and guidance systems in plants will help people design more effective rockets which, like plants, must detect and respond to gravity to be effective.

Randy Moore

See also: Circadian rhythms; Heliotropism; Hormones; Nastic movements; Photoperiodism; Roots; Stems; Thigmomorphogenesis.

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TUNDRA AND HIGH-ALTITUDE BIOMES

Categories: Biomes; soil

Regions where no trees grow because of frozen soil or extreme water runoff due to steep grades (at high altitudes) are known as tundra. High altitude biomes have similar limitations on the growth of plant life.

Tundra landscapes appear where long, cold winters, a permanently frozen subsoil, and strong winds combine to prevent the development of trees. The resulting landscapes tend to be vast plains with low-growing forbs and stunted shrubs. Vast areas of this biome encircle the northernmost portions of North America and Eurasia, constituting the *Arctic tundra*. Climatic conditions atop high mountains at all latitudes are similar; these small, isolated areas are called the *alpine tundra*.

Permafrost

The low temperatures of the tundra regions cause the formation of a permanently frozen layer of soil known as *permafrost*. Characteristic of Arctic tundra, permafrost, which varies in depth according to latitude, thaws at the surface during the brief summers. As the permafrost below is impenetrable by both water and plant roots, it is a major factor in determining the basic nature of tundra.

The alternate freezing and thawing of soil above the permafrost creates a symmetrical patterning of the land surface characteristic of Arctic tundra. Perhaps the best known features of the landscape are stone polygons that result when frost pushes larger rocks toward the periphery, with smaller ones occupying the center of each unit. This alteration of the tundra landscape, called *cryoplanation*,

Image Not Available

is the major force in molding Arctic tundra landscapes.

In contrast, alpine tundra generally has little or no permafrost. Even though alpine precipitation is almost always higher than for Arctic tundra, steep grades result in a rapid runoff of water. Alpine soils are, therefore, much drier, except in the flat alpine meadows and bogs, where conditions are more like those of Arctic areas.

Vegetation

Both Arctic and alpine tundra regions are composed of plants that have adapted to the same generally stressful conditions. Biodiversity of both plants and animals—the total number of species present—is low compared to most other ecosystems. Plant growth is slow because of the short growing seasons and the influence of permafrost. Most tundra plants are low-growing perennials that reproduce vegetatively rather than by seed. Often they grow in the crevices of rocks that both shelter them in the winter and reflect heat onto them in summer.

Common plants of the low-lying Arctic tundra sites include various sedges, especially cottongrass, and sphagnum moss. On better-drained sites, biodiversity is higher, and various mosses, lichens, sedges, rush species, and herbs grow among dwarfed heath shrubs and willow. The arrangement of plants within a small area reflects the numerous *microclimates* resulting from the peculiar surface features.

Alpine plants possess many of the features of Arctic plants. However, because strong winds are such a prominent feature of the alpine environment, most of the plants grow flat on the ground, forming mats or cushions.

Below alpine tundra and south of Arctic tundra, there is the *boreal* (also known as *taiga*) biome, dominated by coniferous forest. Between the forest and tundra lies a transitional zone, or ecotone. This ecotone is characterized by trees existing at their northern (or upper) limit. Especially in alpine regions, stunted, gnarled trees occupy an area called *krummholz*. In North America, the krummholz is much more prominent in the Appalachian Mountains of New England than in the western mountains.

Conservation

Like all world biomes, tundra regions are subject to degradation and destruction, especially as a result of human activities. Because of low human population density and their unsuitability for agriculture, tundras generally are less impacted by humans than are grasslands and forests. However, tundra ecosystems, when disturbed, recover slowly, if at all. As most tundra plants lack the ability to invade and colonize bare ground, the process of ecological succession that follows disturbances may take centuries. Even tire tracks left by vehicles can endure for decades. The melting of permafrost also has long-lasting effects.

The discovery of oil and gas in tundra regions, such as those of Alaska and Siberia, has greatly increased the potential for disturbances. Heavy equipment used to prospect for fossil fuels and to build roads and pipelines has caused great destruction of tundra ecosystems. As the grasses and mosses are removed, the permafrost beneath melts, resulting in soil erosion. The disposal of sewage, solid wastes, and toxic chemicals poses special problems, as such pollutants tend to persist in the tundra environment longer than in warmer areas.

Animals of the Arctic tundra, such as caribou, have been hunted by the native Inuit, using traditional methods for centuries without an impact on populations. The introduction of such modern inventions as snowmobiles and rifles has caused a sharp decline in caribou numbers in some areas.

Although efforts at restoring other ecosystems, especially grasslands, have been quite successful, tundra restoration poses difficult problems. Seeding of disturbed Arctic tundra sites with native grasses is only marginally successful, even with the use of fertilizers. In alpine tundra, restoration efforts have been somewhat more successful but involve transplanting as well as seeding and fertilizing. A recognition of natural successional patterns and long-term monitoring is a necessity in such efforts.

Thomas E. Hemmerly

See also: Arctic tundra; Asian flora; Biomes: definitions and determinants; Biomes: types; European flora; Forests; Lichens; North American flora; Rangeland; South American flora; Taiga.

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ULVOPHYCEAE

Categories: Algae; microorganisms; *Protista*; taxonomic groups; water-related life

One of four classes in the phylum Chlorophya, *the green algae, the ulvophytes* (Ulvophyceae) *include both freshwater and marine species of green algae classified in six orders. Members of this class display varying shapes and range in size from a few cells to long filaments, sheets, or coenocytic masses of cells. Two of the more familiar species are the green, leafy sea lettuce,* Ulva lactuca, *and the egg-shaped* Ventricaria.

The name *Ulvophyceae* is derived from a Latin word designating plants that live in marshes. Carolus Linnaeus referred to algae with the taxonomic term *Ulva* in his *Species plantarum* (1753). In 1978 Kenneth D. Stewart and Karl R. Mattox identified *Ulvophyceae*, or the ulvophytes, as a distinct phyletic line in the division *Chlorophyta*. The classification of *Ulvophyceae* was modified as botanists gained new insights into its ultrastructure.

Using electron microscopes, botanists detected that *Ulvophyceae* algae exhibit unique flagellar apparatus and root systems. *Ulvophyceae* taxonomy was developed according to these physical characteristics. During the 1980's, botanists assigned six orders to class *Ulvophyceae*: *Ulotrichales*, *Ulvales*, *Cladophorales*, *Dasycladales*, *Caulerpales*, and *Siphonocladales*.

By 1990 cladistic analysis of *Ulvophyceae* genetic material caused researchers to reconsider the evolutionary relationships and lineages of *Ulvophyceae* orders. Molecular comparisons suggest that ulvophytes might be basal to (evolutionary predecessors of) those green algae classified in *Chlorophyceae* and *Pleurastrophyceae*. Investigations continue to advance comprehension of *Ulvophyceae*'s role in plant evolution.

Structure

The ultrastructure of species of *Ulvophyceae* usually is radially symmetrical and consists of motile cells with flagella, basal bodies positioned in a counterclockwise rotation, cruciate microtubular roots, and persistent mitotic spindles that do not collapse during teleophase. Many ulvophytes are macroscopic and appear as filamentous or as flat sheets of cells. Others are microscopically small. Some are scaly or slippery. The sea lettuce (*Ulva*) and *Ventricaria* are the most familiar representatives of *Ulvophyceae*.

In the order *Ulotrichales*, species in the genus *Ulothrix* consist of single-nucleus cells arranged to form unbranched filaments. A cell at each filament's basal end is a rootlike holdfast that adheres plants to surfaces. Plants in the order *Siphonocladales* often resemble bubbles and are found on shells or stones in tropical waters. The plants in order *Ulvales* have a flat or hollow thallus (body). Members of *Enteromorpha* in this order consist of tubular strands that can attain widths of 5 centimeters (2 inches). Some species in the genus *Ulva* are as large as 65 centimeters (25.6 inches).

Members of *Codium magnum* in order *Caulerpales* sometimes reach lengths of 8 meters (26.25 feet). Order *Cladophorales* includes both branched and unbranched filamentous algae. Members of *Cladophora* (also sometimes classified in the order *Siphonocladales*) have branching filaments, which often grow tightly together and are formed by multinucleate cells with thick walls. Some members of order *Dasycladales* are extinct. Fossils indicate that these ulvophytes first lived during the Middle Silurian period, about 420 million years ago.

Sexual reproduction in *Ulvophyceae* is significant because ulvophytes are the only members of *Chlorophyta* that reproduce by an alternation of generations, with haploid and diploid thalli. Instead of zygotes, spores are the site of meiosis. Species also form dense stands as a result of vegetative reproduction of fragments, which usually sink instead of float. Temperature and sunlight regulate the rate of growth.

Distribution

Ulvophytes are usually found in marine environments, especially along coasts and in harbors, although freshwater species thrive in shallow parts of lakes and streams. Other habitats include rocks and soil. These algae live primarily in small clumps but occasionally form mats near the water surface as dense as five tousand fronds per square meter (11 square feet). They occasionally live at maximum depths of 10 meters (33 feet), although some species have been discovered as deep as 99 meters (325 feet). Ulvophytes prefer still, clear water but can survive in brackish and polluted environments.

Plants in class *Ulvophyceae* are indigenous to tropical regions in the Pacific, Indian, and Atlantic Oceans and the Red Sea. Some species are unintentionally transported on ships to other regions. If conditions are suitable, ulvophyte colonies multiply by as much as 28 percent daily, invading territory and competing with native plants. In 1984 *Caulerpa taxifolia* was discovered in the Mediterranean Sea. By 1996 that species had spread from covering an area of one square meter (11 square feet) to invading 3,096 hectares (7,647 acres) in seventy-seven places in the Mediterranean. Ulvophytes often adapt to new environments by deviating from their original characteristics—for example, lengthening and increasing the number of fronds to adjust to lower water temperatures.

Uses and Cultural Impact

Several *Ulvophyceae* species are valued by humans for their nutritional qualities, texture, and flavor. Rich in vitamins and minerals, especially iron and iodine, *Ulva* are sources of protein, sugar, starch, and roughage. *Ulva lactuca*, commonly called sea lettuce, is collected for salad, soup, and sauce ingredients. *Ulva* is also cultivated as livestock feed and fish bait.

Many ulvophytes have medicinal characteristics and are able to soothe burns. Soaps, oils and shower gels, and nutritional supplements often include ingredients from ulvophytes. Some animals symbiotically rely on *Ulvophyceae*. For example, sea slugs gather chloroplasts from *Codium*, which continue to undergo photosynthesis in the slugs' respiratory chambers, enhancing their oxygen supply. *Ulva* is cultivated to absorb nitrogen and phosphorus in water at abalone farms. Ulvophytes indicate environmental quality and are used to detect metal contamination and eutrophication, because they quickly accumulate in areas where large amonts of polluting substances cause those conditions.

Ulvophytes also can be toxic. *Caulerpa taxifolia* emits terpene caulerpenyne, which discourages predators from eating algae. *Cephaleuros* causes red rust, a fungus that can be economically disastrous for tea, pepper, and citrus growers. Sometimes considered a pest or pollutant, filamentous algae can destroy water quality necessary to sustain life, interfere with commercial and recreational uses, and deplete oxygen, causing fish kills. *Codium* can destroy oyster beds. Algae decomposition, especially when plants wash onto beaches and rot, results in unbearable stenches caused by the ulvophytes' sulfur content. *Green tides* resulting from an overabundance of ulvophytes thriving on nutrients in agricultural effluent are problematic. These thick clumps of algae prevent other plant and animal organisms from having access to sufficient quantities of crucial sunlight and oxygen.

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See also: Agriculture: marine; Algae; Animal-plant interactions; Aquatic plants; Culturally significant plants; Eutrophication; Green algae; Marine plants.

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USTOMYCETES

Categories: Fungi; taxonomic groups

The Ustomycetes *are a group of the basidiosporic fungi that includes about a thousand species. These fungi all produce spores in a sorus, a mass of spores that is produced on the surface of a plant host.* Ustomycetes *are all parasites of plants, and some are serious pathogens. Most produce hypertrophy (excessive cell growth) in plant tissues.*

One of three main classes of *Basidiomycota*, the ustomycetes include several different orders. *Cryptobasidiales* is a small order of fungi found in tropical areas of South America and Africa. The only species in the *Cryptomycocolacales* is a parasite of ascomycetes. The *Exobasidiales* produce galls on leaf tissue of plants in the *Ericaceae* and *Commelinaceae* families. The *Graphioales* produce black sori on the leaves of *Palmae*. The *Platygloeales* produce small gelatinous to waxy basidiocarps and are saprophytes or mycoparasites. The *Sporidiales* are yeastlike saprophytic fungi. The remaining order, the *Ustilaginales* contains almost all of the fungi of the ustomycetes.

Reproduction

The reproduction of the ustomycetes begins when a haploid hypha from a germinating basidiospore combines with a compatible hypha from another germinating spore. The resultant dikaryotic hypha then ingresses into the plant host. The hypha begins to parasitize the host, allowing the fungus to increase in mass. The fungus needs actively growing tissue to be able to reproduce. After the fungus has gained sufficient energy, the hypha begins to fragment into small cells, which become thick-walled chlamydospores. These spores are dark in color and form the sorus.

The chlamydospores undergo genetic change, and a diploid nucleus is produced. The nucleus then undergoes meiosis and produces haploid nuclei. The chlamydospore germinates, forming a small length of hypha called a metabasidium. The nuclei migrate into the metabasidium, and small basidiospores are produced. The basidiospores often form a yeastlike phase as they reproduce by cell division. This mechanism is unique among the fungi, as most spores, once formed, are unable to divide into two new units. Ustomycetes also have a yeastlike phase when they are grown in axenic culture. Spore release is passive.

The Smuts

The ustomycetes in the order *Ustilaginales* are important plant parasites, known commonly as smuts, and can affect most meristematic areas of plants. Some of these cause considerable economic damage to plants. The smuts cause hypertrophy (excessive growth) of growing tissues. Infection is by dikaryotic hyphae that can penetrate into the meristems of ovaries, leaves, and even roots of plants. The resultant mass of cells can produce a large growth that is unsightly.

The *Ustilaginales* are divided into two families based on the location at which the basidiospores are produced on the metabasidium. In the *Tilletiaceae*, the spores are located terminally, while in the *Ustilaginaceae*, the spores are located laterally.

One of the more visible smuts is caused by *Ustilago maydis*, which infects corn. *Corn smut* has been recorded for thousands of years and is depicted in Mayan and Incan drawings of corn. The fungus infects the developing ovum by penetrating the silk at the time of pollination. Pollination does not occur, but rather the fungus becomes established and fungal tissue begins to grow in place of the developing ovum. A mass of fungal tissue forms under the seed coat. The resulting gall can be more than an inch in length. These are often found on ears of corn as large gray or black growths. Thousands of years ago, it was believed that these growths were divine in origin, and any infected ears were separated. The infected ears were then used as offerings in religious ceremonies. The smut galls were often consumed by the religious leaders. This practice may have preserved corn for future generations. Seed corn can become coated with chlamydospores at the time of harvest. These spores can germinate at the time of planting and infect the germinating seed. Death of the seedling is possible.

Other kinds of smut include *bunt* and *stinking smut*, which infect wheat. With bunt, the seed becomes infected but does not show any symptoms. The mycelium of the fungus remains dormant in the seed. The following year, as the seed germinates, the mycelium remains associated with the meristem. When the wheat plant produces its inflorescence, the fungus causes sori to be produced instead of ovaries. With stinking smut, the chlamydospores are transmitted on the surface of the seeds. Basidiospores are produced, and the mycelium infects the developing plant. When the inflorescence is produced, the ovaries appear enlarged, and the "seed" produced will have a sorus occupying the entire interior. The sori have a distinctive dead fish odor, accounting for the name.

While many smuts attack ovaries, some smuts cause sori to be formed on leaves. *Striped smut* occurs on some turf grasses, while other smuts can cause spots on leaves of plants.

Most inflorescence smuts occur only once a year and do not affect more than about 5 percent of the seeds. They are disseminated by wind. They can be more damaging, however, if crops are staggered in the same growing season.

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See also: *Basidiomycetes*; Basidiosporic fungi; Diseases and disorders; Fungi; Rusts.

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VACUOLES

Categories: Anatomy; cellular biology; physiology; transport mechanisms

Vacuoles are receptacles within plant cells that hold water, enzymes, acids, waste products, pigments, or other substances that serve the plant.

Vacuoles are the largest organelles in most mature plant cells. Frequently constituting more than 90 percent of the volume of a cell, the vacuole presses the rest of the protoplasm against the cell wall. Vacuoles are surrounded by a single fragile membrane called the vacuolar membrane, or *tonoplast*. The contents of the vacuole, referred to as *vacuolar sap*, is 90 to 98 percent water. The vacuole of a typical plant cell occupies approximately 500,000 cubic micrometers. It would take approximately two million of these vacuoles to equal the volume of a sugar cube.

Almost all plant cells contain vacuoles. Not all mature cells of plants, however, contain a single vacuole. For example, the cells of the tissue that produces the wood and bark of trees contain many small vacuoles during winter, when the tissue is dormant. When the tissue becomes active in spring and summer, these small vacuoles fuse into single, large vacuoles.

Storage Reservoirs

Vacuoles were discovered in 1835 and were thought to have relatively little function. It is now known that vacuoles are versatile organelles that have many important functions, including that of storage reservoirs. Vacuoles store waste products that would be dangerous if they accumulated in the cell's cytoplasm. Many of these waste products, such as nicotine, other alkaloids, and cyanide-containing compounds, are poisons that help protect the plant against predators. Vacuoles are also temporary, controlled repositories for useful materials such as potassium, chloride, and calcium ions. Ions such as sodium (Na^+) and chloride (Cl^-) are moved across the tonoplast by *active transport*, an energy-dependent means of transport in cells. These ions are important for cellular metabolism. For example, absorption or release of calcium from vacuoles regulates calcium-dependent enzymes in the cell's cytoplasm.

Vacuoles store many economically important products. For example, proteins are stockpiled in vacuoles of storage cells in seeds. Latex is stored in vacuoles of rubber plants. Vacuoles of many plants store large amounts of amino acids, which are used as a reservoir of nitrogen. Vacuoles of beet roots and sugarcane store large amounts of sugar. Large amounts of salt are also accumulated in vacuoles. The sap in most vacuoles has concentrations of salts similar to that of seawater. In marine algae and plants that grow in the salty soils of deserts and ocean shores, vacuoles often accumulate salts, such as potassium chloride and sodium chloride, to levels several thousand times greater than that of the soil or brackish water in which the plants grow. Sometimes the concentration of a particular salt in the vacuole is so great that it precipitates as crystals. For example, calcium oxalate crystals are common in vacuoles of many plants such as dumb cane (*Dieffenbachia*), which has toxic levels.

Organic acids such as oxalic acid and malic acid are also accumulated. These acids make vacuoles slightly acidic. For example, the typical pH of a vacuole is near 5.5, while that of the cytoplasm is near 7.5. (A pH of 7.0 is neutral.) The vacuoles in citrus fruit contain large amounts of citric acid. Consequently, these vacuoles are very acidic, thus accounting for the tart, sour taste of the fruit.

Water Management

When vacuoles absorb salts, they also absorb water. This water swells the vacuole, much as air inflates a tire. The water entering the vacuole creates a pressure inside the vacuole called *turgor pressure* and presses the surrounding layer of cytoplasm against the edge of the cell. Turgor pressure is what makes nonwoody plant tissue firm. When the vacuole loses water, the turgor pressure is lost, and the tissue wilts. Thus, leaves of plants that lack water wilt, while those of well-watered plants remain firm.

The turgor pressure generated in vacuoles is important for cell growth because it stretches the cell wall of the plant. During cell growth, cells secrete protons into their cell walls. These protons weaken chemical bonds in the cell wall and can stretch it to a larger size. Plant hormones, such as auxins, control the secretion of protons. This type of pressure-driven growth by plant cells is energetically "inexpensive," because it involves little more than absorbing water. This contrasts sharply with the growth of animal cells, which lack vacuoles. Animal cells must expand by making energy-rich cytoplasm, including large amounts of proteins and lipids.

Plant Movement and Gas Exchange

Vacuoles are important for the movements of many plants. For example, leaf movements in the sensitive plant (*Mimosa pudica*) and Venus's flytrap (*Dioneae muscipula*) are based on the tonoplast's ability to absorb or lose water quickly. Cells in specialized regions of the leaves quickly transport salts out of their cells. When they do, water from the cells' vacuoles also leaves the cells. This "deflates" the cells, and the tissue shrinks, thus moving the leaf.

Gas exchange in the leaves is also influenced by vacuoles. Pores through which gases enter and exit leaves are called *stomata*, and they are bordered by specialized cells called *guard cells*. When the vacuoles of these cells absorb water, the cells become turgid and bow apart, thereby creating a pore through which gases move. Thus, water uptake by vacuoles of guard cells correlates with stomatal opening and gas exchange. When water leaves the vacuoles of guard cells, the cells wilt and the pore closes, which stops gas exchange. Gas exchange is crucial because it brings carbon dioxide into the leaf for photosynthesis and releases oxygen into the atmosphere. Many factors control water absorption by guard cells, including light, wind, temperature, and water availability.

Digestive Centers

Vacuoles function as digestive centers of cells: They contain a variety of digestive enzymes, such as phosphatases and esterases, that can degrade (break down) many different kinds of molecules. Vacuoles use these enzymes to degrade and recycle the parts of damaged or old, unneeded organelles. Small vacuoles fuse with old or damaged organelles and, by means of enzymes, digest the organelles. The parts of the digested organelle are then recycled by the cell.

Pigment Holders and Pumps

Many cells have vacuoles that contain water-soluble pigments called *anthocyanins*. These pigments are responsible for the red and blue colors of many vegetables (turnips, radishes, and cabbages), fruits (cherries, plums, and grapes), and flowers (geraniums, roses, delphiniums, peonies, and cornflowers). Anthocyanins help attract pollinating insects to the flowers. Sometimes these pigments are so bright that they mask the chlorophyll, as in the ornamental red maple. The red color of garden beets is caused by another vacuolar pigment, called betacyanin.

Many protozoa and unicellular algae contain specialized vacuoles called *contractile vacuoles*. These vacuoles pump excess water from cells. As a result of this secretion, pressure does not build inside the cells. Contractile vacuoles are rare in marine algae and are absent in terrestrial plants.

Growth, Development, and Transport Models

Vacuoles perform many functions that are critical to plant growth and development. For example, the cellular expansion that produces leaf movements and *tropisms* results largely from water uptake by vacuoles. Similarly, the absorption and loss of water by vacuoles of guard cells regulates photosynthesis, the process that fuels life on earth.

Vacuoles are increasingly used as tools for studying transport across membranes. Ions and sugars move quickly across the tonoplast; this movement makes isolated vacuoles a model system for studying transport of materials across membranes. The movement is controlled by specific proteins that transport each ion or sugar across the membrane.

Many economically important chemicals, including drugs, dyes, spices, and other materials, such as rubber, are contained in vacuoles. Biologists are trying to understand how plant cells make and package these chemicals in vacuoles. Biotechnologists hope to use this knowledge to increase production of these chemicals. Far from being the inert structures they were once believed to be, vacuoles are critical to many aspects of plant life.

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See also: Cytoplasm; Leaf anatomy; Plant cells: molecular level; Plant tissues; Respiration; Tropisms.

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VEGETABLE CROPS

Categories: Agriculture; economic botany and plant uses; food

Vegetables are plant products, either fruits or other fleshy parts of the plant, consumed in human diets. Although the word itself has no precise taxonomical significance, agriculturally vegetables constitute a significant sector of world food crops.

Although most of the world's people consume "vegetables" daily, the word itself has no precise botanical or scientific meaning. Various *vegetative* (nonreproductive) parts of plants are eaten as vegetables, but reproductive parts of plants such as cucumbers and tomatoes, which are technically fruits, are also consumed as "vegetables."

Vegetative "vegetables" include the stems of celery, the tubers Irish (white) potatoes, and asparagus shoots. Other vegetables commonly consumed include roots: sweet potatoes, carrots, parsnips, and radishes, among others. Leaves eaten as vegetables include lettuce, spinach, collards, and cabbage.

Reproductive plant parts that are considered vegetables include broccoli (flower buds); cauliflower (flowers); green beans, squash, and tomatoes (fruits); and green peas and lima beans (seeds). Many more vegetables can be identified for each of those categories of reproductive parts.

PhotoDisc

Reproductive plant parts that are considered vegetables include these squash. "Vegetables" are often, strictly speaking, the fruits of plants.

The plant crops discussed here include those that are generally eaten along with meat as a part of the main course of a meal, as opposed to the fruits, which are generally sweet and are consumed as desserts. Interestingly, whereas many fruits are commonly referred to a vegetables, most foods commonly referred to as "fruits" tend also, in the strict botanical sense of the word, to be fruits.

Origins

Early humans during the Neolithic (Stone) Age were hunter-gatherers who foraged wild plants and ate them both raw and cooked. Gradually, the plants that were most useful were domesticated. Domesticating these plants involved both the selection of superior plants and improving the conditions under which they are grown. Improvements included loosening the soil and applying various materials as fertilizers. Nearly all the vegetable crops now cultivated are known to have been domesticated more than two thousand years ago.

Knowledge about the origins of agriculture, including the domestication of plants, comes from a variety of sources. Before the birth of Christ, the Greek botanist Theophrastus in the third century B.C.E. listed in his *Peri phyton historias* (also known as *Historia plantarum*; "Enquiry into Plants," 1916) crops known to have been grown at that time. A few centuries later, the Roman Pliny the Elder made similar observations. In modern times, two economic botanists summarized the accumulated knowledge relating to economic plants, including vegetable crop plants. The Swiss Alphonse de Candolle wrote *Origine des plantes cultivées* (1882; origin of cultivated plants). Nikolai I. Vavilov, a Russian, gained fame as a result of his work (translated into English as *The Origin, Variation, Immunity, and Breeding of Cultivated Plants*, 1951). Among the conclusions reached by Vavilov, Candolle, and others is that agriculture originated not in a single region, as previously thought, but more or less simultaneously in widely separated "centers of origin" on several of the world's continents.

Vegetables meet the variety of nutritional needs of humans. In addition to providing varying amounts of carbohydrates, fats, and proteins, they supply needed vitamins and minerals so necessary in the diet. Also, vegetables supply the insoluble fiber, or "roughage," that is essentail in maintaining intestinal regularity and preventing colon cancer.

Root Crops

A "root crop" in the commercial/agricultural sense includes any plant crop in which an underground part is dug from the soil and eaten as a vegetable. Botanically, the edible part may be a root, rhizome (underground stem), corm (compressed underground stem surrounded by dry scales), or bulb (short underground stem covered by fleshy leaf bases). The objective is to harvest these plant parts soon after carbohydrates and other nutrients have been stored there for the future use of the plant.

Most root crops have larger amounts of carbohydrates and less protein and oil than grains (cereals) or legumes. Because of their bulk, root crops cost more to ship than do grains and most other food crops. Therefore, root vegetables tend to be consumed locally. Nevertheless, measured in tons, root crops are comparable to grain crops on a worldwide basis. The most important root crops are the

Irish (white) potato, the sweet potato, and cassava. These three are to root crops what maize, wheat, and rice are to grain crops. They, together with root crops of secondary importance, are discussed below. The common name of each crop plant is followed by its scientific name and family name.

White Potato

The common potato, *Solanum tuberosum* (family *Solanaceae*), is the most important nongrain food item of the world. However, it has been known outside the Americas for only a few centuries. Spanish explorers of the sixteenth century found potatoes growing in what is now the nation of Colombia in South America. It had long been grown by Native Americans in the cool, high elevations of the Andes Mountains south to the present country of Chile. Soon after discovery by Europeans, the potato was introduced into Spain and from there into other parts of Europe, including the British Isles. Throughout many of these regions, it became an important staple in the diets of most citizens.

When a fungal disease, potato late blight, wiped out most of the potato crop in Ireland in the mid-1840's, a severe famine (the Irish Potato Famine) resulted, causing large numbers of people to emigrate to the United States, Canada, and other countries. As a result, the popularity and cultivation of potatoes spread in North America, and the potato became known as the Irish potato, to distinguish it from the sweet potato.

The potato is a crop of cool regions. Potato plants are grown from sections of the tuber cut into segments, each containing an "eye" (bud). The resulting plants produce tubers that are harvested, usually by digging machines, later the same growing season. Principal potato-growing regions of the United States include Idaho, Maine, and New York. Many potatoes are also grown in northern Europe.

The potato is an economical source of starch used for both food and industrial purposes. Protein content is only about 2 percent. Purchases of whole potatoes declined throughout the later decades of the twentieth century, but that decline was offset by the increased consumption of processed potato products such as potato chips, ready-mix mashed potatoes, and frozen french fries.

Cassava

Manihot esculenta (*Euphorbiaceae*), also called manioc and tapioca, is an important root crop and a staple item in the diets of more than 500 million people of tropical regions. The starch storage roots are produced by the perennial plant, which is native to tropical America. It is believed to have been domesticated in Brazil, where it is known to have been grown around 2000 B.C.E. In addition to Latin America, it is important in Africa and other tropical regions.

There are several advantages to growing and using cassava as a food plant. After clearing the land, farmers can plant stem sections. Storage roots can be harvested in only eighteen months or can be left in the ground and dug up later. In addition to providing high yields per acre, cassava has the advantage of being resistant to diseases. Furthermore, it survives in poor soil and both dry and wet tropical climates.

One of the disadvantages of cassava is its low protein and vitamin content. Thus, an overdependence on cassava often results in severe nutritional deficiencies. Also, the roots often contain poisonous cyanide-type compounds that must be removed before consumption. As the amounts of these compounds vary with the variety of cassava and the conditions under which they are grown, processes for removal of the toxins can be problematic. Traditionally, in Brazil, the shredded roots are ground by hand, after which the pulp's mass is dried over fires to yield a subsistence product known as *farinha*. Also, a large, round flatbread is made by spreading the pulp on a griddle. In Africa, roots are produced from "sweet" varieties (in which only small quantities of toxins are present). There, the roots are peeled, boiled, dried, and eaten as a lumpy, starchy vegetable with little flavor. In temperate regions, a product called *tapioca*, made from processed roots, is used for puddings.

Sweet Potato

Ipomoea batatas (*Convolvulaceae*), or the sweet potato, a relative of the morning glory, is a trailing tropical vine. Unlike those of the cassava, the edible parts of the sweet potato are true roots. Evidence indicates that it is a native of South America, but it is known to have been cultivated more than a thousand years ago in Polynesia. It was also known in New Zealand before Europeans had ships that could cross the oceans. How the sweet potato was carried across the Pacific remains a mystery.

The sweet potato is cultivated today around the world, in the tropics as a perennial, and in temperate regions as an annual. In the latter case, the stem sections of the vine are planted in the spring, and the roots are dug up later the same season.

Sweet potatoes contain much more protein than either white potatoes or cassava; also, they have significant amounts of vitamin A. However, sweet potatoes do not store as well as cassava and are not grown in as high a quantity. In the United States, they are prepared much like white potatoes. Large amounts are also fed to animals or used as sources of industrial products. China is the leading producer of sweet potatoes.

Other Root Crops

Perhaps the most important world root crop, after those listed above, is the yam, *Dioscorea alata* (family *Dioscoreaceae*). Not to be confused with sweet potatoes, which are often called "yams" in the southern United States, the true yam is, like the white potato, a tuber. Also like potatoes, yams are propagated using sections of tubers with the buds. The resulting plants are deep-rooted climbing vines. One problem in harvesting them is the large amount of labor required to dig the tubers. However, yams are well adapted to tropical rain forests. Yams are prepared as are white potatoes and have a similar nutritional value. In addition to *Dioscorea alata*, native to China, several other *Dioscorea* species are cultivated as root crops.

Several plants of the arum family, *Araceae*, are grown as root crops. The most important is taro, *Colocasia esculenta*. Taro is believed to have originated in southern Asia; it spread from there to India and also through the islands of the South Pacific. Later it was introduced into the Mediterranean, tropical Africa, and the West Indies. The plant is closely related to "elephant ear," which is grown as an ornamental. The edible portions include both tubers and corms. Visitors to Hawaii are familiar with the viscous preparation poi, which made from taro.

Onions and their close relatives of the genus *Allium* (family *Liliaceae*) have a long and esteemed reputation in the culinary arts. Native to Central Asia and the Near East, they have long been cultivated. The bulbs, after being dug, can be consumed directly or stored. Onions (*A. cepa*) produce a single large bulb; garlic (*A. sativum*), several smaller ones. The bulb of the leek (*A. ampeloprasum*) is continuous with the leaf blade above.

Stem and Leaf Crops

Cole crops include cabbage and its close relatives, all of the species *Brassica oleracea* (family *Brassicaceae*), along with other plants of this family. There is evidence that from cabbage, native to northern Europe, each of the cole vegetables has resulted from a different modification of the stems or leaves. Cabbage has long been an important crop in Germany, where it is used to make sauerkraut. Other vegetables of this group include brussels sprouts, cauliflower, kohlrabi, broccoli, and kale.

The aster family (*Asteraceae*) also includes several plants grown as vegetables. Lettuce (*Lactuca sativa*) is believed to have been derived from a plant native to the Mediterranean region. It has been grown for centuries and used for salads, much as it is today. Selection has resulted in numerous varieties including leaf lettuce and romaine lettuce. In the United States, iceberg lettuce is the familiar, popular type seen in supermarkets. Plants known as endive and chicory are also used as salads. Both are cultivars of *Cichorium intybus*.

Several other common vegetables, of various families, are grown for their edible stems or leaves. The principal edible parts of celery, *Apium graveolens* (family *Apiaceae*), are the stalks or leaf petioles. Spinach, *Spinacia oleracea* (family *Chenopodiaceae*), is used raw in salads and as a cooked vegetable. Asparagus, *Asparagus officinalis* (family *Liliaceae*) is a perennial from which young shoots are cut each spring.

Thomas E. Hemmerly

See also: African agriculture; Agricultural revolution; Agriculture: traditional; Agriculture: world food supplies; Asian agriculture; Australian agriculture; Central American agriculture; European agriculture; Fruit crops; Fruit: structure and types; Green Revolution; Horticulture; Legumes; North American agriculture; Plant domestication and breeding; Plant tissues; Roots; South American agriculture.

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VESICLE-MEDIATED TRANSPORT

Categories: Cellular biology; physiology; transport mechanisms

Large substances such as proteins, some amino acids, and polysaccharides are transported into and out of plant cells by vesicle-mediated transport, which involves interaction with and fragmentation of the cell membrane to create a membrane-bound vesicle for internal distribution or external export. Once formed, the vesicle can be transported to its destination within the cell.

Plant cells use several methods to transport ions, polar molecules, and macromolecules through the cell membrane. Some of these can permeate the member via membrane via osmosis. Small substances, mostly ions, can diffuse through pores composed of transmembrane proteins. Other substances, however—such as glucose, glycogen, and some amino acids—must be transported by membrane-bound carrier molecules in a process called vesicle-mediated transport.

Also called *bulk transport*, vesicle-mediated transport is an active process that involves the cell membrane (plasma membrane) and consumes energy. Vesicle-mediated transport also provides a mechanism that enables a cell to "hoard" needed nutrients against a concentration gradient. The product of vesicle-mediated transport is a saclike vesicle, typically about 0.05-0.1 micrometer in diameter, comprising a fragmented portion of the cell membrane that bounds and contains the substances being transported. Vesicle-mediated transport of substances into plant cells is called *endocytosis* (*endo* means "within"; *cytosis*, "cytosol" or "cytoplasm"), and movement of substances out of cells is called *exocytosis*. The three forms of endocytosis are pinocytosis, phagocytosis, and receptor-mediated endocytosis.

Pinocytosis

Pinocytosis is called "cell drinking" because during the process fluids and dissolved solutes are taken into the cell. Pinocytosis involves the formation of membrane-bound vesicles at the cell membrane surface, called pinocytotic vesicles, which are then taken into the cell interior and released. Under certain circumstances, pinocytosis enables a cell to take in fluid at a much faster rate than during normal osmosis. Pinocytosis may augment osmosis or may function entirely independently; cells in an isosmotic solution, for example, can acquire large volumes of additional fluid via pinocytosis.

Studies of plant cell uptake of heavy metals such as lead have clarified much of the processes involved in pinocytosis. Pinocytosis occurs in special depressions in the cell membrane. Each depression, or *pit*, consists of one or more proteins called clathrin. Clathrin is a complex protein that consists of three large and three small polypeptide chains bound together to form a tripodlike configuration called a *triskelion*.

During pinocytosis, clathrin-coated pits form around a droplet of extracellular fluid as well as any ions contained within the fluid droplet. The membrane-bound droplet then invaginates via a deep groove through the membrane, pinching off within the interior as a minute, fluid-filled vesicle. The whole process takes only a few seconds.

Phagocytosis

Phagocytosis is called cell eating (*phago* for "eating," and *cytosis* meaning "cell") and refers to the cellular intake of large and generally insoluble molecules and macromolecules that cannot be taken into the cell using other membrane transport mechanisms. Phagocytosis differs from pinocytosis in that little fluid is taken into the cell.

Many small single-celled organisms such as amoebae feed by phagocytosis. Some of the more specialized forms of phagocytosis in plants include uptake of food by slime molds and the intake of nitrogen-fixing bacteria such as *Rhizobium* into the root nodules of legumes as they form.

The products of phagocytosis are typically solid substances rather than fluid and are contained within a vesicle called a *phagosome*. Some examples of phagocytosis involve extensions of the plasma membrane called *pseudopodia*, which surround the substance. The ends of the pseudopodia fuse to encircle the substance, which is then transported through the membrane and budded off into the cytoplasm. Inside the cell at least some phagocytic vesicles bind with one or more structures within the cytoplasm for further processing. Others are transported and their contents emptied into cell vacuoles or other cytoplasmic organelles.

Receptor-Mediated Endocytosis

Receptor-mediated endocytosis is an efficient process whereby nutrients and other essential macromolecules are taken into the cell. During receptor-mediated endocytosis, specific receptor sites located on the plasma membrane bind to target molecules in the extracellular fluid medium. Most of the receptor sites in plant cell membranes are glycoproteins which bind to specific sites on the target macromolecules, called ligands. Some receptor sites are located throughout the cell membrane, but others are found in clathrin-coated depressions or pits in the membrane. During receptor-mediated endocytosis, the receptor sites located in membrane depressions selectively bind with target substances to form a receptor-ligand complex. Following this, several receptor-ligand complexes may combine to form clusters around which a portion of the cell membrane encircles, producing a vesicle that invaginates inward to pinch off as a coated vesicle. Once inside, changes in the acidity (pH) within the cytoplasm separate the substance from the protein coating. The substance diffuses or is dissolved within the cytoplasm, and the protein coating is recycled back to the cell membrane.

Exocytosis

Exocytosis is the reverse of endocytosis. During exocytosis a vesicle-bound substance is transported through the membrane from the interior to the exterior of the plant cell. Exocytosis represents the method by which plant cells secrete or excrete substances out of the cell by means of membrane-bound sacs. A common example found in most plant cells during initial growth involves exocytosis of precursor molecules that will form the cell wall. During the process, the precursor molecules bind to the interior of the plasma membrane, then evaginate into the region where the cell wall is developing.

Exocytosis begins in the cytoplasm when a substance or a membrane-bound substance in the cytoplasm migrates to and fuses with the cell membrane. A pit or groove evaginates outward through the cell membrane, and the membrane-bound substance is transported to the cell surface. In some examples of exocytosis, the membrane opens at the cell surface and the interior substance diffuses into the extracellular fluid. In other cases, the vesicle is secreted or excreted as a membranous sac into the extracellular fluid.

Plant hormones, other secretory products, and waste are the most common substances removed from the cell by exocytosis. Following exocytosis, the vesicle generally dissolves, and the substance diffuses into the extracellular fluid.

Dwight G. Smith

See also: Active transport; Cells and diffusion; Endocytosis and exocytosis; Liquid transport systems; Membrane structure; Osmosis, simple diffusion, and facilitated diffusion; Plasma membranes; Water and solute movement in plants.

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VIRUSES AND VIROIDS

Categories: Cellular biology; diseases and conditions; medicine and health; microorganisms

Viruses are extremely small parasites that have none of the structures characteristic of living cells. Many viruses are little more than a protein-coated and particle-containing DNA or RNA. The protein coat is specifically adapted for breaching the plasma membranes of host organisms. Viroids are even simpler parasites comprising small, single-stranded molecules of RNA with no protein coat. They are the smallest known agents of infectious disease.

The concept of a virus dates back to the late nineteenth century investigations of the mosaic disease of tobacco by Dmitri Iosifovich Ivanovsky in Russia and Martinus Willem Beijerinck in Holland. They found that the agent that caused a mosaic pattern of light and dark green areas on tobacco leaves was smaller than a bacterium, being able to pass through a filter known to exclude bacteria. Subsequently, similarly small agents were shown to cause disease in animals.

Particle Components

As their extremely small size suggests, virus particles do not contain everything needed to reproduce themselves. They can multiply only within the cells of living organisms. Virus particles, also known as *virions*, universally contain one or more deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) chains. Encoded in the sequence of nucleotides of the DNA or RNA is all information needed for virus reproduction. Virions also contain one or more types of capsid proteins, which protect the nucleic acid from destruction by the environment. Virions of some viruses contain additional coatings, including membranes derived from cell membranes containing distinctive, virus-encoded proteins.

Despite their simplicity and small size, viruses are not the smallest infectious agents of plants. That title belongs to viroids: small, circular RNA molecules with extensive secondary structures. They do not encode proteins and are not encapsulated. Viruses are classified based on the type of nucleic acid strands contained in virions, their mode of replicating the strand or strands, and the shape of virions.

Viruses may have RNA or DNA as genetic material. These nucleic acids may be single-stranded or double-stranded. If single-stranded, the instructions for making protein may be on the packaged strand (*positive sense*), on its complement (negative or *antisense*), or on both strands (*ambisense*). The genome of the virus may be in one nucleic acid strand or distributed among several. The sizes of plant viral genomes vary from about four kilobases (kb) to about twenty kb. Exceptions are the phycodnaviruses of algae whose DNAs are over three hundred kb. Virions may be roundish in shape (in actuality an intricate geometrical form called an icosahedron), rod-shaped, or filamentous.

Replication and Evolution

Most known plant viruses have positive sense RNA as genetic material. However, examples of negative sense and ambisense virion RNAs are known. Virus-encoded RNA replicase enzymes make strands complementary to the virion strands and then use the complements to make strands for packaging in progeny virions. The single DNA strands of begomoviral virion DNA are made by host-encoded DNA polymerases. Spanning the

RNA and DNA worlds, the virion DNA of plant equivalents of retroviruses is copied into RNA by host enzymes. The RNA is then copied into DNA by a virus-encoded enzyme.

Mistakes in viral replication are so frequent, and replication so prolific, that the population of viral genomes in an infected organism is a collection of many different sequences, called a *quasispecies*. Quasispecies allow viruses to evolve rapidly when novel environments act on them, to select a better adapted variant. The study of bacteriophages, viruses that infect bacteria, has contributed to understanding how plant viruses evolve and function.

Viral genomes are collections of gene modules, each with a different purpose. Viruses also evolve by exchanging modules. A *reassortant* arises when a novel mixture of RNA or DNA strands is packaged, while a *recombinant* arises by exchange of only part of one strand. Therefore, one virus may have multiple origins, one for each module. Relationships that have not been obscured by evolutionary divergence suggest modules themselves have multiple origins.

Viral Gene Function

Gene modules are classified into those coding for structural (virion-associated) proteins and those coding for nonstructural proteins. Structural proteins are those that can be found in virus particles, including capsid and envelope proteins and, in some viruses, include replication proteins. Plant viruses are unique in having a module required for movement of infection from one cell to the next. Indeed, an insect-infecting virus can spread in plants engineered to make a movement protein of a plant virus. Movement proteins alter plasmodesmatal connections between cells, but how they allow virus movement from cell to cell is still under intensive study. Movement of some viruses may depend on an as-yet-undetermined pathway for intercellular RNA movement.

Viruses also move from the infected leaves to other leaves. This movement follows the phloem pathway used by the plant to transport sucrose, with the infection moving from source leaves to sink leaves. Some viruses require the coat protein for long-distance movement. A few viruses move in the xylem. Movement of a virus from one plant to another requires a *vector* (another organism that assists in transmission); numerous insect species, nematodes, and fungi can transmit specific viruses. Specific viral proteins interact with a host-component to assure transmission specificity. Some viruses, such as tobacco mosaic virus, and viroids are transmitted only mechanically, by contact with animals or farm equipment.

Disease and Control

Viruses first grabbed scientists' attention because they cause disease. In plants, symptoms associated with virus infection include leaf discoloration, foliar distortion, and fruit blotches. It is now known, however, that many viral infections are unapparent. Specifically what causes symptoms is not known.

Most plants are not susceptible to most viruses. A virus may be unable to replicate in cells of the plant species. The plant may mount a hypersensitive response in which it kills its own cells at the site of infection, to limit the infection. Overproduction of RNA, such as occurs during RNA virus infection, can lead to induction of an RNA destruction mechanism. Some viruses have evolved suppressors of that defense pathway. Systemic acquired resistance


Digital Stock

Viruses, such as this Ebola *virus shown at 108,000 × magnification, are extremely small parasites that have none of the structures characteristic of living cells. Many are little more than a protein-coated and particle-containing DNA or RNA.*

is a pathogen-nonspecific state of resistance induced by infection with any kind of pathogen.

Infection of crop plants by viruses causes large agricultural losses. Control methods have been developed. Culling is the removal of infected plants. Controlling vectors with pesticides can limit the spread of viral outbreaks. Breeding genes from resistant plant species or varieties into the crop variety is a standard approach. Such resistance may break down as viruses evolve to overcome the new genes. In cross protection, plants are purposely inoculated with a mild strain of the virus and become resistant to other strains. Cross protection led to the biotechnological pathogen-derived resistance, in which protection comes from a viral DNA element incorporated into the plant chromosome.

Ulrich Melcher

See also: Bacteriophages; Cell-to-cell communication; DNA in plants; Plant biotechnology; Plant diseases and disorders; Proteins and amino acids; RNA; Viral genetics; Viral pathogens.

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WATER AND SOLUTE MOVEMENT IN PLANTS

Categories: Physiology; transport mechanisms

Plants have two separate transport systems for conducting essential nutrients and water into and through the plant. These take the form of two types of vascular tissue. One, for water and minerals, the xylem, originates in the root and moves water and minerals upward. The second, the phloem, moves dissolved carbohydrates out of the leaves to other plant parts in which they are used for growth or stored.

Vascular plant tissue is designed to meet the nutritional transport needs of land plants. Xylem tissue has two types of transport cells; both are nonliving when functional. The smaller in diameter is the *tracheid*. These have a narrow bore and tapering, overlapping ends. These tapered ends have numerous *pits*, which are narrow passages to adjacent cells. Water passes through the cell to the next cell through these pits. Because of the narrow openings from one cell to the next, the flow of water tends to be rather small.

The second cell type in the xylem is the *vessel element*. These cells have a much larger diameter than the tracheids and have endwalls that rarely overlap and are totally open. This second type is very much like a section of water pipe, with no endwalls at the end of each section to restrict the flow of water.

The structure of the phloem is similar to that of the xylem in that two cell types are found. Unlike the cells in the xylem, however, only one of the phloem cells, called the *sieve element*, actually transports fluids; the other is called the *companion cell* and seems to be involved in unloading the phloem.

Water Movement in the Xylem

One of the early explanations for water and mineral movement in plants was "root pressure." The water in the xylem in the root contains ten to fifteen times the mineral content of the soil water, an accumulation that cannot be explained by diffusion or osmosis. Botanists now realize that the *root hairs*, those fingerlike outgrowths of the epidermal cells that expand the surface area of the roots to hundreds of square meters, and the cells of the cortex are able to use energy to collect mineral ions, such as magnesium ions, which are then transported into the xylem in the root.

As mineral ions accumulate in the root's xylem, water diffuses into the root as well. This accumulation of mineral ions and water creates a type of pressure called *turgor pressure*. This pressure is identical to the pressure in the water pipes of a house. Any time a faucet is opened, water moves toward the opening. This movement is called bulk flow or *convective movement* or *hydraulic lift*.

Root pressure is generally limited by two factors. The first is the large amount of energy needed to accumulate mineral ions from the soil. The second is the problem associated with the narrow passages between tracheids. As a result, root pressure is generally limited to plants of a few meters in height or less. While root pressure is easily demonstrated in the laboratory, it is clearly not able to move water to the tops of trees, which may reach a height of 130 meters (400 feet) or more.

Cohesion-Adhesion Theory

The means whereby nutrients and water are transported through large plants and trees is explained by the *cohesion-adhesion theory*. Leaves are the primary sites of photosynthesis in most plants. During photosynthesis atmospheric carbon dioxide is required to make glucose, which is converted to sucrose for transport. As a result the leaves' surface is covered by small openings called *stomata*. As carbon dioxide is entering the leaf, water is evaporating from the leaf in a process called *transpiration*. Transpiration is driven by the much lower water content of the atmosphere compared to the water content of the leaf.

Transpiration generates a *tension*, from $^{-}0.1$ to $^{-}5$ megapascals in the xylem of the leaf. This tension is transmitted through the solid water columns of the xylem to the roots and increases the uptake of water in the root. At the more negative part of this range, water should exist as a gas rather than a liquid. That, however, is not the case, because the cell wall, with its massive number of $^{-}$OHs, stabilizes the water via *adhesion*—that is, by forming hydrogen bonds with water molecules, which are also hydrogen bonded to each other via *cohesion*. One might expect the water column to break under its own weight (called *cavitation*), but that does not occur either. Lyman Briggs (1950) demonstrated that a small column of water requires at least $^{-}25$ megapascals before it will cavitate. For example, as oil in an oil lamp is used in the burning end of the wick (transpiration), more oil is pulled (via adhesion and cohesion) up the wick (similar to a stem or root) from the oil in the base of the lamp (similar to the soil). The moving stream, called the *transpiration stream*, transports water, mineral ions, and sometimes other materials from the roots to the leaves.

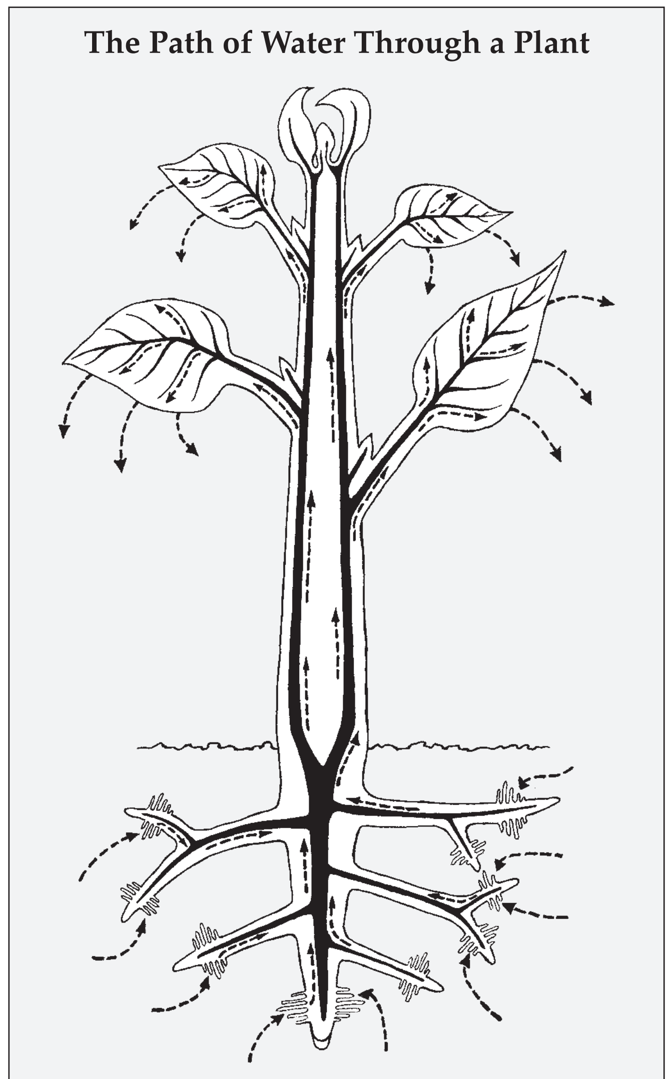
Evidence for the Cohesion-Adhesion Theory

Evidence to support the cohesion-adhesion theory was provided by Per Scholander (1965). He reasoned that if the xylem were under tension when a twig is cut from the plant, the water columns in the xylem would pull back to a position that could be supported by atmospheric pressure. If this twig were placed in a closed chamber with the cut surface exposed and the pressure were increased gradually in the chamber, it should be possible to force the water columns out to the cut surface of the twig. The pressure would be a direct measure of the tension in the xylem but of opposite sign, that is if 2 megapascals were necessary to get the water out to the cut surface the twig, it must have been under $^{-}2$ megapascals, since tension is a negative pressure.

Scholander built a small aluminum chamber with an associated pressure gauge and gas supply, called the Scholander Pressure Chamber. He then traveled about and measured the tension in numerous parts of many trees, under a variety of environmental conditions. He and many others since have reported tension in the $^{-}0.1$ to $^{-}5$ megapascals range for leaves, twigs stems, and roots, with the values becoming more negative as one takes samples higher on the same plant.

The Problem of Transpiration

Transpirational water loss is a major loss to the plant. As much as 95 percent of all the water entering the roots is lost by transpiration. Transpiration is under environmental control. Stomatal opening is controlled by the carbon dioxide level of the interior of the leaf; as carbon dioxide inside decreases, the stomata open. With the stomata open, a drop in humidity, an increase in temperature, an increase in air currents, or all these conditions will cause an increase in transpiration and the tension in the xylem.



Kimberly L. Dawson Kurnizki

Water moves into plants through roots but can rise only so far by means of "root" pressure or turgor pressure. The cohesion-adhesion theory has been used to explain water movement in larger plants and trees.

Transpiration will continue until darkness or until the water in the plant is so reduced that the plant wilts.

When the xylem is under tension, air bubbles may enter the water columns; these are called *embolisms*. When a water column is broken by an embolism, it will not transport water. Thus, water transport is reduced. There is some evidence that these embolisms may be repaired.

Movement in the Phloem

Movement of materials in the phloem—again, the conducting tissue that is responsible for moving food manufactured in the leaves to other parts of the plant, including the roots—is driven by pressure rather than by tension. The leaves are the primary sites for photosynthesis and thus its product sucrose; leaves, therefore, may be called the *source*. These carbohydrates are loaded into the phloem in the leaf, up to 1.2 moles per kilogram of water. With more solute in the phloem, water diffuses into the phloem from the xylem. This loading of sucrose and influx of water generate pressure, which is transmitted throughout the phloem. Any site in the plant, known as a *sink*, which is actively using carbohydrates for the production of new cells in fruits or the storage of starch in the roots, relieves the pressure, and the *assimilate stream*, as the fluid in the phloem is called, will move in the direction of the relief, much like a dripping faucet. This assimilate flow will continue as long as carbohydrates are being consumed in an area. As a result of high levels of carbohydrates in the source and the use of carbohydrates in the sinks, the rate and direction of flow of materials in the phloem are controlled. Sinks may change from hour to hour during the day, sometimes sending materials to the roots, other times sending materials to the flowers or even developing leaves.

Evidence for Pressure in Phloem Transport

Evidence for pressurized phloem transport is easily collected using aphids. Aphids have sharp, hollow snouts, which they are able to insert into sieve cells very accurately. To investigate phloem transport, scientists have allowed aphids to infest a plant. Once they are settled, it is fairly easy to sever the snouts from the bodies of the aphids. These snouts will continue to "bleed" phloem sap for several days. Bleeding could not occur if the phloem were under tension, which supports the theory of pressurized phloem transport.

Additional evidence for pressurized phloem transport was provided by Ernst Munch in 1927 as a laboratory model. He attached two dialysis bags together by way of a glass tube. Into one of the bags he placed a sucrose solution (the source), and water was placed in the other (the sink). When both bags were placed in water, the water diffused into the sucrose solution. This generated a pressure that was transmitted via the tube to the other bag and caused water to flow out of the second bag. Thus, the materials in the sucrose bag were transported to the other bag.

James T. Dawson

See also: Active transport; Angiosperm cells and tissues; Cells and diffusion; Endocytosis and exocytosis; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Plant tissues; Root uptake systems; Roots; Leaf anatomy; Shoots; Stems; *Tracheobionta*; Vesicle-mediated transport.

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WETLANDS

Categories: Ecosystems; water-related life

Wetlands, transitional areas between aquatic and terrestrial habitats, are home to a variety of flood-tolerant and salt-tolerant plant species.

Wetlands represent one of the most biologically unique and productive of all natural habitats. In their unaltered state, these water-influenced areas are used by a variety of wildlife species. These habitats also have the ability to take up and store water during floods, and their soils and plants have the ability to remove nutrients and heavy metals from water. The recognition of these values helped to slow the rate of wetlands loss to such uses as agricultural development and urban expansion. A desire to protect remaining wetland acres has led to a significant movement for wetlands preservation.

Definition of Wetlands

Ecologists recognize wetlands as a type of *ecotone*. Ecotones are unique areas that represent a transition from one type of habitat to another. Often, these transitional areas have characteristics of both habitats. Wetlands are areas located between aquatic, water-based habitats and dry land. Because they are located at the edge of an aquatic habitat, wetlands are always influenced to some degree by water. They are not always underwater, as are aquatic habitats, and they are not always dry, as are terrestrial habitats.

The most important environmental factor in wetlands is the periodic or frequent occurrence of water. This presence of water influences both the nature of the soil and the flora and fauna of a region. Soils which experience periodic coverage with water become anoxic, develop a dark color, and give off an odor of hydrogen sulfide. These soil characteristics differ from those of upland soils and give wetland soils their unique hydric nature. In these soils influenced by water, only flood-tolerant *hydrophyte* species can exist. Hydrophytic plants vary in their tolerance to flooding from frequent (such as bald cypress) to infrequent (such as willows).

In defining a particular area as a wetland, often all three of the components listed above are used: water, hydric soils, and hydrophytic plants. However, the presence of water is not always a reliable indicator because water rarely covers a wetland at all times. Often, a wetland is dry during a period of low river flow or during a low tide. For this reason, only hydric soils and hydrophytic plants should be used as reliable indicators of a wetland.

Classification of Wetlands

The broadest classification of wetlands includes two categories: freshwater and saltwater wetlands. *Freshwater wetlands* occur inland at the edges of rivers, streams, lakes, and other depressions that regularly fill with rainwater. *Saltwater wetlands* occur along the coast in bays, where salt water and fresh water mix and wave energy is reduced.

Of the two categories, freshwater wetlands are by far the most common. Freshwater wetlands are subdivided into two categories: tree-dominated types and grass-dominated types. Tree-dominated freshwater wetlands include areas that are frequently covered with water (such as cypress swamps) and those that are only occasionally covered with water (such as bottomland forests). Grass-dominated types include freshwater marshes, prairie potholes, and bogs.

While freshwater marshes are widespread, prairie potholes and bogs occur regionally in the United States. *Prairie potholes* are located in the central portion of the United States, while *bogs* are found in the Northeast and Great Lakes regions.

Saltwater wetlands are also subdivided into tree-dominated and grass-dominated types. Tree-dominated types include tropical *mangrove swamps*. Grass-dominated types can be further subdivided into salt marshes and brackish marshes. *Salt marshes* occur in bays along the coast where salt

Interior wetlands on Otter Island at the ACE Basin National Estuarine Research Reserve in South Carolina.

water and fresh water mix in almost equal proportions. *Brackish marshes* occur farther inland than salt marshes do; their mix contains less seawater and more fresh water. Both grass-dominated types are common in bays along the Gulf of Mexico and the East Coast of the United States.

The Biota of Wetlands

The most noticeable feature of all wetlands is the abundance of plant life. A variety of plant species thrive in wetlands, but each occurs only in a particular kind of habitat. Freshwater wetlands that are frequently flooded provide a favorable habitat for water-tolerant trees, such as bald cypress and water tupelo, and water-tolerant herbaceous plants, such as cattail, arrowhead, bulrush, spike rush, water lily, and duckweed. Less frequently flooded freshwater areas support trees such as willow, cottonwood, water oak, water hickory, and red maple. Seawater areas in tropical bays favor the development of mangroves, while temperate bays favor the development of cordgrass.

Wetland plants provide a habitat for a variety of animals. Cypress swamps and cattail marshes support a large assortment of animals, including alligators, ducks, crayfish, turtles, fish, frogs, muskrat, wading birds, and snakes. Likewise, mangrove prop roots provide attachment sites for a variety of invertebrates and shelter for numerous small fish, while upper branches provide roosting and nesting sites for birds. In salt marshes, mussels live among cordgrass roots, while snails, fiddler crabs, oysters, and clapper rails live among plant stalks. When water covers cordgrass at high tide, plant stalks shelter small fish, crabs, and shrimp seeking refuge from large predators.

The Value of Wetlands

The amount of plant material produced in wetlands is higher than that produced in most aquatic and terrestrial habitats. This large amount of plant material supports an abundance of animal life, including commercially important species such as crayfish, ducks, fish, muskrat, shrimp, and crabs.

The biotic value of wetlands is well recognized, but it represents only a part of their total value. Wetlands provide "services" for other areas that often go unrecognized. For example, freshwater wetlands are capable of storing large amounts of water during periods of heavy rainfall. This capability can be important in minimizing the impact of flooding downstream. Saltwater wetlands along coastlines are an effective barrier against storms and hurricanes. These natural barriers hold back the force of winds, waves, and storm surges while protecting inland areas. Wetlands are also capable of increasing water quality through the trapping of sediment, uptake of nutrients, and retention of heavy metals. Sediment trapping occurs when moving water is slowed enough by grass and trees to allow suspended sediment particles to settle. Wetland plants take up nutrients, such as nitrates and phosphates, from agricultural runoff and sewage. For this reason, wetlands are used as a final treatment step for domestic sewage from some small cities. Wetland soils are capable of binding heavy metals, effectively removing these toxic materials from the water.

Wetlands Loss and Preservation

It is estimated that the United States once contained more than 200 million acres of wetlands. Less than half this amount remains today. Once considered wastelands, wetlands were prime targets for "improvement." Extensive areas of freshwater wetlands and prairie potholes have been drained and filled for agricultural development. Saltwater wetlands have been replaced by urban or residential development and covered with dredge spoil. Wetlands loss rates have slowed, but an estimated 300,000 acres continue to be lost each year in the United States. The loss of wetlands habitat threatens the survival of a number of animal species, including the whooping crane, American crocodile, Florida panther, manatee, Houston toad, snail kite, and wood stork.

Since the 1970's the rate of wetlands loss has slowed for several reasons. One is the passage of federal and state laws designed to protect wetlands; another is the efforts of conservation organizations. At the federal level, the single most effective tool for wetlands preservation is Section 404 of the Clean Water Act. Section 404 requires that a permit be issued before the release of dredge or fill material into U.S. waters, including wetlands. At the state level, Section 401 of the Clean Water Act allows states to restrict the release of dredge or fill material into wetlands. There are several conservation organizations that support wetlands preservation, including Ducks Unlimited, the National Audubon Society, the National Wildlife Federation, and the Nature Conservancy. These organizations keep the public informed regarding wetlands issues and are active in wetlands acquisition.

Steve K. Alexander

See also: Aquatic plants; Biomes: types; Ecosystems: studies; Halophytes; Pacific Island flora; Peat; Rice.

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WHEAT

Categories: Agriculture; economic botany and plant uses; food

Wheat (Triticum sativum) *is the world's most important grain crop, serving as a natural food source for much of the world's population. The wheat grain is easily refined to raw foods such as flour, which can be used in countless recipes.*

Throughout the world, large portions of agricultural land are devoted to the production of wheat. Wheat is the national food staple for more than forty nations and provides 20 percent of the total food calories for the world's population; it is the major staple for about 35 percent of the people of the world. In the United States, wheat constitutes a large part of the domestic economy, makes up a large part of the nation's exports, and serves as the national bread crop.

The cultivation of wheat is older than the written history of humankind. Its place of origin is unknown, but many authorities believe that wheat may have grown wild in the Tigris and Euphrates Valleys and spread from there to the rest of the Old World. Wheat is mentioned in the first book of the Bible, was grown by Stone Age Europeans, and was reportedly produced in China as far back as 2700 B.C.E. Wheat was brought to the New World by European settlers and was being grown commercially in the Virginia Colony by 1618.

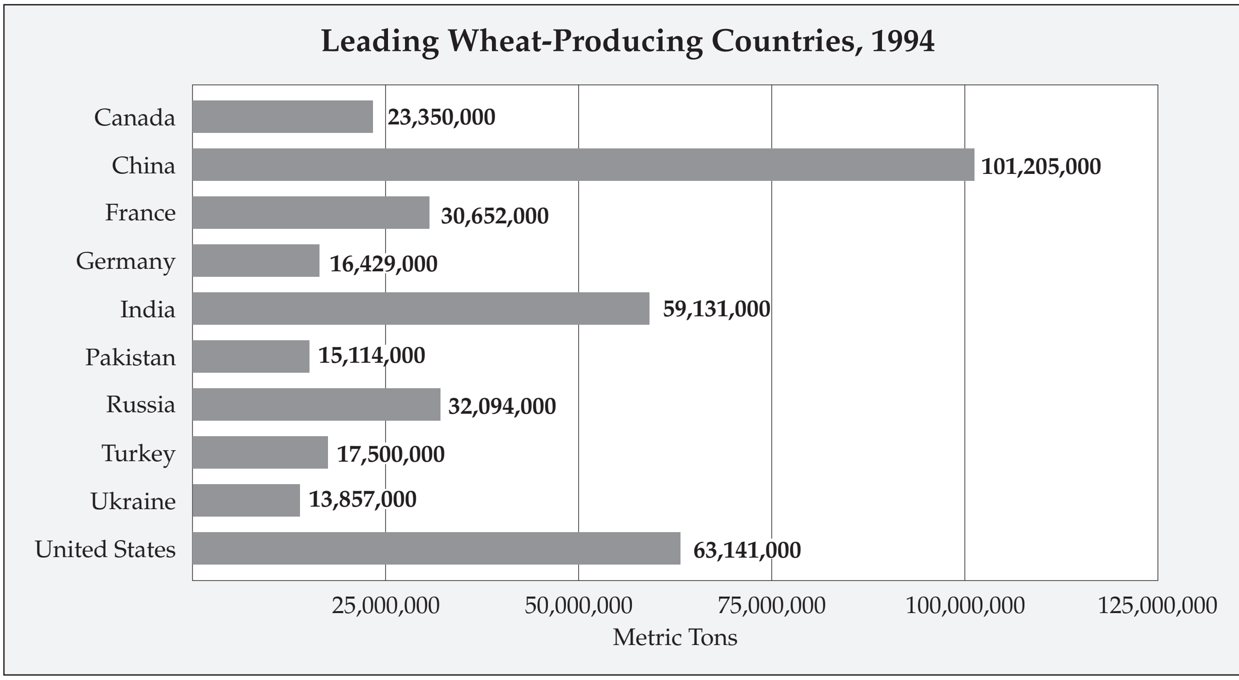
Botany and Classification

Wheat is an annual grass, but its structural morphology varies considerably, depending on the type. The wheat flowers and subsequently the seed are borne on spikes originating from the top of the plant. Wheat is widely adapted throughout the world and can grow in many climates. It can be found growing from near the equator to 60 degrees north latitude. About the only places wheat does not grow are those with climates that continually stay hot and moist.

Most commercially grown wheats can be separated into either hard grain wheat or soft grain wheat. Hard wheat is usually dark in color and possesses no white starch, while the soft wheat is generally much lighter in color and shows a white starch. Both hard and soft wheat contain a protein

PhotoDisc

After wheat flowers, the seeds are borne on spikes originating from the top of the plant.



Note: World total for 1994 was approximately 528 million metric tons.
Source: U.S. Department of Commerce, *Statistical Abstract of the United States, 1996*, 1996.

called gluten, which enables leavened dough (dough after yeast has been added) to rise by trapping the gas bubbles produced during fermentation by the yeast, but hard wheat contains more glutin than does soft wheat. As a result, the hard wheats are much more desirable for making bread. The weaker flour produced by the soft wheats is preferred for making biscuits, crackers, pie crusts, and starchy breakfast foods. The most common types of commercially planted wheat are common wheats, durum wheat, and club wheat.

The common wheats include hard red winter wheat, grown in Texas and northward up through Kansas; hard red spring wheat, grown in the north central states (North and South Dakota, Idaho, Montana, and Minnesota); soft red winter wheat, grown in the east-central United States (Ohio, Michigan, Missouri, Illinois, and Indiana); and white wheat, grown around the Great Lakes and in the far West. Hard red winter wheat and hard red spring wheat are primarily used in making bread, while soft red winter wheat and white wheat are used chiefly for making cakes, cookies, pies, and other pastries. *Durum wheat* is a very hard wheat also grown in the north-central United States. Durum wheat is primarily used for making pasta such as macaroni and spaghetti. Club wheat, also grown in the far West, is used to make the starchy flours required for making pastries. Additional wheat types include poulard, emmer, spelt, polish, and einkorn; these types are of little importance in the United States.

Production and Harvest

Production begins with the selection of the seed. So that high yields can be obtained, extreme care is taken to select only the highest-quality seed. For winter wheat, the seed is planted in the fall, generally at the time of the average first frost. This timing allows the crop to make a stand before winter but is not so early that it begins rank growth or starts to send up tall shoots. Spring wheat is generally planted as early as is practical in the spring, which is usually early March in the areas where spring wheat is normally grown. In the United States, almost all wheat is planted by drilling the seed into the soil. Drilling provides for the best germination and the least amount of winter killing.

Harvest time for wheat is determined primarily by the moisture content of the grain. Most wheat in the United States is harvested with mechanical combines, and the ideal seed moisture for combine harvest is 12 to 13 percent. After harvesting, the grain is taken to the mill. During the milling process, the grain is washed and scoured to remove fuzz and foreign material. The grain is then tempered by soaking in water to toughen the bran. After tempering, the grain is crushed by a series of corrugated rollers. The bran, produced primarily in the seed coat, is then separated from the starch. The milled flour is often chemically bleached to improve the color and baking quality and enriched with vitamins and minerals to replace those lost by removing the bran. The average flour yield is 70 to 74 percent of the weight of the grain.

D. R. Gossett

See also: Agriculture: world food supplies; Alternative grains; Corn; Grains; Grasses and bamboos; Green Revolution; High-yield crops; Rice.

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WOOD

Categories: Anatomy; economic botany and plant uses; forests and forestry

Wood is a fibrous plant tissue that functions in support and water conduction. It composes the bulk of stems and roots in the magnoliids and eudicots of the angiosperms (phylum Anthophyta*), as well as in the conifers (phylum* Coniferophyta*). It is formed by thickening growth, which persistently adds new layers that accumulate as a cylinder of wood between the pith and the bark.*

Secondary Xylem

Technically, wood is secondary *xylem*. The growth in girth that produces it is called secondary growth. This growth occurs after the stem or root segment has completed its increase in length, or primary growth. Secondary growth also yields, in much smaller amounts, secondary phloem, which becomes a part of the bark.

Secondary growth results from divisions of the cells in a layer called the *vascular cambium*, located between the bark and wood. Cambial cell divisions that are oriented toward the interior of the stem or root (that is, on the pith side of the cambium) result in a new layer of secondary xylem cells at the periphery of the layers formed previously. Cambial cell divisions oriented toward the exterior (on the bark side) of the stem or root add a new layer of secondary phloem to the inside of the bark. The angiospermous group *Monocotelydones* (the monocots) forms neither secondary xylem nor secondary phloem, because the fibrous conducting tissues are arranged in scattered bundles rather than in layers.

Wood Structure and Growth Rings

Wood is composed of cells arranged in two orientational systems. Most of the cells are oriented axially, in approximate alignment with the long axis of the stem or root. The rest are oriented radially, perpendicular to the long axis. The axial, or longitudinal, cellular system functions in both support and water conduction. In conifers, which include pines, spruces, and firs, this system is composed mainly of tracheids, with some parenchyma cells. In angiosperms, which include oaks, ashes, and elms, the axial system contains, in addition to tracheids and parenchyma, vessel members and fibers. Vessel members are one of angiosperm wood's most distinctive features because they commonly enlarge greatly in diameter. The radial system in both gymnosperms and angiosperms is composed mainly of parenchyma cells. These are aggregated into rays, which conduct nutrients from the phloem to the interior of the stem or root.

In temperate-zone trees, the vascular cambium usually lays down a single increment of secondary xylem each year, during the warm season. The wood formed early in the growing season, called earlywood, is less dense, and in some species has a different cell composition than the latewood. Because of the within-increment contrast in cell characteristics, the increments appear as annual growth rings on cross sections. Trees growing in relatively uniform tropical climates do not form annual rings because growth is not generally limited to a particular season.

Softwoods and Hardwoods

Angiosperm woods are often referred to as *hardwoods* and coniferous woods as *softwoods*. Although these terms are generally accurate, some hardwoods are actually softer than some softwoods. For example, the conifers known as "hard pines" are technically "softwoods," and basswood is technically a "hardwood," yet hard pines are much harder than basswood. Softwoods compose much of the commercial lumber in the Northern Hemisphere.

Sapwood and Heartwood

Because each new increment of wood is produced at the periphery of the preceding increment, the wood that is nearest the bark is the youngest. Eventually, the older wood, which is deeper within the tree, loses its capacity to function in conduction and storage. It accumulates oils, resins, tannins, and other substances. This darker, nonconducting, inner wood is called *heartwood*. The lighter, functioning, outer wood that surrounds it is called *sapwood*. The relative amounts of heartwood and sapwood, and the degree of their color contrast, vary with the species.

Reaction Wood

Leaning branches or trunks produce a specialized kind of wood, called *reaction wood*, that generally helps the stem return to a more vertical orientation. In conifers, reaction wood develops on the undersides of leaning branches or trunks and is called compression wood. In angiosperms, it develops on the upper sides and is called tension wood. In leaning conifer stems, the growth rings are much wider on the compression-wood side of the stem than in the ordinary wood on the opposite side.

Wood's Appearance

Certain characteristics that affect wood's appearance are quite variable. Color is one. For example, black walnut, widely considered North America's finest cabinet wood, owes its aesthetic appeal largely to its heartwood, which is often a rich chocolate brown, in contrast to the much lighter heartwood of many other species. Grain, texture, and figure also affect the appearance of wood. Grain is considered straight if the longitudinal wood cells closely parallel the stem's long axis. Deviations produce spiral, wavy, and interlocked grains. Texture, which refers to the sizes and proportional distribution of the various kinds of wood cells, may be coarse or fine. Figure, or distinctive markings and patterns on longitudinal wood surfaces, results from basic anatomical structure, irregular coloration, and defects or from irregular patterns as in "bird's-eye maple."

Knots

During the course of secondary growth, the bases of the branches that had formed when a tree was younger are typically buried within the trunk or within a larger branch, through addition of successive increments of woody tissue. That part of a branch that becomes overgrown by secondary growth is called a *knot*. Knots generally degrade the quality and value of lumber.

Jane F. Hill

See also: Angiosperm cells and tissues; Angiosperms; Conifers; Dendrochronology; Forest and range policy; Forest management; Forests; Gymnosperms; Logging and clear-cutting; Petrified wood; Plant tissues; Stems; Timber industry; Wood and charcoal as fuel resources; Wood and timber.

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WOOD AND CHARCOAL AS FUEL RESOURCES

Categories: Economic botany and plant uses; forests and forestry

Globally, the amount of wood and charcoal used for fuel exceeds the combined amount of wood used for all other purposes. Between 60 percent and 95 percent of the total energy needs of some developing countries are met by wood.

Wood is one of the oldest energy sources. Rough wood and bark may be burned directly for fuel, or wood may be converted into charcoal by charring in a kiln from which air has been excluded. According to the Food and Agriculture Organization of the United Nations, more than half of all the wood utilized in the world at the end of the twentieth century was used for energy production. Wood provides for as much as 60 to 95 percent of the total energy needs of some developing countries, but it provides less than 5 percent of the total energy required in most developed countries. As a rough estimate, around two billion people use wood for their cooking and heating. In some developing areas of the world, fuelwood demand is greater than the supply; particularly in parts of Africa, consumption significantly exceeds replacement of the stock of trees.

Wood fuel also finds some use in industry, as in the paper industry. Industries often burn waste material from other manufacturing processes. Bark removed from raw logs, sawdust, planer shavings, sander dust, edges, and trim pieces may all be burned to generate power while disposing of the unwanted material. Small wood particles such as sawdust and shavings may be compressed to produce briquets or "logs" for use as fuel.

Increasing numbers of forests are being planted and cultivated for the sole purpose of energy production. Entire trees are chipped and burned for energy production at the end of a rotation. These forests may be known as *forest plantations*, *tree farms*, or *energy forests*. This type of wood production and fuel use has the potential to reduce dependency on *fossil fuels*. Energy forests remove carbon from the atmosphere over their life span, then release this carbon in various forms during combustion for energy production.

Types of Combustion

The direct burning of wood occurs when the surface is intensively irradiated so that the temperature is raised to the point of spontaneous ignition, anywhere from 500 to more than 900 degrees Fahrenheit (260 to 500 degrees Celsius), depending on the conditions. More common is indirect combustion, in which the wood breaks down into gases, vapors, and mists, which mix with air and burn.

PhotoDisc

Wood provides as much as 60 to 95 percent of the total energy needs of some developing countries but less than 5 percent of the total energy requirement in most developed countries. However, wood fuel also finds some use in industry, as in the paper industry.

About 1.4 pounds (0.6 kilogram) of oxygen are required for the complete combustion of a pound of wood. At normal atmospheric concentrations, this implies that about 6 pounds (2.7 kilograms) of air are needed for the complete combustion of a pound of wood. During combustion, gases such as carbon dioxide and carbon monoxide, water vapor, tars, and charcoal are produced, along with a variety of other *hydrocarbons*. Dry wood or bark and charcoal burn relatively cleanly; wetter wood produces a larger amount of emissions. Collectors may be used to remove *particulate matter* from industrial sources. It is less feasible to reduce emissions from cooking stoves (either chemically or mechanically), however, and cooking stoves are a major source of human exposure to emissions from wood burning in much of the world.

Charcoal

Charcoal is lighter than wood and has a higher energy content. It takes approximately 3 pounds (1.4 kilograms) of wood to produce 1 pound (0.45 kilogram) of charcoal. The exact conversion ratio depends on the tree species, the form of wood utilized, and the kiln technology used. Charcoal is more efficient to transport than wood, and it can be burned at higher temperatures. It is used both for domestic purposes and, in some countries—Brazil is one—as an industrial fuel. In general, charcoal is considered a cleaner, less polluting fuel than wood in that its combustion produces fewer particulates. Charcoal was used extensively as an energy source for smelting and metalworking from prehistoric times into the Industrial Revolution, but coal eventually became the principal alternative energy source for these processes in areas where it was available. Today, petroleum and natural gas are major sources of energy for industrial processes.

Energy Content

The average recoverable heat energy from a pound of wood is about 8,500 British thermal units (Btu's). The value ranges from 8,000 to 10,000 Btu's per pound for different species. In some efficient processes, 12,500 Btu's can be recovered from a pound of charcoal. If wood with a high moisture content is burned, some of the energy produced by combustion is absorbed as the moisture evaporates, reducing the recoverable energy.

Impacts on Environment and Health

Traditional uses of wood fuel for cooking and home heating utilize woody material obtained from tree pruning or *agroforestry* systems. These uses are *sustainable* and have relatively little environmental impact in areas with low human population levels, but they may be associated with serious air pollution problems as well as widespread *deforestation* and *erosion* if they are the major sources of energy for a large or concentrated population. In most of the areas that have deforestation problems, the problem is primarily attributable to changes in land use, particularly the opening of land for agriculture and grazing. Fuelwood is often recovered during such land-use changes, but the need for fuelwood production is often a secondary cause or by-product of deforestation.

Industrial power production that utilizes available technology to ensure high-temperature, virtually complete combustion minimizes hydrocarbon and particulate emissions and can be designed to meet most existing air quality standards. Less efficient domestic combustion may be associated with unacceptable levels of human exposure to airborne particulates, carbon monoxide, and other hydrocarbons produced by incomplete combustion. The health effects of exposure to domestic wood fires are difficult to determine, since they often occur along with other factors known to increase health risks.

David D. Reed

See also: Coal; Deforestation; Forest and range policy; Forest management; Peat; Reforestation; Sustainable forestry; Timber industry; Wood.

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WOOD AND TIMBER

Categories: Economic botany and plant uses; forests and forestry

The use of products derived from woody plants, notably timber, takes advantages of wood's insulating ability, strength, workability, and abundance as a construction and engineering material.

No other material has all the advantages of wood. One material may equal wood in insulating quality but lack its abundance and low cost. Another may rival it in strength but fail on the point of workability. A third may rank with it in workability but fail to measure in durability. If wood were a newly discovered material, its properties would startle the world.

Since the human race first started to build crude shelters at the dawn of civilization, wood has been available as a construction material. Wood has long been used in the construction of buildings, bridges, and boats. As technology developed, wood also found a variety of less readily recognizable forms, such as paper, films, and pulp products, many of which are mainstays of daily life.

Woody material is produced in many plants, but its most useful manifestation is in the limbs and trunks of *trees*. There is a great diversity of tree species, and most climatic zones have at least one tree that has adapted to the prevailing conditions within that area. Thus, wood is available in most inhabited regions of the world. Wood has played a dominant role as a construction and engineering material in human society, yet humankind has lived with this material for so long that its significance is easily overlooked.

Hardwoods and Softwoods

Trees are broadly classified into *hardwoods* and *softwoods*. These terms can be misleading, as they are not connected to the actual hardness of the wood. Hardwoods are broad-leaved, deciduous trees. Softwoods, on the other hand, have narrow, needlelike leaves and are usually evergreens. Oak, birch, and basswood are common hardwood species, whereas longleaf pine, spruce, and cypress are softwoods. While some hardwoods (for example, oak) are really hard, many others (basswood) are nevertheless softer than the average softwood. In fact, balsa is classified as a hardwood, even though it is one of the softest woods in the world.

By far, the majority of timber used in building structures comes from the softwood category. Douglas fir, southern pine, and redwood are some of the important softwood species widely employed in structural applications. They are relatively strong and can be used in structural elements such as joists, beams, and columns. By comparison, the stronger hardwood species, such as oak, are relatively heavy, hard to handle, and hard to nail. As far as construction is concerned, their utility is limited; they are generally only used in flooring, cabinetry, and furniture.

Supply and Disposal

Wood is a renewable resource. It does not exist in finite quantities; rather, it is constantly produced in growing trees. If forests are carefully managed, timber can be harvested on a sustained-yield basis, year after year. Wood is also a reusable resource. The recycling of timber from old buildings is well documented. The ease with which wood can be cut, joined, and worked into various shapes permits the extension of its functional life beyond that of many other construction materials.

Wood is a biodegradable natural product: It can be reduced to its constituent carbohydrates and extractives through degradation. After wood has reached the end of its useful service, it can be disposed of with little damage to the environment. Unlike plastics or chemicals, timber has a very low pollution potential. A study quantified the pollution potential of various construction materials, finding that steel is five times more polluting than timber, while aluminum and concrete blocks are respectively fourteen and twenty-four times more polluting. From an environmental standpoint, timber is recognized as the most appropriate construction and engineering material.

Logging

Tremendous quantities of timber are consumed each year throughout the world. In the early and mid-1990's, an average of about 3.5 billion cubic meters of timber was harvested annually. The majority of hardwood harvest is used for fuel, while softwoods are primarily used in construction and manufacturing. To produce the large quantities of timber needed annually, logging operations have become highly organized and technologically advanced. When trees are removed in harvest, steps are taken to provide for forest renewal and to prevent soil erosion. Such steps include leaving some trees to produce seeds, transplanting young trees, and other methods of reseeding.

Sometimes a "prelogging" operation is undertaken before the main harvest. In this phase, the small trees are removed for conversion into poles, posts, and pulpwood. During harvest, various types of machinery are used to cut trees close to the ground. The limbs are then removed from the fallen trees, and the trunks are bucked into various lengths and transported to sawmills for further processing. The remaining tree limbs are converted into chips for sale to pulp and paper mills. Fre-

U.S. Lumber Consumption
(in millions of board feet)

	1970	*1976*	*1986*	*1991*	*1992*
Species group					
Softwoods	32.0	NA	48.0	44.0	45.7
Hardwoods	7.9	NA	9.0	10.8	10.3
End Use					
New housing	13.3	17.0	19.3	15.0	
Residential upkeep and improvements	4.7	5.7	10.1	11.6	
New nonresidential construction	4.7	4.5	5.3	5.4	
Manufacturing	4.7	4.9	4.8	5.6	
Shipping	5.7	5.9	6.8	8.2	
Other	6.8	6.7	10.9	8.8	

Source: U.S. Department of Commerce, *Statistical Abstract of the United States, 1996*, 1996.

quently, roads are built to facilitate the transportation of trunks and the deployment of heavy logging equipment. At the conclusion of harvest, refuse should be disposed of so that it will not interfere with the growth of new trees.

Owing to careful management of forests and improved efficiency of logging operations, the supply of timber in the United States currently renews itself at a higher rate than the removal level. It must be pointed out, however, that growth in world population will inevitably bring about an increase in timber consumption. The adequacy of timber supply will be a matter of concern in the future.

Physical Structure and Strength

As a material of botanical origin, wood is composed of hollow, elongated fibers. These fibers are usually arranged parallel to one another in the direction of the length of the trunk. They are cemented together by a substance known as *lignin*. The fibers in softwoods are longer than those in hardwoods. The length of the fibers, however, is not a criterion of the strength of the wood. Owing to the parallel arrangement of their fibers, wood possesses different mechanical properties in different directions and is said to be *anisotropic*. As an example, timber is five to ten times as strong in compression parallel to the grain as it is perpendicular to the grain. The varying strength of timber in different directions must be taken into consideration in construction design. By contrast, metals are *isotropic* and have the same characteristics in any direction.

The strength of timber is affected by its moisture content. Wood in a living tree typically contains more moisture than the surrounding atmosphere. When a piece of timber is cut from the log and exposed to air, its moisture content decreases to an equilibrium value determined by the temperature and relative humidity of ambient air. Should wood dry below a value called the *fiber saturation point*, it becomes stronger and stiffer. That is why higher design stresses are allowed for timber which is used under relatively dry conditions, such as a girder in a building, than for timber used under relatively moist conditions, such as in a waterfront house or in a bridge.

Wood has a very high strength-to-weight ratio. Compared with many other construction materials at the same weight, wood is stronger. For instance, in bending tests, Douglas fir has a strength-to-weight ratio which is 2.6 times that of low-carbon steel. Wood also has very high internal friction within its fibrous structure and is therefore a good absorber of vibrations. It has much greater damping capacity than other materials, particularly the metals. That explains why wood is the preferred material for construction of houses in earthquake-prone regions. Finally, timber structures can be designed to withstand impact forces that are twice as large as those they can sustain under static conditions. Materials such as steel and concrete do not permit such increase in the applied forces. This exceptional impact strength of wood is utilized in timber structures such as bridges or the landing decks of aircraft carriers.

Insulation and Fire Resistance

Due to its fibrous composition, wood has excellent insulating properties. At a low moisture content, wood is classified as an electrical insulator. This is what makes wood such a common material for high-voltage power-line poles and for tool handles. Wood is also an effective thermal insulator. The thermal conductivity of timber is only a fraction of that of metals and other common construction materials. For example, bricks are about 6 times more conductive than timber, and glass and steel are respectively 8 and 390 times more conductive.

By using stud walls or layers of spongy materials, thermal insulation of timber structures can be further enhanced. In addition, timber structures may be designed to provide a very degree of acoustical insulation. (Sound is transmitted through vibration of air particles.) Because of its high vibration-damping capacity, wood is also a good acoustical insulator.

It is well known that wood is combustible. On the other hand, wood that is thick enough is also fire-resistant. Because of the low thermal conductivity of wood, the high temperatures of a fire cause a temperature rise for only a short distance into the wood from the surface exposed to the fire. This is the reason larger timber members may continue to support a structure in a fire long after an insulated steel member has collapsed because of elevated temperatures. In fact, buildings framed with large timber members have been given the highest rating by fire underwriters among all common buildings erected.

Fabrication and Workability

Wood may be cut and worked into various shapes with the aid of simple hand tools or with power-driven machinery. It therefore lends itself not only to conversion in a factory but also to fabrication on-site. It is the latter fact that principally keeps conventional wood-frame construction fully competitive with any method of prefabrication of houses yet employed.

Timber can be joined with nails, screws, bolts, and connectors, all of which require the simplest kinds of tools and produce strong joints. Timber may also be joined with adhesives, which can produce a continuous bond over the entire surface to which they are applied and develop the full shear strength of the solid timber. This use of adhesives provides a means of fabricating timber members of different shapes and almost unlimited dimensions. The prefabrication of large wood trusses, laminated beams and arches, and stress-skin panels has permitted wood to remain extremely competitive as a building and engineering material.

Durability

Wood is remarkably resistant to decay and is inert to the action of most chemicals. It is widely used in facilities for bulk chemical storage; the timber may be in direct contact with the chemicals. When wood is exposed to atmospheric conditions, it slowly erodes under the action of weather at a rate of about 0.25 inch per century. If properly used, wood lasts for a long time. Decay and insect damage are often significant problems, but these can be minimized by following sound methods of design in construction and by using properly seasoned timber. In situations where biological wood-destroying agents are difficult to control, the decay resistance of timber can be maintained by impregnation with suitable preservatives.

Significance of Wood

Wood has remained a primary construction material for thousands of years, essentially because no competitive material has all the advantages of wood. The importance of wood as a raw material for pulp and paper is also profound. No other natural substance can meet the increasing demands of modern society for paper and other pulp products. It is also unlikely that a synthetic material can be made economically to rival wood as a source of pulp, particularly in light of the limited supply and high cost of petroleum. On the other hand, methods for converting wood into various chemicals are continually being developed. There is potential for using wood as a raw material to produce chemicals that are now obtained from petroleum.

Future Prospects

Tremendous progress was made in the late twentieth century in transforming wood from a material of craftsmanship to one of engineering. Reliable structural grading, improved fastenings, efficient fabrication, and glue-laminating have all contributed to making wood a truly modern construction material. Timber connectors and other improvements in fastenings have permitted the use of small timber members for larger spans.

The increasing popularity of glue-laminated wood products is of particular significance. A glue-laminated timber member typically has greater strength than a solid sawed member of the same size. It may also have superior surface properties such as higher fire resistance. The laminated arches used in churches and buildings are common examples of this application. Other examples include the exterior waterproof laminations in such structures as bridges and ships.

Fai Ma

See also: Asian agriculture; Conifers; Deforestation; Dendrochronology; European flora; Erosion and erosion control; Forest and range policy; Forest fires; Forest management; Forests; Logging and clear-cutting; North American flora; Old-growth forests; Petrified wood; Plant tissues; Rain-forest biomes; Reforestation; Savannas and deciduous tropical forests; Sustainable forestry; Taiga; Timber industry; Wood; Wood and charcoal as fuel resources.

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YEASTS

Categories: Economic botany and plant types; food; fungi; microorganisms; taxonomic groups

The term "yeast" does not refer to any recognized taxonomic name but instead describes fungi that are unicellular and usually reproduce asexually by budding. The term yeast is also used, more specifically, for those species in the genus Saccharomyces *that are used to leaven bread and ferment alcoholic beverages.*

Among mycologists, there is some disagreement over what should be called a yeast. Many mycologists use the term to describe any fungus that has a unicellular budding form at any time in its life. They often use the term "monomorphic" to describe those that are always unicellular and the term "dimorphic" to describe those that can have both unicellular and filamentous growth. Others, however, reserve the name yeast for those species that are permanently unicellular and use the term "yeastlike" to describe those fungi that can alternate between mycelial and unicellular forms. Because some species that have traditionally been called yeasts have later been shown to have a mycelial form, the former broader definition will be used here.

Taxonomy

Yeasts are found in all three major fungal phyla, *Zygomycota*, *Ascomycota*, and *Basidiomycota*, but the vast majority are ascomycetes. As in many fungi, the placement of some species in the proper phylum is made difficult by the lack of data on sexual reproduction. In others, the sexually reproducing, or telomorph, form and the asexually reproducing, or anamorph, form have been assigned different names. In addition, dimorphic fungi were often assigned different names for their yeast and mycelial phases. *Mucor indicus* (synonymous with *Mucor rouxii*) is a zygomycote yeast. Basidiomycete genera include *Filobasidiella* (anamorph: *Cryptococcus*), *Rhodospiridium*, and *Ustilago*. Some ascomycote genera are *Saccharomyces*, *Candida*, *Blastomyces*, and *Ajellomyces* (anamorph: *Histoplasma*).

Reproduction

The most common reproductive mechanism seen in yeasts is *budding*. During this asexual process the nucleus divides, and a small section of the original cell containing one of the new nuclei begins to bulge from the original cell. The cell and the bud begin to separate by the formation of a new cell wall called, at this stage, the *cell plate*. The bud grows and, usually, separates from the original cell. In some species, buds do not separate and, after they have grown, may produce buds of their own. This pattern leads to a connected group of cells produced by sequential budding referred to as a *pseudomycelium*. Yeasts may bud new cells from any part of the original cell (called multilateral budding) or from just the tips of the cell (called polar budding). The release of a bud often leaves a bud scar, and the scarred area is usually not able to produce another bud.

Other methods of reproduction include fission, in which the original cell divides equally, and the production of various kinds of spores occurs both asexually and sexually.

Cells

Like all fungi, yeasts are eukaryotic organisms that can exist in haploid, diploid, and dikaryotic (two haploid nuclei per cell) states. Unlike filamentous fungi, in which the zygote is the only diploid cell, ascomycote yeasts such as *Saccharomyces* can have a prolonged diploid state after the haploid nuclei of the dikaryote fuse. Cell components of yeasts are quite similar to those of filamentous fungi. One exception is that monomorphic yeasts have much lower levels of chitin in their cell walls, and the small amount that is present is found mainly in the bud scars.

Uses

Both brewing and bread making, which use various *Saccharomyces* species, have existed for millennia. Four-thousand-year-old tomb paintings in Egypt depict both, but only since the mid-1800's has the involvement of yeast in these processes been studied. In both, complex carbohydrates are converted to glucose, and the yeast ferments glucose, producing ethyl alcohol and carbon dioxide. *Saccharomyces cerevisiae* is the most common baker's yeast, although *Candida milleri* is important in the production of sourdough breads. In beer brewing, the bottom-fermenting *Saccharomyces carlsbergensis*, which tolerates cold (10 degrees Celsius) is the most commonly used yeast. Wines, a few beers, and most ales use *Saccharomyces cerevisiae*, a top fermenter that requires higher temperatures (20-25 degrees Celsius).

Yeasts are also important in the development of flavor and texture in certain cheeses. Production of Limburger, Camembert, Brie, and Swiss cheeses all rely on yeast fermentation. Because of their high nutrient content, yeasts themselves are important foods and food additives. Yeasts have also been used in the production of various industrial chemicals and biochemicals, including glycerol, ethanol, B vitamins, and polysaccharides. With the advent of modern genetic techniques, yeasts are being engineered to produce many other useful products.

Pathogens

Many yeasts can cause disease in plants or animals. *Histoplasma capsulatum*, *Blastomyces dermatiditis*, and *Cryptococcus neoformans* are all dimorphic fungi that can cause systemic infection in humans when the fungi are in the yeast form. *Candida albicans*, also dimorphic, is an opportunistic human pathogen which is pathogenic in its filamentous form. Most *Candida* infections, such as vaginal yeast infections and thrush, are superficial, but systemic infections can occur in immunocompromised individuals. *Pneumocystis carini*, which causes respiratory infections in patients with acquired immunodeficiency syndrome, was originally classified as a protist but is now thought to be a dimorphic fungus. The dimorphic genera *Ustilago* and *Taphrina* both contain many plant pathogens.

Richard W. Cheney, Jr.

See also: Ascomycetes; *Basidiomycetes*; Basidiosporic fungi; Deuteromycetes; Ethanol; Eukaryotic cells; Extranuclear inheritance; Fungi; Genetically modified bacteria; Glycolysis and fermentation; Model organisms; *Ustomycetes*; Wheat; Zygomycetes.

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ZOSTEROPHYLLOPHYTA

Categories: Evolution; paleobotany; seedless vascular plants; taxonomic groups

The Zosterophyllophyta *are a phylum of extinct seedless vascular plants that have been recovered from fossils in the stratum ranging from the Early to the Late Devonian, approximately 408 million to 370 million years ago.*

Today, scientists believe that zosterophyllophytes and lycopods arose at about the same time from a common but unknown ancestor. The zosterophyllophytes went extinct, but the lycopods have survived until today.

Characteristics

The *Zosterophyllophyta* evolved independently from the *Rhyniophyta*, but both groups shared a number of characteristics. Their aerial stems arose from a horizontal axis, the rhizome, when one of two branches formed by the forking rhizome turned and grew upward. Some of the zosterophyllophytes had no leaves, the common condition in the rhyniophytes. The two groups were distinguished by sporangial position and the presence or absence of a coiled stem that grew in length by unrolling like a New Year's Eve noisemaker. In the rhyniophytes, the sporangia were borne at the branch tips. In the zosterophyllophytes, the sporangia were borne on short branches along the sides of the stem. Growth from a coiled stem is characteristic of most zosterophyllophytes but does not occur in the rhyniophytes (or lycopods).

The zosterophyllophytes formed dense stands that could cover hundreds of square meters. Most of the plants existed in a vegetative state (lacking reproductive organs) for most of their lives. Their ability to grow and reproduce asexually through K- and H-branching allowed them to spread and dominate an area (a characteristic known as turfing). H-branching occurred when the aerial stem forked twice in rapid succession. One of the two branches formed by the first forking was short and ran parallel to the ground. This short axis forked again, and one of the new branches turned upward, while the other returned to the ground. Viewed from the side, the pattern resembled a capital H. In K-branching, a short branch on the rhizome forked, giving rise to two new axes. The upper axis was coiled and became a stem. The lower axis was not coiled and became a root. Viewed from the side, the branching pattern resembled a capital K.

Taxonomy

Zosterophyllophyta contains two orders: the *Zosterophyllales*, whose members have completely naked stems, and the *Sawdoniales* (also called prelycopods), whose aerial stems bear flaps of photosynthetic tissue (enations) that lacked vascular tissue. Typical members of the *Zosterophyllales* are *Zosterophyllum* and *Rebuchia*. Members of the *Sawdoniales* include *Bathurstia*, *Crenaticaulis*, and *Serrulacaulis*.

Zosterophyllales

All members of this order have naked stems which bear clusters of oval to kidney-bean-shaped sporangia on short side branches at the stem tip. Depending on the species, the sporangia may be arranged either spirally, like the red line on a barber pole, or in two vertical rows. For most species of *Zosterophyllum*, only the aerial stems are known. The lower portions of these stems lack a cuticle (a surface covering secreted by the plant to retard water loss). Since a cuticle was absent, the lower portions of *Zosterophyllum* probably grew in standing water. Although the aerial stem normally branched by forking, occasionally H-branching also occurred. The oldest fertile specimens (*Z. myretonianum* and *Z. fertile*) are from 412 million to 406 million years old. In a specimen of *Zosterophyllum*, from Bathurst Island in Arctic Canada, the aerial stems grew from a horizontal rhizome that bore rootlike structures on its lower surface.

Rebuchia resembles *Zosterophyllum* in all features except sporangial position. The sporangia of *Rebuchia* are borne on short side branches at the stem tip. They arise in two rows on opposite sides of the stem, but the stalks on which they are borne curve so that the sporangia all lie on the same side of the stem when mature.

Sawdoniales

Members of the *Sawdoniales* have spherical sporangia that are located on short side branches at various places along the stem. Flaps of photosynthetic tissue (enations) are present. These lack vascular tissue and do not influence the growth of the adjacent vascular tissue in the stem. The enations are arranged either randomly or in one or two rows. The sporangia are not associated with the enations. In the lycopods, the sporangia sit on the upper surface of vascularized leaves (called sporophylls), which are spirally arranged. *Bathurstia*, *Crenaticaulis*, and *Serrulacaulis* are typical sawdonialeans whose wedge-shaped enations lacked vascular tissue.

The enations of *Bathurstia* are arranged randomly on the stem. The sporangia are grouped together in two rows on opposite sides of the stem tip. *Bathurstia* exhibited K-branching. In *Crenaticaulis*, two rows of triangular, rounded (that is, crenate) enations were located on opposite sides of the stem. Subordinate branches, which were once thought to be rhizophores similar to those of *Selaginella*, are found just below each fork of the main axis. These subordinate branches are clearly stems, while rhizophores are rootlike. Therefore, the subordinate branches do not indicate a close relationship with the lycopods, as scientists once thought. *Sporangia* arose in two rows on opposite sides of the stem. Rootlike structures were found on some specimens of *Crenaticaulis*, and root hairs may be present. The gametophyte of *Crenaticaulis* was similar in appearance to *Sciadophyton*. In *Serrulacaulis*, two rows of triangular, pointed (that is, serrate) enations were located on opposite sides of both the aerial stem and rhizome. Sporangia occur alternately in two rows on one side of the stem. Rhizoids were seen coming from the rhizome.

Herbivory

The spinelike enations found on sawdonialeans were not adaptations to prevent insects from eating the plant (herbivory). All the known contemporary insect herbivores were too small to be affected by them. Wounds found on fossil plants are consistent with sap-sucking and not chewing insects. Insect coprolites (fossil fecal material) containing a mixture of vegetative plant cell types and spore masses are known but were produced by detritivores (animals that eat dead plant material). No evidence for any herbivore that chewed and digested living plant material has been found prior to 345 million years ago.

Asteroxylon mackiei

For some researchers, the most important member of the *Sawdoniales* (formerly *Asteroxylales*) was *Asteroxylon*, a plant from the Rhynia Chert of Scotland. The naked rhizome of *Asteroxylon* grew along the ground and branched by forking into two new axes. Because *Asteroxylon* was a large plant, its water and anchorage needs could not be met with rhizoids alone. Enationless, rootlike structures (possibly adventitious roots) depart from the rhizome and penetrate the soil. The aerial stem that arose from the rhizome had a single central axis from which the lateral branches arose. The aerial stem was densely covered with spirally arranged enations, which superficially resembled leaves but lacked vascular tissue. A vascular trace did leave the central vascular cylinder of the stem and traveled to the base of the leaf but did not enter it. Sporangia were found scattered among the enations. Each sporangium was borne on short stalk containing vascular tissue.

The sporangial position and overall appearance of *Asteroxylon* is very similar to that of the living lycopod, *Huperzia* (*Lycopodium*) *selago*. The sporangia of *Huperzia* are also scattered on short axes among the leaves of the stem. The enations of *Asteroxylon* lacked vascular tissue, a characteristic of the leaves (microphylls) of the lycopods, which initially prevented researchers from classifying *Asteroxylon* as a lycopod. By redefining a microphyll as a stem outgrowth which influences the growth of the adjacent vascular tissue in the stem, *Asteroxylon* can be classified as a lycopod because a vascular trace did run up to the leaf base although it did not enter the leaf. Vascular tissue might never have formed in the microphyll of *Asteroxylon*, or the vascular tissue that was once present might have been lost. *Asteroxylon* is now placed in the *Drepanophycales* along with *Drepanophycus* and *Baragwanathia*.

Baragwanathia

Baragwanathia's stem is covered with long, thin microphylls, each with a single vein. The sporangia are borne on the stem among the microphylls and appear to be spirally arranged. *Baragwanathia* may be the oldest lycopod, although this statement does cause controversy. The age of oldest specimens from Australia has been disputed. Some researchers believe that they are more than 414 million years old, while others claim that the sediments in which *Baragwanathia* was found are less than 406 million years old. If the older age is accepted, *Baragwanathia* is older than the simpler rhyniophytes (*Aglaophyton*) and zosterophyllophytes (*Zosterophyllum*) and contemporaneous with the cooksonioids. An older *Baragwanathia* supports an evolutionary origin for the lycopods distinct from that of the rhyniophytes and prevents the zosterophyllophytes from being the direct ancestors of the lycopods. Therefore, the *Sawdoniales* are mistakenly called prelycopods. The evolutionary development of microphylls through the sequence of naked stems, enations, and finally microphylls using *Asteroxylon* as an intermediate is also not possible. The similarity between the *Sawdoniales* and the lycopods is an example of convergent evolution.

Gary E. Dolph

See also: Adaptive radiation; Evolution of plants; Fossil plants; Lycophytes; Paleobotany; Plant tissues; *Rhyniophyta*; Shoots; Species and speciation; Stems; *Trimerophytophyta*.

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ZYGOMYCETES

Categories: Fungi; taxonomic groups

Zygomycetes are a group of fungi that constitute the phylum Zygomycota. *Also called zygote fungi, zygomycetes include about 750 species. Most are saprobes, living on decaying plant and animal matter in the soil; some are parasites of plants, of insects, or of small soil animals; some cause the familiar soft fruit rot and black bread mold; and a few occasionally cause severe infections in humans and farm animals.*

Zygomycetes share many common features with members of other phyla in kingdom *Fungi*. They are rapidly growing, nonphotosynthetic organisms that characteristically form filaments called hyphae. Hyphae are highly branched to form an interwoven network mass called mycelium. All zygomycetes are terrestrial and reproduce by means of spores. No motile cells are formed at any stage of their life cycle. The primary component of their cell wall is chitin, and the primary storage polysaccharide in the cytoplasm is glycogen. Most zygomycetes have coenocytic hyphae, within which the cytoplasm can frequently be seen streaming rapidly. Both sexual and asexual reproduction occurs in zygomycetes.

Members of *Zygomycota* play important roles both ecologically and economically. Some species (such as *Rhizopus stolonifer*) cause soft fruit rot, posing a problem for transport and storage of many fruits. The same fungi may also feed on bread and other bakery foods, a potentially serious health hazard. Others, such as *Glomus versiforme*, may form intimate and mutually beneficial symbiotic associations with plant roots called mycorrhizae (literally, "fungus roots").

Yet another group of zygomycetes, the *trichomycetes*, form a fascinating relationship with arthropods. Trichomycetes are found in the larvae of aquatic insects, millipedes, crayfish, and even crustaceans living at the bottom of the ocean near hydrothermal vents. They usually reside in the guts of these animals and are thought to provide vitamins to their hosts. Members of zygomycetes in the order of *Entomophthorales* have great ecological significance based on their parasitic relation with insects and other small pest animals. They are being increasingly used in the biological control of insect pests of crops.

Reproduction and Life Cycle

Even though by appearance all haploid hyphae of zygomycetes look identical, they are actually of two different mating types. When the two hyphae are in close proximity, hormones are released that cause an outgrowth near their hyphal tips to come together and develop into gametangia. Although some species are homothallic (self-fertilizing), most *Zycomycota* species are heterothallic, requiring a combination of + and – strains for sexual reproduction. The two strains "mate" sexually through the combination of two gametangia. In the process, the walls between the two touching gametangia dissolve, fusing their haploid nuclei to form diploid zygospores (hence the name *Zycomycota* for this phylum). Zygospores have very thick walls and thus are very hardy, able to tolerate extreme environment conditions. Zygospores are dispersed through the air and can remain dormant until conditions are favorable for growth. Zygospores then undergo meiosis and germinate, producing structures on which sporangia (spore cases) are formed. The sporangia produce and disperse numerous haploid spores, marking the beginning of the asexual part of the reproductive cycle.

During asexual reproduction, haploid spores released by sporangia germinate on food such as fruits, bread, and dung, producing haploid hyphae. These hyphae in turn may produce more hyphae or additional spores within sporangia through mitosis, and the cycle begins again. Asexual reproduction via haploid spores of sporangia is universal among all species of zygomycetes. Two examples illustrate the important role of zygomycetes in human lives: *Rhizopus stolonifer* and *Glomus versiforme*.

Rhizopus stolonifer

This is one of the best-known and most familiar members of phylum *Zygomycota*. *Rhizopus stolonifer* is a black mold that forms cottony masses on the surfaces of moist, carbohydrate-rich foods and similar substances that are exposed to air. This organism is a serious pest for stored fruits and vegetables, bread, and other types of staple food. Many people are familiar with rotten fruits or aged bread that are covered by *R. stolonifer*.

The life cycle of *R. stolonifer* is similar to those of other species of *Zygomycota*. The mycelium of *R. stolonifer* is composed of several distinct types of haploid hyphae. Most of the mycelium consists of rapidly growing, coenocytic hyphae, which grow through the substrate (such as orange or bread), absorbing nutrients. From coenocytic hyphae, arching hyphae called stolons are formed. The stolons form rhizoids wherever their tips come into contact with the substrate. From each of these points, a sturdy, erect branch arises, which is called a sporangiophore. Each sporangiphore produces a spherical sporangium at its apex. A sporangium begins as a swelling sac, into which a number of nuclei flow. The sporangium is eventually isolated from other hyphae by the formation of a structure called a septum. The protoplasm within is cleaved, and a cell wall forms around each spore. The sporangium wall becomes black as it matures, giving the mold its characteristic color. Each mature spore, upon dispersal, is capable of germinating under adequate conditions to produce a new mycelium. Each year *R. stolonifer* causes an estimated loss of millions of dollars to farmers, fruit growers, and consumers.

***Glomus versiforme* and Mycorrhizae**

As one of the most important groups of zygomycetes, *Glomus versiforme* and related genera grow in intimate associations with the roots of plants, forming mycorrhizae. Mycorrhizae not only dramatically increase the surface area of roots for absorption but also help convert nutrients in soil into forms usable by plants. For many forest trees, if seedlings are grown in a sterile nutrient solution and then transplanted to grassland soil, they grow poorly and may eventually die from malnutrition.

However, if a small amount of forest soil containing the appropriate fungi (including *G. versiforme*) is added to the soil around the roots of the seedlings, normal growth is restored. Studies have found that in forest soil *G. versiforme* and related fungi ensure the formation of mycorrhizae and restore the normal growth of seedlings.

Mycorrhizae occur in most groups of vascular plants. The fungal partner *G. versiforme* helps plant roots to absorb and transfer essential nutrients such as phosphorus, zinc, manganese, and copper. By extending several centimeters out from colonized roots in all directions, the plants are able to obtain nutrients from a much larger volume of soil than would be possible otherwise. In return, *G. versiforme* obtains carbohydrates from the host plants. Some fungi may simply attach to the outer surface of the root to form a sheath of hyphae around the root called ectomycorrhizae. In addition to surface extension, other fungi may penetrate into the root to form endomycorrhizae. Of the two major types of mycorrhizae, endomycorrhizae occur in about 80 percent of all vascular plants. The *G. versiforme* hyphae penetrate the cortical cells of the plant root, where they form either minute, highly branched, treelike structures called arbuscules or swellings called vesicles. Such endomycorrhizae are particularly important in the tropics, where soils tend to be positively charged and thus retain phosphates so tightly that this nutrient is available only in very limited supplies for plant growth. Since the impoverished farmers there are often unable to afford fertilizers, endomycorrhizae play a critical role in making phosphates available to crops in these regions. The commercial applications of endomycorrhizae to crops in other regions to reduce fertilizer use and increase yields appear to be an increasingly attractive possibility as well.

Yujia Weng

See also: Ascomycetes; *Basidiomycetes*; Basidiosporic fungi; Chytrids; Community-ecosystem interactions; Deuteromycetes; Diseases and disorders; Fungi; Lichens; Mycorrhizae; Nitrogen; Nitrogen fixation; Nutrient cycling; Nutrients; Oomycetes; Rusts; *Ustomycetes*; Yeasts.

Sources for Further Study

Ayres, P., and P. Nigel. "Weeding with Fungi." *New Scientist*, September 1, 1990, 36-39. Describes an herbicide made from fungi, which can devastate weeds but not crops. Could be an ideal form of weed control.

Christensen, C. M. *Molds, Mushrooms, and Mycotoxins*. Minneapolis: University of Minnesota Press, 1975. Well-organized and thoughtful discussions on some fungi and their ecological and economic importance.

Dix, N. J., and J. Webster. *Fungal Ecology*. London: Chapman & Hall, 1995. A easy-to-read yet comprehensive account of fungal diversity in various ecological communities. Includes informative discussions on the critical roles fungi play in maintaining the health of ecosystems.

Matossian, M. K. *Poisons of the Past: Molds, Epidemics, and History*. New Haven, Conn.: Yale University Press, 1989. A very good summary on the effects of food poisoning resulting from bread molds on human history. A useful reference book for public health.

Smith, D. C., and A. E. Douglas. *The Biology of Symbiosis*. Baltimore, Md.: Edward Arnold, 1987. An outstanding, concise account of biological symbiosis, including several chapters on symbiotic relationships between fungi and plants.

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BIOGRAPHICAL LIST OF BOTANISTS

Adanson, Michel (1727-1806), French naturalist and African explorer. He collected biological specimens in Senegal, 1749-1753, and published *Histoire naturelle du Sénégal* (1757). He was the first to develop a natural classification of plants, in *Familles des plantes* (1763, 2 vols.), though he was strongly influenced by his studies with Bernard de Jussieu in developing his "natural method." Many of his specimens and manuscripts still exist.

Albertus Magnus (c. 1200-1280), German natural philosopher. He was the most important medieval European student of plants, and he achieved such a prominent role both in the Church and in education (Thomas Aquinas was a student) that his *De vegetabilibus et plantus* (c. 1250) was highly regarded. In writing it, he was inspired by an uncritical *De Plantis* that was wrongly attributed to Aristotle, and he lacked access to the works of Theophrastus. However, his training in the authentic writings of Aristotle prepared him well for his task. Book 7 in *De vegetabilibus* is the best general work on agriculture since that of Lucius Columella.

Arber, Agnes Robertson (1879-1960), English botanist and historian of herbals. She studied under Ethel Sargent, who inspired her interest in comparative anatomy. She married the Cambridge University paleobotanist E. A. N. Arber. She published three anatomical monographs, *Water Plants* (1920), *Monocotyledons*: *A Morphological Study* (1925), and *Gramineae* (1934). She first published her study of early printed herbals in 1912, then largely rewrote a second edition (1938). She also published three books on her philosophical perspectives as a biologist (1950-1957). She was the first woman botanist elected a fellow of the Royal Society of London, and she received the Linnean Society's Gold Metal in 1948.

Banks, Joseph (1743-1820), English botanist and science administrator. He inherited enough wealth to follow his interests, and his friendship with England's King George III facilitated his activities on behalf of science. Although he entered Oxford University, its resources for botanical education were slight, and he left in 1766 in order to spend eight months exploring Labrador and Newfoundland. He returned with the beginnings of the renowned Banks Herbarium and was elected to the Royal Society of London. He also was a naturalist on the first voyage of Captain James Cook (1769-1771); this voyage made them both famous. From his presidency of the Royal Society (1778-1820), he dominated British science and exerted a broad influence in Europe. He was also influential in the early development of the Royal Botanic Gardens at Kew.

Bartram, John (1699-1777) and William (1739-1823), America's most prominent early native botanists. John was the son of a farmer and became one himself, near Philadelphia. However, his fascination with plants extended far beyond utilitarian uses, and Philadelphia provided both the personal connections and books to study botany. His exploratory expeditions throughout the British colonies began in 1738, and he supported them by selling his collected plants and seeds to supporters in England and Europe. In 1753 he first took along his son, William, on a trip into the Catskill Mountains, and they collected plants in Florida in 1765. In recognition of his discoveries and shipments of plants to England, he was appointed botanist to the king in 1765. Both Bartrams published accounts of their explorations and botanical discoveries. William was a skilled illustrator of plants and animals, and his *Travels Through North and South Carolina, Georgia, East and West Florida* (1791) was widely read.

Bary, Anton de (1831-1888), German founder of mycology. He was the son of a physician who encouraged his early interest in fungi and algae. De Bary earned a medical degree at the University of Berlin (1853), with a dissertation on sexual reproduction of plants. He practiced medicine for a while, then taught botany and worked as Hugo von Mohl's assistant at the University of Tübingen. De Bary demonstrated in 1853 that rusts and smuts of cereals and other plants are not diseased cells but fungal parasites. In 1855 he succeeded Karl Nägeli as botanist at Freiburg im Breisgau. After the Franco-Prussian War, de Bary became rector of the University of Strasbourg. In 1858 he demonstrated sexual reproduction in fungi. In 1861 he began publishing his studies on the potato blight that had devastated Ireland. Although it seemed to have only one host, he later showed that wheat rust has a two-stage life cycle, its other host being common barberry. He coined the terms "mutualism" and "symbiosis" in his monograph, *Die Erscheinung der Symbiode* (1879). He also made important contributions to bacteriology.

Bauhin, Jean (1541-1613) and Gaspard (1560-1624), Swiss botanists. Their father was a prominent physician who fled France because of the persecution of Protestants. Jean studied botany in Zurich under Konrad Gesner and in 1560-1565 helped Gesner compile his *Historia plantarum*, which Gesner did not live to publish. The same fate befell Jean's own *Historia plantarum universalis*, which describes and gives synonyms of 5,226 species. It appeared in three well-illustrated volumes in 1650-1651. Gaspard studied botany under his older brother, Jean, and traveled to Italy and France to study medicine. Gaspard's two main botanical works, *Prodromos* (1620) and *Pinax theatri botanica* (1623), distinguished between genus and species and introduced binomial nomenclature for about six thousand species.

Bawden, Frederick Charles (1908-1972), English virologist and plant pathologist. An early interest in gardening and botany led him to obtain a Ministry of Agriculture scholarship to Cambridge University. Upon graduation, he became assistant to R. N. Salaman, director of the Potato Virus Research Station at Cambridge. Bawden and his collaborator, N. W. Pirie, discovered that plant viruses are nucleoproteins. This was an early step toward molecular biology. In 1940 he became head of the Plant Pathology Department at the Rothamsted Experimental Station. Later he became director of Rothamsted. His work carried him frequently to Africa and Asia as a consultant. He also served as president of several important organizations, including the Institute of Biology.

Beijerinck, Martinus Willem (1851-1931), Dutch botanist. His early interest was botany, but he majored in chemical engineering at the Delft Polytechnic School. Upon graduation in 1872, he taught botany while working on a doctoral degree in botany at Leiden, which he earned in 1877. In early 1880's he became interested in tobacco mosaic disease (his father was a tobacco dealer) and attempted unsuccessfully to discover a bacterial cause. He became a bacteriologist at the Dutch Yeast and Spirit Factory and discovered a bacterium that lives in nodules on leguminous plants and converts atmospheric nitrogen into soil-fertilizing compounds. In 1895 he returned to the Delft Polytechnic School as professor of microbiology and discovered that the causative agent for tobacco mosaic disease can pass through a porcelain filter that traps bacteria. After determining that the cause was not a toxin, he concluded in 1898 that it was a molecule, which he called a "filterable virus," and suspected was a liquid. American biochemist Wendell Meredith Stanley isolated tobacco mosaic virus in 1935.

Bentham, George (1800-1884), English botanist. He accompanied his father, a government official, to St. Petersburg (1805-1807) and while there learned Russian, French, German, and Latin. As an adult, he read botanical works in fourteen languages. By age seventeen, he and his family had moved to France and his mother's enthusiasm for gardening had aroused his interest in botany. He borrowed her copy of Jean-Baptiste Lamarck and Augustin de Candolle's *Flore française*, which awakened his lifelong interest in systematic botany. His first publication was in French, a catalog of the plants of the Pyrenees and Languedoc (1826), but it was only in 1833, after inheriting enough wealth to be independent, that he became fully committed to botany. In 1854 he transferred his herbarium of 100,000 specimens and his library to the Royal Botanic Gardens at Kew, where he was given research facilities. His major work was coauthored with the gardens' director, Joseph Hooker; their *Genera plantarum ad exemplaria imprimis in herbariis kewensibus servata definita* (1862-1883, 3 vols.) was a monumental achievement.

Bessey, Charles Edwin (1845-1915), American botanist. The son of an Ohio schoolteacher, Bessey devoted his own career to teaching and research, but in higher education. He earned a bachelor's degree at Michigan Agricultural College and then taught at Iowa's College of Agriculture (1869-1884). In 1884 he became professor of botany at the University of Nebraska, where he remained for the rest of his career. He was equally prominent as an author and as a professor. His botany textbooks dominated the field from 1880 to 1915, but he was also influential as an investigator of the evolution of flowering plants. His evolutionary classification was founded upon the classifications of George Bentham and Joseph Hooker and of Adolf Engler and Ludwig Prantl. Bessey published "Evolution and Classification" in 1893, and his system achieved its final form in *The Phylogenetic Taxonomy of Flowering Plants* (1915). Although not an ecologist, he steered several students in that direction, most notably Frederic E. Clements.

Biffen, Rowland Harry (1874-1949), English botanist and agronomist. He studied botany at Cambridge University and, after graduating, participated in an expedition to Brazil and Mexico to study rubber production. This experience turned his interests toward agriculture. He became a lecturer at Cambridge's new School of Agriculture in 1899 and served as its professor of agricultural botany (1908-1931). He realized the importance of Gregor Mendel's laws of genetics for improving crops, and in 1905 he bred a rust-resistant strain of wheat. He also directed the Plant Breeding Institute at Cambridge (1912-1936). He won the Royal Society's Darwin Medal in 1920 and was knighted in 1925.

Blackman, Frederick Frost (1866-1947) and Vernon Herbert (1872-1967), English plant physiologists. Their father was a physician whose botany books attracted their interest. Although Frederick studied medicine, he became a plant physiologist at Cambridge University, where he studied plant respiration. He showed that stomata control gas exchanges between plants and their environment. His skills as both experimentalist and teacher attracted outstanding students who continued his studies. Vernon followed in his brother's footsteps, studying medicine and then botany. He conducted cytological researches on the nucleus of *Pinus sylvestris* and on the *Uredineae*, demonstrating alternation of generations in rust fungi. He was the first professor of botany at Leeds University (1907-1915), after which he joined the Imperial College of Science, Technology, and Medicine in London, where he did agricultural research until he retired in 1942.

Blakeslee, Albert Francis (1874-1954), American botanist. He obtained a doctorate from Harvard University in 1904, with a dissertation on his discovery of sexual fusion in several species of fungi. In 1907 he joined the faculty of Connecticut Agricultural College (now the University of Connecticut), where he established a botanical garden and taught what was probably the first course in genetics in the United States. In 1915 he moved to the Carnegie Institution's Station for Experimental Evolution and served as its director (1934-1941). In 1937 he discovered that the alkaloid colchicine, from the autumn crocus, produces polyploidy in plant chromosomes. In 1942 he became a professor at Smith College and founded its Genetics Experiment Station, funded initially by the Carnegie Institution. He was active in many national scientific organizations and served as president of five of them.

Borlaug, Norman E(rnest; 1914-), American agronomist and plant pathologist. He received his bachelor's (1937), master's (1941), and doctoral (1942) degrees from the University of Minnesota, in plant pathology and forest management. The Rockefeller Foundation hired him to breed disease-immune crops that could grow in Mexico's varied ecosystems. He developed a high-yield dwarf spring wheat. In response to German bacteriologist Paul Erhlich's 1968 prediction that the world would soon face massive famine, Borlaug concluded that high-yielding crops could avert catastrophe. In 1963 the Rockefeller Foundation and Mexico established the International Maize and Wheat Center, which he headed. By 1968 he increased Pakistan's wheat yield by 70 percent and ushered in the Green Revolution, which saved millions of lives and won him a Nobel Peace Prize in 1970. Controversy followed, however, because of the necessity of inorganic fertilizer and irrigation to achieve widespread results. He responded that with higher production per acre, less land fell victim to slash-and-burn agriculture, more than offsetting the environmental stresses of his methods.

Bose, Jagadis Chandra (1858-1934), Indian physicist and physiologist. He graduated from a Jesuit college in Calcutta, then went to Cambridge University, where he graduated in natural science in 1884. He then became professor of physics at Presidency College, Calcutta, where he remained until he retired in 1915. Early on, his research turned from the properties of radio waves to a comparison of the comparative responses of plant and animal tissues. Today he is seen as a pioneer in biophysics, but at the time, many viewed his researches as far-fetched. He was knighted in 1917 and became a fellow of the Royal Society of London in 1920. In 1917 he founded the Bose Research Institute, where he developed sensitive automatic recorders of plant growth.

Brongniart, Adolphe-Théodore (1801-1876) and Alexandre (1770-1847), French paleontologists. Alexandre studied both geology and medicine and in 1794 became professor of natural history at École Centrale des Quatre-Nations. In 1820 he became professor of mineralogy at the Muséum d'Histoire Naturelle. He independently discovered the value of fossils to identify strata, though William Smith's discussion of this was published before Brongniart's. Alexandre trained his son, Adolphe, and they collaborated on important projects. Adolphe, however, focused more narrowly on botany and paleobotany at a time when most paleontologists studied fossil animals. His *Prodrome d'une histoire des végétaux fossilles* (1828) was an early synthesis of paleobotany, and his *Tableau des genres de végétaux fossiles* (1849) synthesized twenty-five years of research. Afterward, he devoted his research to the systematics of living plants, especially those from Neo-Caledonia.

Brown, Robert (1773-1858), British botanist. Although he was primarily a taxonomist, he discovered the cell nucleus, protoplasmic streaming, and Brownian motion. Botany was only a hobby at first, as he trained and served as an army surgeon. However, in 1798 he attracted the interest of Joseph Banks, who arranged for him to accompany a naval expedition to Australia in 1801 under Matthew Flinders. Brown collected plants there and in Tasmania, Norfolk Island, and at the Cape of Good Hope. Upon returning to England, Banks arranged for the Admiralty to support Brown for five years while he described the more than four thousand plants he had collected. Brown became an officer of the Linnean Society of London and was its president (1849-1853). In 1820 he inherited Banks's library, herbarium, an annuity, and the use of Banks's Soho Square house. Brown gave the library and herbarium to the British Museum in exchange for its creation of a botany department under his directorship. He became one of Europe's leading botanists.

Brunfels, Otto (c. 1488-1534), German monk, physician, and botanist. He received a master of arts degree in 1508-1509 and then entered a monastery. However, he became swept up in the Protestant Reformation and left the monastery in 1521. He married in 1524, and his widow helped publish his manuscripts posthumously. His most important work was *Herbarium vivae eicones ad nature imitationem* (1530-1540, 3 vols.); a German version was titled *Contrafayt Kreüterbuoch* (1532-1540, 2 vols.). This work pioneered the transition from medieval herbalism to modern botany. Although his text drew heavily upon ancient and medieval sources, he added German names and illustrations drawn from live plants. Most of the approximately 230 species described were indigenous to the Strasbourg region and included more than 40 species not previously described.

Burbank, Luther (1849-1926), American horticulturist. He was the son of a Massachusetts farmer and received a good education but did not go to college. In 1871 he bought land and became a truck-gardener for five years. In 1872 he bred a potato with attractive shape and white skin that became known as the "Burbank potato." He sold sixty bushels of them to a seedsman and with the money moved to Santa Rosa, California, where he devoted his career to plant breeding. He introduced more than eight hundred new plants to gardeners and farmers. His breeding methods began well before the rediscovery of Gregor

Mendel's genetic laws in 1900, and Burbank's methods never caught up with the scientific techniques developed by university geneticists. Consequently, his credibility as a cereal breeder was questioned, but his empirical achievements were nevertheless impressive.

Calvin, Melvin (1911-1997), American plant physiologist. He trained in college as a chemist, and when he became a faculty member at the University of California at Berkeley in 1937, he joined an organic chemistry research group. During World War II he studied ways to produce oxygen. In 1946 he became director of the bio-organic chemistry group at the Lawrence Radiation Laboratory; in 1960 the group became the Laboratory of Chemical Biodynamics. Calvin's work at the Lawrence Laboratory gave him the opportunity to use radioactive tracers, particularly carbon 14, to follow the complex steps in photosynthesis, for which he won the Nobel Prize in Chemistry in 1961. He identified eleven intermediate compounds plants create between the intake of simple ingredients and the formation of energy compounds. He also developed a theory on the chemical evolution of life.

Camerer, Rudolph Jakob (1665-1721), German botanist. He came from a long line of physicians and pharmacists. At a time when medicines were still made mainly from plants, it was natural for him to become director of the Tübingen Botanic Garden. He read Nehemiah Grew's (1682) and John Ray's (1686) comparisons of the stamen and pollen in flowers to male organs and semen of animals. Because Camerer's microscopic studies indicated that these claims were plausible, he concluded that many species are hermaphroditic, while other flowers are monoecious or dioecious (though the latter terms came later). He then conducted experiments by removing male flowers from the vicinities of female flowers of mulberry. The female plants produced seeds, but none were fertile. This was the first important experiment in plant physiology. The results of his experiments over several years were published in 1694.

Candolle, Augustin Pyramus de (1778-1841) and Alphonse de (1806-1893), Swiss botanists. Augustin fell in love with the Swiss mountain flora at age fourteen. In 1796 he went to Paris to study medicine but became so excited about science from his contacts with Georges Cuvier, Jean-Baptiste Lamarck, and other scientists at the Muséum d'Histoire Naturelle that he abandoned medicine for botany. While in Paris, his many botanical publications earned him a professorship of botany in Montpellier (1808-1816). In 1816 his hometown, Geneva, established a professorship of natural history for him, where he spent the rest of his life. In 1820 he published an important, lengthy essay in a science encyclopedia, "Géographie botanique," that went beyond Alexander von Humboldt's perspectives by emphasizing the competition between species as an important factor influencing distribution. Augustin de Candolle's most significant work was *Prodromus systematis naturalis regni vegetabilis* (1824-1873, 17 vols.), which is not limited to descriptions of plants but includes ecology, phytogeography, biometry, agronomy, and evolutionary allusions. Alphonse was born in Paris and lived in Montpellier until 1816, when the family returned to Geneva. He earned a bachelor's degree in science in 1825, then a doctorate in law in 1829. His legal training facilitated his participation in Geneva's civic life. He succeeded his father in 1835 as professor of botany and director of the university's botanical garden. Alphonse's greatest work is his *Géographie botanique raisonnée* (1855, 2 vols.), which is worldwide in scope. Two other notable works were his *Histoire des sciences et des savants depuis deux siècles* (1873) and *Origine des plantes cultivées* (1882; *Origins of Cultivated Plants*, 1884). Furthermore, he continued his father's *Prodromus systematis naturalis regni vegetabilis* (1844-1873, vols. 8-17).

Carson, Rachel Louise (1907-1964), American marine biologist, author, and environmentalist. As an undergraduate at the Pennsylvania College for Women (now Chatham College), she was undecided about whether to major in English or biology. A professor persuaded her to choose biology, but she spent the rest of her life using both literary and scientific skills to persuade people to appreciate and preserve nature. She earned a master's degree at Johns Hopkins University before joining the U.S. Fish and Wildlife Service as an author-editor. She published three best-selling books on the sea (1941-1954), but enduring fame came with *Silent Spring* (1962), her eloquent and meticulous attack on the careless, widespread use of insecticides, especially DDT. Such sprays killed not only herbivorous insects, she showed, but also their predators and pollinating insects. She died of cancer before DDT was banned in the United States in 1972.

Carver, George Washington (c. 1864-1943), American agricultural scientist. He was born into slavery in Missouri, but emancipation enabled him to get a public education in Kansas and a college degree from Iowa State University in Ames in 1894. He joined its faculty and received a master's degree in agriculture in 1896. He then became director of the agricultural experiment station at Tuskegee University in Alabama. He devoted his career to developing sustainable agriculture for the South, emphasizing peanuts and sweet potatoes as supplements or alternatives to cotton. He found new uses for peanuts and sweet potatoes, such as dyes, milk substitutes, and cosmetics.

Cesalpino, Andrea (1519-1603), Italian physician, botanist, and philosopher. He studied philosophy and medicine at Pisa University, received a doctorate in 1551, and in 1555 succeeded his teacher Luca Ghini as medical professor and director of the botanical garden. In 1592 he became physician to Pope Clement VIII and professor at Universita degli Studi "La Sapienza," Rome. His *De plantis libri XVI* (1583), heavily influenced by Aristotle and Theophrastus, was the first true textbook of botany. He considered the fruit the most important part of the plant and made it the basis for his classification system of about fifteen hundred species, while still using of the Greek division of plants into trees, shrubs, shrubby herbs, and herbs. He denied the sexuality of plants. He first provided a system of plants based on a coherent set of principles, though his narrative (rather than an outline) presentation of it limited its influence.

Clements, Frederic Edward (1874-1945), American plant ecologist. A native of Lincoln, Nebraska, he attended the university there and studied under Charles Edwin Bessey, who ran the state's phytogeographic survey. Clements collaborated with fellow student Roscoe Pound on the survey, developing methodologies which Clements used in his doctoral research. (Pound became a law professor.) Clements taught botany at Nebraska (1897-1906) and married his doctoral student Edith Schwartz, who was often his assistant or collaborator. They bought a cabin in a Pike's Peak canyon that became a summer laboratory. Although he also taught botany at the University of Minnesota, 1907-1917, Clements was much more interested in research than teaching, and in 1917 he became a full-time research associate at the Carnegie Institution in Washington, D.C. *Plant Succession* (1916) was his most important book, which developed his main ecological ideas about discrete communities that are adapted to a climate; if disturbed, a community grows through a series of stages and returns to a climatic climax. He was the most productive publisher in plant ecology of his time, and his books were both influential and controversial, as his theories went beyond the supporting evidence.

Cohn, Ferdinand Julius (1828-1898), Polish botanist and bacteriologist. He came from Breslau's Jewish ghetto but was allowed to attend the city's gymnasium. He became interested in botany at Breslau University but was barred because of religion from taking the degree examinations. He transferred to the University of Berlin, where he was introduced to microscopic studies, and he received a doctorate at age nineteen. In 1849 he returned to Breslau (now Wrocław) and in 1850 became a Privatdozent at Breslau University, working under Jan Purkinje in his Institute of Physiology. In 1850 Cohn began researches on unicellular algae and similarities to protozoa, and in 1855 he demonstrated sexuality in unicellular algae. About 1870 he turned to bacteria and soon developed a classification system that became accepted. However, he also studied bacterial physiology and proved that bacteria are killed at 80 degrees Celsius. Cohn became professor of botany in 1872. In 1887 the university provided him with an institute of plant physiology, and he received many international honors.

Colonna, Fabio (1567-1650), Italian jurist and botanist. He studied law but suffered from chronic epilepsy. Ancient pharmacists and physicians had allegedly used a medicinal plant to cure epilepsy, but it was uncertain to which species the ancient name applied. Colonna's efforts to determine its identity drew him into botany. He departed from Andrea Cesalpino's classification of plants by fruits, believing that flowers provide better evidence of relationships. He was the first botanist to make comparative studies of flowers and to establish plant genera based on his findings. His two books, *Phytobasanos* (1592) and *Ecphrasis* (1616), first used illustrations engraved on copper plates rather than on wood, enabling him to achieve greater floral detail than before.

Columella, Lucius Junius Moderatus (early first century C.E.), a Roman from Cadiz, Spain, and author on agriculture. His is the third and most detailed Latin agricultural treatise, which includes information on the cultivation of many different kinds of food plants. He explained grafting techniques and knew that both manure and legumes improve soil fertility. His *De re rustica* (*De re rustica*, 1968-1979, 3 vols.) is published in a modern Latin-English edition.

Cordus, Euricius (1486-1535), German teacher, physician, and botanist, and **Valerius (1515-1544),** pharmacist and botanist. Euricius, the youngest of thirteen children, adopted his nickname, "Cordus" (last-born), as a surname. He became a schoolmaster, but because his income did not adequately support his own family, he went to Italy in 1519 and studied medicine. In 1523 he became a municipal physician, and in 1527 he became professor of medicine at the new Protestant University of Marburg. While Martin Luther reformed religion, Cordus attempted to reform the understanding of names of medicinal plants, in his *Botanologicon* (1534). Valerius studied at Marburg under his father and after receiving a bachelor's degree in 1531 went to Leipzig to study pharmacy. Next, he went to Wittenburg, where he wrote a *Dispensatorium*, which was published posthumously (Nuremberg, 1546); it was Germany's earliest city-sponsored pharmacopoeia, which discussed about 225 medicinal plants and minerals. With later editions, its use spread far beyond Germany. More purely botanical were his *Annotationes in Dioscoridis de materia medica libros* (1549), *Historiae stirpium libri IV* (1561), and *Stirpium descriptionis liber quintus* (1563), which describe about five hundred species. His descriptions were based on his own studies and are presented in an organized, thorough fashion.

Correns, Karl Franz Joseph Erich (1864-1933), German botanist and geneticist. He studied botany at the University of Munich under Karl Nägeli and married Nägeli's niece. He did graduate work at Berlin and Tübingen and then taught at several universities. When the Kaiser-Wilhelm Institut für Biologie was founded in 1913, he became its director. His fame came from his rediscovery in 1899 of Gregor Mendel's laws of heredity. Correns followed Hugo de Vries's example of publishing his own findings, while acknowledging Mendel's priority. He devoted the rest of his career to testing and refining these laws.

Cowles, Henry Chandler (1869-1939), American plant ecologist. He studied science at Oberlin College, and when he went to the University of Chicago as a graduate student in 1895, his main interest was in geology. However, in 1896 Professor John Merle Coulter persuaded him to switch to botany. Cowles read Johannes Warming's introduction to plant communities (1895) and decided to study the vegetation of the Lake Michigan sand dunes. His main publications were based on his doctoral dissertation, "The Ecological Relations of the Vegetation of the Sand Dunes of Lake Michigan" (1899) and "The Physiographic Ecology of Chicago and Vicinity" (1901), showing that while habitat influences the type of vegetation, vegetation can also influence the character of habitat. Although his publications (1899-1911), were well received, he eventually focused his career on effective teaching at the University of Chicago.

Crick, Francis (1916-   ), English molecular biologist. He earned a bachelor's degree in physics in 1937, and his graduate education was interrupted by World War II. He became interested in biology in 1946 upon reading Erwin Schrödinger's *What Is Life?* In 1947 Crick began working at Cambridge University and soon undertook doctoral research on protein structure, using X-ray diffraction. When James Watson came to the Cavendish Laboratory, he and Crick collaborated on an attempt to discover the structure of deoxyribonucliec acid (DNA). With advice and data from various colleagues, they were successful in 1953 and won the Nobel Prize in Physiology in 1962. Their work was a major component of a new science, molecular biology, to which Crick continued making contributions in his subsequent career.

Curtis, John Thomas (1913-1961), American plant ecologist. He was a small-town boy who became friends with a curator at the Milwaukee Public Museum, who inspired him to study wild plants, especially orchids. Curtis attended the local Carroll College, majored in biology, and wrote a senior thesis on orchid seeds, germination, and growth. In 1934 he entered graduate school at the University of Wisconsin to study plant physiology, with a minor in plant pathology. His master's thesis and doctoral dissertation were also on orchid seed germination. In 1937 he became an instructor in botany at the University of Wisconsin and in 1938 began teaching plant ecology. He had long been interested in the environments of different orchid species, and his ecological interests expanded after he became director of research at the university arboretum. During World War II he conducted a statistical study on the phytosociology of the tropical vegetation of Haiti, which changed the direction of his research. Back in Wisconsin in 1946, he embarked on a long-term study of its vegetation. He attracted a half-dozen outstanding graduate students to assist the project with doctoral dissertations, and he synthesized the findings in *The Vegetation of Wisconsin: An Ordination of Plant Communities* (1959). Besides being a valuable account of a state's vegetation, this book is also his definitive account of his continuum concept, showing that the notion of distinct plant communities is often an illusion.

Darwin, Charles (Robert) (1809-1882) and Erasmus (1731-1802), English naturalists. Erasmus Darwin studied medicine at Cambridge and Edinburgh and became one of the most prominent physicians of his day. In 1766 he became a founding member of the Lunar Society, a group of amateur, radical scientists who met in Birmingham. Three of his four books were on botany; his earliest speculations on evolution were in *The Botanic Garden* (2 parts, 1789-1791), and he developed further those ideas in *Zoonomia* (1794-1796, 2 vols.) and *The Temple of Nature* (1803). When published, his evolutionary ideas fell on deaf ears, but Charles Darwin developed a high regard for his grandfather and read his books—initially, before developing his own ideas on evolution and again after he began searching for explanations of evolution. Charles attended the same universities as his grandfather but found himself unsuited to the medical profession. He was willing to go into the Anglican ministry because such as career would leave time for natural history, but he received an offer to sail as naturalist on a naval survey ship *Beagle*, which mapped the coastlines of South America (1831-1836). His contacts with science professors had prepared him for the task, and on the voyage he collected specimens and observations that turned him into an evolutionist in July, 1837. His early researches were in zoology and geology, and it was only in the final writing of *On the Origin of Species by Means of Natural Selection* (1859) that he shifted his emphasis to botany. That was partly because of his reliance on the judgment of Joseph Hooker and Hewett Watson. Today, Charles Darwin's fame rests mainly on his 1859 work, but he wrote sixteen works—all highly regarded—seven of which are partly or wholly on plants.

De Duve, Christian (1917-   ), Belgian cytologist and biochemist. He was born near London during World War I and grew up speaking four languages. He received his medical degree in 1941, and during World War II he was confined in a prison camp until he escaped. He studied the action of insulin on glucose uptake for his philosophy doctorate in 1945 and published his dissertation that year as a book. In 1947 he joined the faculty of Louvain University, and in 1962 he became a professor at Rockefeller University while still serving half-time at Louvain. His insulin studies led to enzyme research. He pioneered the use of the centrifuge and electron microscope in cytology and discovered two new organelles: lysosome and peroxisome, for which he shared a Nobel Prize in 1974.

Dioscorides, Pedanius (c. 50-70 C.E.), Greek physician-pharmacist who spent one or two years traveling with the Roman army, collecting medicinal plants in the Mediterranean region. His pharmacopoeia is in Greek but is known by a Latin title, *De materia medica* (c. 78; *The Greek Herbal of Dioscorides*, 1934). It is organized by plant species and is the earliest known dictionary of plants, giving descriptions and locations for more than five hundred species. During the 1500's and 1600's *De materia medica* became one of the foundations of modern botany and was translated into English in 1655 (though not published until 1934).

Dodoens, Junius Rembert (1517-1585), Belgian botanist and physician. He studied medicine at the University of Louvain and served as a municipal physician in his hometown, Mechelin (1548-1574). He was inspired by the herbals published by Otto Brunfels, Jerome Bock, and Leonhard Fuchs. His first brief botanical book, *De frugum historia liber unus* (1552), was on cereals, vegetables, and fodders. In 1554 he incorporated it into his own large Flemish herbal, *Cruydeboeck* (*A New Herbal: Or, Historie of Plants*, 1586). There were also Latin and French editions of his herbal, with new species being introduced into later editions. He described and illustrated for the first time about one hundred plants. He left his town to become physician to Emperor Maximilian II (1574-1580), and in 1782 he became professor of medicine at the University of Leiden.

Dokuchaev, Vasily Vasilievich (1846-1903), Russian geologist and soil scientist. From a family of priests, in 1867 he entered the St. Petersburg Ecclesiastical Academy but soon abandoned it for St. Petersburg University. In 1871 he received a master's degree, with a thesis on the alluvial deposits of the Kachna River, near his birthplace. He remained connected to St. Petersburg University and that city's other scientific institutions. He founded Russia's first department of soil science. He received a doctorate in 1878 with his dissertation, "Methods of Formation of the River Valleys of European Russia." He then studied the formation of topsoils, and he helped prepare a soil map of European Russia. A severe drought in 1891 turned his attention to steppe soils and farming methods. He believed soil science must incorporate the study of bedrock, climate, topography, and the influences of plants, animals, and humans.

Douglass, Andrew Ellicott (1867-1962), American astronomer and dendrochronologist. His interest in astronomy and mathematics developed during high school and continued at Trinity College in Hartford, Connecticut. He graduated with honors in 1889 and became an assistant at the Harvard University Observatory, which sent him on an expedition to Peru for three years. In 1894 wealthy Bostonian Percival Lowell hired him to find a site for an observatory in Arizona Territory, which he did, west of Flagstaff. Douglass remained there in various occupations until he joined the University of Arizona faculty in Tucson in 1906. In 1916 an endowment established The Steward Observatory, which was completed in 1922. Douglass was interested in the influence of sunspots on weather and therefore studied tree rings as indicators of climate. Tree rings seemed to confirm an eleven-year cycle of sunspots. He also worked with archaeologists to develop a history of southwestern U.S. climate from tree rings extending from 11 C.E.

Dutrochet (René Joachim) Henri (1776-1847), French plant and animal physiologist. He was born into an provincial aristocratic family that lost its wealth and power in the French Revolution. He went to Paris, studied medicine, and then became an army surgeon. At age thirty-four he abandoned medicine for science and became interested in gas exchanges between the atmosphere and the tissues of plants and animals. He concluded that respiration is essentially the same in plants and animals. In 1832 he showed that stomata connect with passageways deep in plant tissues and that only green parts can absorb carbon dioxide and change light energy into chemical energy. In 1831 he demonstrated that mushrooms are fruiting bodies of fungal mycelia.

Englemann, George (1809-1884), German-American botanist. His parents ran a girls' school in Frankfurt and encouraged his interest in plants, which developed when he was fifteen. He received a medical degree in 1831 from the University of Würzburg, with a thesis on plant and animal monstrosities. In 1832 he immigrated to a relative's farm 20 miles from St. Louis as a base for studying American botany, and in 1836 he began keeping meteorological observations which he continued until his death. In 1840 he started a clearinghouse for collectors and buyers of Western plants. He collected Western plants and wrote monographs on cacti, conifers, grapes, dodders, mistletoes, yuccas, rushes, and quillworts. In 1859 he was mainly responsible for persuading Henry Shaw to establish the Missouri Botanical Garden in St. Louis. Two of Englemann's notable discoveries were the pollination of yuccas by pronuba moths and that American wild grapes are immune to phylloxera infection.

Flemming, Walther (1843-1905), German cytologist. He studied at three other universities before taking his medical degree at the University of Rostock (1868). He also did research at several universities before becoming professor of anatomy at Kiel University in 1876, where he remained, living with his sister Clara. By 1879 he had investigated all stages of mitotic cell division and published his results in three famous articles (1879-1881). In 1880 he coined the term "chromatin" for the stainable threads (chromosomes) in the cell nucleus. He concluded that the heads of spermatozoa are composed entirely of chromatin. In 1887 he described meiotic cell division in spermatozoa but did not fully distinguish it from mitosis. He also developed two new staining methods.

Fritsch, Felix Eugen (1879-1954), English algologist. He earned a bachelor's degree in botany from London University in 1898 and a philosophy doctorate at Munich in 1899. He appreciated the German emphasis on physiology and ecology, in contrast to English emphasis on anatomy and morphology. In 1901 he worked at the Jodrell Laboratory at Kew, and in 1902 he became assistant lecturer at University College, London. He began his long-lasting studies on periodicity in phytoplankton. In 1905 he earned a science doctorate at London and became assistant professor at University College. In 1911 he took charge of botany at Queen Mary College, where he collaborated with assistant lecturer Edward Salisbury on five widely used textbooks (1914-1928). In 1927 Fritsch published a revised, rewritten edition of G. S. West's *Treatise of the British Freshwater Algae* and urged formation of a freshwater biological station. In 1929 the Freshwater Biological Association was formed, with him serving as chairman until his death. A biological station at Wray Castle was also established in 1929. Fritsch was elected fellow of the Royal Society of London in 1932 and received its Darwin Medal in 1950. He published his greatest work, *The Structure and Reproduction of Algae*, in two volumes (1935-1945). He retired in 1948 and thereafter worked at the Botany School, Cambridge University. He was president of the Linnean Society of London (1949-1952) and received its gold medal in 1954. He was president of the International Association of Limnology and the Institute of Biology in 1953.

Fuchs, Leonhard (1501-1566), German physician and botanist. While a child, his grandfather, Johann Fuchs, taught him the names of flowers and evidently imparted a lasting interest in them. In 1517 Leonhard graduated from the University of Erfurt and opened a school. He became a Lutheran and was influenced by religious reformism in his scientific outlook. In 1519 he enrolled at the University of Ingolstadt and received his master's degree in 1521 and his medical degree in 1524. In 1526 he became professor of medicine at Ingolstadt but in 1528 resigned to become court physician to a Lutheran ruler. In 1533 he attempted to return to the Ingolstadt faculty but was prevented because of his religion. In 1535 he became professor of medicine at the University of Tübingen, where he remained. He published a popular medical textbook (1531) that he frequently republished in revised and enlarged editions. His lasting fame came from his pharmaceutical herbal, *De historia stirpivm commentarii insignes maximis impensis et vigiliis elaborati adjectis earvndem vivis plvsqvam quingentis imaginibus, nunquam antea ad naturæ imitationem artificiosius efictis & expressis* (1542). Of 487 species and varieties included, more than 100 were recorded in Germany for the first time. Among the species that had never before been illustrated were foxglove and corn. His publications were marred, however, by plagiarism.

Gärtner, Joseph (1732-1791) and Karl Friedrich von (1772-1850), German botanists. Joseph obtained a medical degree at the University of Tübingen in 1753 but never practiced medicine. He had broad scientific interests and turned to botany after attending botanical lectures at Leiden in 1759. He was professor of botany and head of a botanic garden at St. Petersburg (1768-1770), and he explored the Ukraine, discovering many undescribed plant species. In 1770 he returned to live in his hometown, Calw, where he studied carpology. His *De fructibus et seminibus plantarum* (1788-1807, 3 vols.) describes fruits and seeds of 1,050 genera. Karl earned his medical degree from the University of Tübingen, but unlike his father, he did practice medicine, in Calw. However, in 1824 he became interested in plant fertilization and hybridization and devoted the rest of his career to that research. He believed in the stability of species. He published his findings in three major studies (1827-1838, 1844, 1849).

Gesner, Konrad (1516-1565), Swiss physician, naturalist, and philologist. His early studies were in Protestant theology, but by 1535 he had become more interested in Greek, Latin, and Hebrew; then he switched to medicine and received his medical degree at Bern in 1541. Gesner had an early interest in natural history, and his encyclopedic works include not only his *Bibliotheca universalis* (1545-1555, 4 vols.) but also his *Historia animalium* (1551-1587, 5 vols.; history of animals). He did publish a few brief botanical works, but his *Opera botanica* (1751-1771; botanical works) was unfinished when he died during an epidemic of plague. He was the first botanist to emphasize the importance of flowers for determining kinship of species, but the unfortunate publishing history of his botany limited its influence.

Ghini, Luca (c. 1490-1556), Italian botanist. His hometown was near Bologna, and he received his medical degree from the University of Bologna in 1527. The following year he joined its faculty and in 1535 began teaching medical botany. From 1544 to 1554 he taught medical botany at Pisa but then rejoined the Bologna faculty. He collected the first herbarium, and the oldest surviving herbaria are those assembled by two of his students. The botanical garden he created at the University of Pisa is one of the two oldest. Andrea Cesalpino was one of his many students and was his successor as head of the Pisa botanical garden.

Gleason, Henry Allan (1882-1975), American botanist. As a child he enjoyed playing in the woods, but at age thirteen he took a course in botany that focused his interest on the local flora. He earned his bachelor's (1901) and master's (1904) degrees at the University of Illinois and his doctorate (1906) at Columbia University. The writings of Frederic Clements inspired him to make a plant ecological study of the Ozark Mountains and prairies of southwestern Illinois, but he also developed a strong interest in taxonomic botany. In 1910 he became an associate professor at the University of Michigan. However, in 1919 he went to the New York Botanical Garden, where he remained through 1950. Clements had pioneered the use of quadrats and statistics in the study of vegetation but did not persist in this technique. Gleason, however, used the technique to study vegetation and concluded (1920) that species are not distributed in discrete communities, as Clements claimed. Gleason preferred the term "plant association" to "plant communities." However, it was only in the writings of John Curtis and Robert Whittaker in the 1950's that Gleason's claims were taken seriously and gained widespread support.

Goethe, Johann Wolfgang von (1749-1832), German author and naturalist. He obtained a law degree in 1771 but was soon so famous as a poet, novelist, and natural philosopher that he did not practice law. His theorizing in biology was influenced by Baruch Spinoza's philosophy and George-Louis Leclerc de Buffon's natural history. Goethe believed that related species are variations of an archetype and that biologists could gain an understanding of archetypes by comparative studies on species or genera that are its variants. The archetype of a major class has simple components that vary according to the species. For example, flowering plants have cotyledons, inflorescences, stamens, and pistils that are all variations of leaves. He developed this idea from studying the fan palm and explained the concept in *Versuch die Metamorphose der Pflanzen zu erklären* (1790). He also coined the term "morphology." Although he believed that the environment plays a role in the modification of leaves into the variants found in different species, his system was an idealistic substitute for the idea of evolution.

Golgi, Camillo (1843-1926), Italian histologist and pathologist. The son of a Pavian physician, he earned his own medical degree from the University of Pavia in 1865, studying under its first professor of histology. Most of his research was on the histology of nerves. Little progress had been made in this field because of inadequate techniques. Golgi's development of satisfactory techniques enabled him to make the important discoveries leading to his sharing the Nobel Prize in Physiology in 1906. In 1898 he examined the histology of an owl's brain and discovered a small organelle in the cytoplasm of nerve cells, now called the Golgi body. It was not an important discovery at the time because he could not explain its function.

Gray, Asa (1810-1888), American taxonomic botanist. He was from upstate New York and studied medicine there but became more interested in the botany he studied than in medicine, in which he earned a degree in 1831. In 1832 he began assisting John Torrey, the Untied States' leading botanist, to compile *Flora of North America*. By the time it appeared in 1836, Gray's assistance was so significant that he became coauthor. In 1842 he became professor of natural history at Harvard University, where he remained. He was well positioned to receive specimens from botanical explorers of the West, and much of his time went into describing and organizing American systematic botany. However, in 1851 he traveled to England, where he met and became friends with Joseph Hooker and Charles Darwin. In the correspondence that followed, Darwin confided in Gray in 1857 key details of his theory of evolution. After the publication of Darwin's *On the Origin of Species by Means of Natural Selection* (1859), Gray became Darwin's staunch ally against Gray's antievolution colleague Louis Agassiz. Gray collected the essays he had written on evolution over several years into *Darwiniana* (1876). Under Hooker and Darwin's influence, Gray also became America's leading phytogeographer.

Greene, Edward Lee (1843-1915), American botanist. His mother was a skilled gardener, and Greene at age six began reading her copy of Elmira Lincoln's *Familiar Lectures on Botany* (1842). A neighbor in southern Wisconsin, the naturalist Thure Kumlien, encouraged Greene's botanical interests. In 1859 Greene entered Albion Academy, but his education was interrupted by the Civil War, in which he was a Union Army private (1862-1865). He carried with him Alphonso Wood's *Classbook of Botany* and sent specimens and seeds from his travels to his mother and Kumlien. Greene returned to Albion and graduated in 1866. He taught school for several years, became an Episcopal priest in 1873, and joined the Roman Catholic Church in 1885. He also was professor of botany at the University of California at Berkeley (1885-1895). Greene was a diligent explorer of western America, but he was also a controversial botanist because he published names of new species of plants that other botanists challenged. Nevertheless, he was elected president of the Madison Botanical Congress in 1893 and served as an associate of the National Museum, Smithsonian Institution (1904-1914). He ended his career by writing *Landmarks of Botanical History* (1983, 2 vols.), which defended his distinctive perspective.

Grew, Nehemiah (1641-1712), English plant anatomist. The son of a Nonconformist Protestant clergyman-schoolmaster, he was allowed to earn a bachelor's degree at Cambridge University but could not remain there. He obtained a medical degree at the University of Leiden and returned to practice medicine at Coventry. In 1672 the Fellows of the Royal Society of London raised fifty pounds to enable Grew to move to London, where he continued practicing medicine while also investigating plant anatomy. Robert Hooke instructed him in the use of the society's compound microscope. Grew had broader scientific interests than plant anatomy, but in this he excelled. His earlier studies were collected and expanded into *The Anatomy of Plants* (1682), which is well illustrated. He attempted to understand plant physiology by studying anatomy, but that proved to be very difficult. He had no students to continue his work.

Grisebach, August Heinrich Rudolph (1814-1879), German phytogeographer and taxonomist. As a youth he learned botany from his uncle, botanist Georg Friedrich Wilhelm Meyer. Grisebach studied medicine and natural history at Göttingen and Berlin and eventually became professor of botany at Göttingen. From 1839 to 1840 he traveled through the Balkan States and Asia Minor on botanical explorations, and later he explored in Norway (1842), southern France, the Pyrenees (1850), and the Carpathian Mountains (1852). His taxonomic studies included monographs on the *Malpighiaceae*, *Gramineae*, and the genera *Gentiana* and *Hieracium*. He also studied the flora of southeastern Europe, Central America, and Argentina. In phytogeography he was strongly influenced by Alexander von Humboldt, and his own earlier studies culminated in his grand synthesis, *Die Vegetation der Erde nach ihrer klimatischen Anordnung* (1872), which emphasizes the influence of climate on composition and distribution of flora.

Haberlandt, Gottlieb (1854-1945), Hungarian-German botanist. His father was a professor of applied botany and taught him botany as a youth. Haberlandt studied at the University of Vienna and was greatly influenced by Julius von Sachs's textbook of botany. He earned his doctorate in 1876 and then worked under Simon Schwendener at Tübingen, because Schwendener emphasized the combined study of anatomy and physiology. The outcome of Haberlandt's investigations was *Physiologische Pflanzenanatomie* (1884; *Physiological Plant Anatomy*, 1914), which he later revised and enlarged through six editions. His text considered evolutionary and ecological aspects of plants. He also published on other topics, including a travel book, *Eine botanische Tropenreise* (1893), on his experiences in Ceylon and Java from 1891 to 1892.

Hales, Stephen (1677-1761), English plant and animal physiologist. He studied divinity at Cambridge University and received a parish near London in 1709, where he remained. In 1703 he became friends with William Stukeley, who was studying science, and Hales came to share Stukeley's interests. William Harvey had shown the necessity of experimentation in animal physiology, and Hales realized the same is true for plant physiology. In 1706 Hales first attempted to measure the blood pressure of dogs, and in 1712-1713 he took the blood pressure of two horses and a deer. In 1733 he published *Haemastaticks*. However, he found it less convenient to work with animals than with plants, and by 1718 he had begun studying the effect of the sun's warmth on the rise of sap in trees. In 1724-1725 he presented to the Royal Society of London the manuscript of his *Vegetable Staticks*, which was read during several meetings and published in 1727. *Vegetable Staticks* was the founding study in plant physiology.

Hedwig, Johann (1730-1799), Czech-German botanist. He had a childhood interest in plants, and although he studied medicine at the University of Leipzig (receiving his medical degree in 1759), while there he worked as an assistant to the professor of botany and continued to study plants while practicing medicine. His special interest was in mosses and liverworts, and during the 1770's he studied their reproduction and published his findings in 1781. Despite some skepticism, his accounts withstood scrutiny, and he became professor of botany at the University of Leipzig.

Hofmeister, Wilhelm Friedrich Benedict (1824-1877), German botanist. His father, whose business was publishing and selling books on music and botany, was an amateur botanist. The son's initial interest was in entomology, physics, and mathematics. However, he did not go to college and instead followed his father into music publishing, with botany as a hobby. He suffered from severe myopia, which inclined him toward microscopic studies. He was also influenced by Matthias Schleiden's studies on life histories and cell structure, and his first scientific paper (1847) corrected Schleiden's account of fertilization and embryo development in flowering plants. Hofmeister's 1849 book expanded his findings to other species, and his most famous book (1851) generalized about the alteration of generations in plants. The University of Rostock was impressed by his achievements and awarded him an honorary doctorate in 1851. His 1851 book is now seen as the beginning of modern botany. In 1863 he became professor of botany at Heidelberg and in 1872 at Tübingen. In 1868 he published the first textbook on plant morphogenesis.

Hooke, Robert (1635-1703), English scientist. As a child he was fascinated by mechanical devices, and as a teenager that fascination extended to Euclid's geometry. He entered Oxford in 1653 and received a master's degree in 1663. Oxford was the center of English science when he arrived, and he became Robert Boyle's experimental assistant. In 1660 the Royal Society of London was founded, and in 1662 it appointed Hooke curator of experiments, expecting him to demonstrate three or four significant experiments per week. Although an impossible task, Hooke's *Micrographia* (1665) records what he managed to achieve in a few years. He discovered "cells" in a slice of cork and also observed them in a variety of plants. In moss and mold fungus he observed "seeds" small enough to disperse in air, and therefore he doubted the possibility of spontaneous generation. He also concluded that fossils are the remains of living plants and animals; because they do not resemble living species, they represent either extinct species or species that had changed.

Hooker, Joseph Dalton (1817-1911) and William Jackson (1785-1865), British botanists-administrators. William was from a prosperous family but did not attend college. His general interest in nature became focused on botany in 1804 when he discovered a moss that was previously unknown in Britain. Despite his young age, he soon knew Britain's prominent botanists, and in 1809 Joseph Banks arranged for him to join a diplomatic mission to Iceland, where he was the first to botanize. Dawson Turner became his patron, and William married Turner's eldest daughter. In 1820 Banks had him appointed professor of botany at Glasgow, where he was very popular with students and others. In 1841 William became first director of the Royal Botanic Gardens, Kew, where he remained. He was also a very productive botanical author and editor and made Kew into an important scientific and recreational institution. Joseph received a medical degree from Glasgow University but wanted a profession in botany. He followed the examples of Banks, Robert Brown, and Charles Darwin of serving as a naturalist on a naval expedition, 1839-1843, to the South Pacific. He became Darwin's closest friend but resisted Darwin's theory of evolution until he read *The Origin of Species by Means of Natural Selection*. He succeeded his father as a successful director of the Royal Botanic Gardens and outdid his father as a scientist. In both taxonomy and phytogeography, Joseph was a leading botanist of his time.

Humboldt (Friedrich Wilhelm Heinrich) Alexander von (1769-1859), German scientist. He was from a wealthy family and attended the universities of Frankfurt and Göttingen and the Freiburg School of Mines. He studied botany under Karl Ludwig Willdenow and geology under Abraham Gottlob Werner. In 1792 Humboldt entered the Prussian mining service and made effective changes in equipment and the training of miners. He also conducted scientific research until 1798, when he went to Paris to arrange an expedition to Latin America, at his own expense. He and botanist Aimé Jacques Alexandre Bonpland reached Venezuela in July, 1799, and they departed from Cuba in April, 1804. Humboldt then lived in Paris until 1827 and published their findings in elaborate detail. The greatest private scientific expedition in history was documented in the greatest private expedition report in history. Taxonomic botany was greatly advanced, but Humboldt also founded phytogeography as a modern science. In 1829 he explored Siberia with naturalist Christian Gottfried Ehrenberg and mineralogist Gustav Rose. Humboldt achieved great fame both for his scientific and his popular science writings. Charles Darwin was among the many inspired by his works.

Hutchinson, John (1884-1972), English botanist. He became a gardener at the Royal Botanic Gardens, Kew, in 1904 and assistant at the Herbarium in 1905. He botanized in South Africa, 1928-1930. He is best known for his *Families of Flowering Plants* (1926-1934, 2 vols.), which contains his classification of the vascular plants—a revision of Bessey's classification. He was Keeper of the Kew Museums, 1936-1948. Among his later publications are *Genera of Flowering Plants* (1964-1967, 2 vols.) and *Evolution of Flowering Plants* (1969).

Ibn al-ʿAwwam (second half of 1100's), Hispano-Arabic agricultural author. Nothing of his life is known except that he wrote or compiled the most important book on agriculture between the time of Columella and that of Albertus Magnus. *Kit b al-fil ha* discusses 585 plants and more than 50 fruit trees. He had access to Columella and other ancient and medieval authors, and there seems little in his book that is original, but it was a reliable guide for the time. It was translated into Spanish (1802, 2 vols.) and French (1864-1867, 2 vols.).

Ingenhousz, Jan (1730-1799), Dutch-English physician and plant physiologist. He studied medicine in the universities of Louvain, Paris, and Edinburgh and became an expert on smallpox inoculation, even traveling to Vienna to inoculate the royal family. (He stayed on as court physician.) He was inspired by Joseph Priestley's experiments, 1771-1779, on plant and animal gas exchanges under glass enclosures to undertake similar studies. Although Priestley found that plants can restore air exhausted by a candle or a mouse, he did not obtain consistent results because he did not discover that light is also essential for photosynthesis. That connection was established in Ingenhousz's *Experiments upon Vegetables* (1779); he could account for Priestley's inconsistent results by showing that plants produce carbon dioxide at night, just as animals do.

Ivanovsky, Dmitri Iosifovich (1864-1920), Russian botanist and microbiologist. He attended St. Petersburg University in 1883 to study science. In 1887 he and a student of plant physiology, V. V. Polovtsev, were sent to study tobacco blight at plantations in the Ukraine and Bessarabia. They concluded that it was a contagious disease, and Ivanovsky graduated in 1888 with a thesis, "On Two Diseases of Tobacco Plants." In 1890 another disease appeared at tobacco plantations in the Crimea. Ivanovsky's investigation of tobacco mosaic provided the first evidence of pathogenic viruses. In 1895 he earned his master's degree with a thesis on yeast activity under aerobic and anaerobic conditions. He received a doctorate at Kiev in 1903 for his book *Mosaic Disease in Tobacco*, but because this research attracted little attention, he then researched photosynthesis at Warsaw University.

Jacob, François (1920-   ), French microbiologist, geneticist, and physiologist. He studied medicine to become a surgeon, but Germany's invasion of France in 1940 interrupted his education. He escaped to London and became a medical officer in the French Free Army. During the Normandy invasion in 1944 he was wounded severely while assisting an injured officer and was unable to train as a surgeon. He therefore turned to microbiology and received a Ph.D. under André Lwoff's guidance, studying lysogenic bacteria. He then studied sexuality and genetics of bacteria with Elie Wollman; they showed that bacterial chromosomes are circular DNA molecules, with genes that can be mapped experimentally. Next, Jacob and Jacques Monod discovered messenger RNA, leading to their differentiation of ribosomal, messenger, and transfer RNA—all of which assist in protein synthesis. Jacob and Monod hypothesized that chromosomes are divided into "operon" units; an operon is composed of a regulatory gene, an operator site, and several structural genes. This concept helped them explain enzyme induction caused by a sudden increase in food. Lwoff, Jacob, and Monod shared the 1965 Nobel Prize in Physiology for their discoveries on genetic control of enzymes and virus synthesis.

Johannsen, Wilhelm Ludwig (1857-1927), Danish botanist and geneticist. Although Johannsen was a good student, his family could not afford to send him to college, and in 1872 he was apprenticed to a pharmacist. While working in pharmacy he taught himself botany and chemistry, and in 1881 he became an assistant in the new Carlsberg Laboratory. He investigated the metabolism of ripening, dormancy, and germination in fruits and seeds. In 1892 he became a lecturer in botany at the Copenhagen Agricultural College, and in 1893 he discovered a way to end dormancy of winter buds. Despite a lack of a university education, in 1905 he became professor of plant physiology at the University of Copenhagen and in 1917 became its rector. He began studying variability in relation to heredity in the 1890's, improving Francis Galton's statistical methods. He showed that selection for heavier or lighter seeds has no effect on pure strains of peas and beans, but it can affect impure strains. In 1909 he shortened Hugo de Vries's "pangene" to "gene" as the name for the unit of heredity. In 1923 he wrote in Danish a history of genetics that went through four editions.

Jung (Jungius), Joachim (1587-1657), German natural philosopher, botanist, and mathematician.

He was the son of a professor at the Gymnasium St. Katharinen in Lübeck and studied there until he entered the University of Rostock in 1606. He studied mathematics and logic and then transferred to the University of Giessen, where he received his master's degree in 1608. He taught there and elsewhere until 1616, when he reentered the University of Rostock to study medicine. He obtained an medical doctorate from Padua in 1619. During the following decade he practiced medicine and taught mathematics at Rostock. Finally, he became professor of natural science and rector of the Akademisches Gymnasium of Hamburg, where he remained for thirty years. In botany, he developed morphology based upon the writings of Theophrastus and Andrea Cesalpino. He developed a comprehensive terminology for describing precisely all plant parts and their relationships. This brought order to a developing quagmire. His botanical treatises appeared posthumously—*Doxoscopiae Physicae Minores* in 1662 and *Isagoge Phytoscopica* in 1679—but John Ray had access to a manuscript, *Isagoge*, in 1660.

Jussieu, Adrien-Henri (1797-1853), Antoine (1686-1758), Antoine-Laurent de (1748-1836), Bernard (1699-1777), and Joseph (1704-1779), French botanists. Antoine, Bernard, and Joseph were sons of a Lyons apothecary, Laurent de Jussieu. Laurent's fourth son, Christophle, was an amateur botanist and father of Antoine-Laurent, who, in turn, was father of Adrien-Henri. Antoine studied medicine and botany at Montpellier under Pierre Magnol, France's first botanist to attempt a natural classification of plants and originator of the family concept in botany. Antoine received his medical degree in 1707 and went to Paris to study under Tournefort, who died the following year. In 1710 Antoine succeeded Tournefort as professor of botany at the Jardin du Roi, where he concentrated on developing the garden and training other botanists, including his brothers Bernard and Joseph. Bernard went to Paris in 1714 to finish his medical and botanical studies. In 1722 he became *sous-démonstrateur de l'extérieur des plantes* at the Jardin du Roi. He was an effective teacher and was famous for his field trips. He arranged the garden at Trianon, near Versailles, to illustrate his natural system. Joseph also studied medicine and botany, but in addition, he was interested in engineering. In 1735 he joined a scientific expedition to Peru and did not return to Paris until 1771. The intervening years were spent exploring, botanizing, practicing medicine, and building a bridge at Potosí. Antoine-Laurent went to Paris to study medicine, receiving his medical degree in 1770, with a thesis comparing animal and plant physiology. He soon became deputy professor of botany at the Jardin du Roi and in 1774 published a paper on his uncle Bernard's Trianon garden arrangement of plants, as adapted to the Jardin du Roi. Antoine-Laurent made a thorough study of genera and families of flowering plants for his epoch-making *Genera Plantarum Secundum Ordines Naturales Disposita, Juxta Methodum in Horto Regio Parisiense Exaratam, Anno 1774* (1789; *Genera of Plants Arranged According to Their Natural Orders, Based on the Method Devised in the Royal Garden in Paris in the Year 1774*). In 1793 the Jardin du Roi was reorganized as the Muséum National d'Histoire Naturelle, and he became professor of botany. He established a herbarium which absorbed herbaria and libraries confiscated by France's revolutionary armies. In 1800 he became director of the museum. Adrien-Henri followed family tradition, studying medicine and botany, and received a medical degree in 1824 with a thesis on *Euphorbiaceae*. In 1826 he succeeded his father as professor of botany at the Muséum National d'Histoire Naturelle. He was a brilliant teacher, and his textbook went through twelve editions, 1842-1884. He also wrote taxonomic monographs, contributed articles on taxonomic theory, and built up a large herbarium.

Kalm, Pehr (1716-1779), Swedish-Finnish naturalist. He began his higher education at Abo, Finland, and in 1740 went to Uppsala University in Sweden, to finish under Carl Linnaeus. He went on several Scandinavian expeditions and in 1747 became professor of applied science at Abo. In 1748, at the urging of Linnaeus, the Royal Swedish Academy of Sciences sent Kalm to North America to find useful plants for Scandinavia. It was reasonable to travel mainly in Canada because of the similarity of climates, and he spent a few months there on two trips. However, he was attracted to the Philadelphia area, partly by the Swedish settlement in nearby New Jersey, where he met his wife, and partly by the intellectual community, which included John Bartram. He reluctantly departed in 1751 with abundant living and pressed plants, fortunately leaving a set with Linnaeus in Uppsala before continuing on to Abo, where his own collection later was destroyed in a fire. His lasting fame comes from his *En Resa til Norra America* (1753-1761, 3 vols.), which also appeared in German, English, Dutch, and French translations. He was a popular teacher and devoted the rest of his life to Finnish botany, forestry, and agriculture.

Kämpfer, Engelbert (1651-1716), German geographer and botanist. Son of a Lutheran minister, he had a strong urge to travel that was manifested in his attending schools and universities in various places. He finally earned a master's degree in Kraków in 1680 and then studied medicine at Königsberg, 1680-1681, and at Uppsala, Sweden in 1681. He became secretary and physician to the ambassador to Iran, and they left Stockholm in March, 1683, reaching Isfahan a year later. After the ambassador returned to Sweden in 1685, Kämpfer remained in Iran three more years as an employee of the Dutch East India Company. In 1688 he sailed on one of its ships to Southeast Asia and reached Nagasaki, Japan, in 1690, where he remained until November, 1692. He reached Holland in October, 1693, and received a medical degree from Leiden in 1694, with a dissertation on his foreign discoveries. He returned to his hometown, Lemgo, to practice medicine and prepare his journals for publication. He published one book, *Amoenitatum exoticarum* (1712), and after his death Hans Sloane bought his herbarium and manuscript history of Japan; the latter was translated and published in English. Kämpfer's herbarium is in the British Museum, where Carl Peter Thunberg studied it.

Koch, (Heinrich Hermann) Robert (1843-1910), German bacteriologist. He earned a medical degree at Göttingen in 1866, having studied under Jacob Henle. After serving as a field physician in the Franco-Prussian War, he became a country doctor near Breslau. An anthrax epidemic in the area led him in 1876 to verify C.-J. Davaine's contention that rodlike microorganisms found in sheep's blood cause the disease. He learned to cultivate the bacterium in cattle blood at body temperature. He traced its life cycle, including spore formation and germination, and in 1876 took his work to Ferdinand Julius Cohn at the University of Breslau, who studied it and sponsored its publication. In 1877 Koch published *Untersuchungen über die Aetiologie der Wundinfectionskrankheiten (Investigations into the Etiology of Traumatic Infective Diseases*, 1880), in which he modified Henle's criteria for determining contagion into "Koch's postulates." In 1880 he became adviser to the Imperial Department of Health in Berlin and had a laboratory with Friedrich Loeffler as an assistant. In 1881 at the International Medical Congress in London, Koch demonstrated in Joseph Lister's laboratory his pure-culture methods, which Louis Pasteur praised. Returning to Berlin, Koch demonstrated the infectious properties of tuberculosis and was able to overcome great difficulties to isolate the bacterium. His 1882 lecture, "Über Tuberculose," was sensational. He believed at the time that human and bovine tuberculosis was the same but later changed his mind. He went on to numerous other discoveries, becoming one of the main founders of bacteriology.

Kölreuter, Josef Gottlieb (1733-1806), German botanist. He graduated from the University of Tübingen in 1755 with a medical degree and then spent six years as keeper of natural history collections at the Imperial Academy of Sciences in St. Petersburg. There he began studies on plant fertilization and hybridization, continuing these experiments after moving to Karlsruhe as professor of natural history and director of the margrave's gardens. His experiments continued until the death of his patroness, the margrave's wife, in 1786. Despite publication of Rudolph Jakob Camerer's experiments on plant sexuality (1694), doubts lingered among botanists. Kölreuter made thorough studies of pollen, stamen, and stigmas; he showed that many hermaphrodite flowers are not self-pollinating, as their stamens and stigmas ripen at different times. He successfully hybridized two species of tobacco and was pleased to report that the hybrids were infertile but later found he could produce fertile hybrids in the genus *Dianthus*. However, he continued to believe it impossible to produce new species by hybridization. Later hybridizers built upon his work.

Kramer, Paul Jackson (1904-1995), American plant physiologist. He grew up on an Ohio farm with a large library. The first scientific article he read was in the U. S. Department of Agriculture *Yearbook* for 1920, on photoperiodism. At Miami University he majored in botany and after graduating in 1926 worked for several summers for the Department of Agriculture. He entered graduate school at Ohio State University and studied ecology and physiology under E. N. Transeau. He received his Ph.D. in 1931, married fellow botany student Edith Vance, and accepted an instructorship at Duke University. At Duke's School of Forestry Kramer researched and trained students in two related subjects—water absorption and woody plants. He synthesized his and his students' findings in *Plant and Soil Water Relationships* (1949, 2d ed. 1969) and in *Physiology of Trees* (1960); the latter he coauthored with his former student Theodore T. Kozlowski. Neither subject had received much attention before Kramer's researches, but when he retired, they were major components of plant science.

Krebs, Hans Adolf (1900-1981), German-English biochemist. He was son of a surgeon and studied medicine, receiving his medical doctorate at Berlin in 1925. He then practiced medicine and pursued biochemical research at the Kaiser Wilhelm Institute for Biology and at the University of Freiburg. In 1933, because he was Jewish, he lost his position at Freiburg and immigrated to England. In 1935 he became a lecturer in biochemistry at Sheffield University, and by 1945 he was chairman of a research unit in cell metabolism. His research focused on cyclic metabolic pathways. He had already discovered the urea cycle in 1930-1933, and by 1945 he was investigating the citric acid cycle that made him cowinner of a Nobel Prize in 1953.

Kunkel, Louis Otto (1884-1960), American plant virologist. He grew up on a Missouri farm and because of a need to earn a living was not able to enter the University of Missouri until 1906. His bachelor's degree was in education, but he took a master's degree in botany in 1911 and went to Columbia University for a philosopy doctorate in 1914, with a dissertation on fungus physiology. He became a pathologist with the U.S. Department of Agriculture (USDA) and studied diseases of potatoes and cabbage. In 1915-1916 he received a fellowship to study viral diseases of potatoes in Holland, Germany, and Sweden. In 1920 he left the USDA to become pathologist for the Hawaiian Sugar Planters' Association. In four months he discovered that the virus causing cane mosaic was not transmitted by the sugar cane aphid but by another aphid whose usual host had been displaced by sugarcane. In 1923-1932 he was first a pathologist and later an administrator at the Boyce Thompson Institute for Plant Research and afterward at the Rockefeller Institute for Medical Research. Besides his own accomplishments in virology, Kunkel assembled a brilliant research team to study viruses, insect vectors, and disease eradication.

Lamarck, Jean-Baptiste (1744-1829), French botanist, zoologist, and evolutionist. He began his career as a soldier and fought in the Seven Years' War; afterward, while on guard duty in eastern and southern France, 1763-1768, he became interested in French flora. After leaving the army he studied medicine and botany in Paris and published a highly regarded *Flore française* (1779 despite 1778 on title page, 3 vols.; reprinted in 1795 and revised by A. P. de Candolle in 1805). He developed a dichotomous key to the species that was easier to use than Linnaeus's artificial system, and he adopted the natural system of classification being developed by Michel Adanson and the de Jussieus. He also wrote three and a half volumes of the eight-volume *Dictionnaire de botanique* (1783-1795). In 1779 he was elected to the Académie des Sciences as a botanist, and he was employed at the Jardin du Roi, 1788-1793. In 1793, when the Jardin du Roi was reorganized as the Muséum National d'Histoire Naturelle, he was not needed as a botanist and became professor of zoology to study the animals which he named "invertebrates." It was while studying animals that he developed his theory of evolution, first published in 1800 and explained in detail in *Philosophie zoologique: Ou, Exposition des considerations relative à l'histoire naturelle des animaux* (1809, 2 vols.; *Zoological Philosophy: An Exposition with Regard to the Natural History of Animals*, 1914). However, he also introduced his evolutionary ideas into his *Introduction à la botanique* (1803, 2 vols.; introduction to botany).

Lawes, John Bennet (1814-1900), British agricultural chemist. He attended Oxford University and became interested in chemistry but left without a degree. In 1834 he inherited Rothamsted estate, where in 1836 he began adding acids to ground bone for fertilizer, and in 1843 he began manufacturing "superphosphate" fertilizer and used the profits to finance his experiments. He also hired chemist Joseph Henry Gilbert (1817-1901) as his assistant, and they collaborated for more than fifty years, making Rothamsted world famous. They devised a "chessboard" system of random plots for field trials. Work on agricultural use of sewage caused Lawes to be appointed a member of a Royal Commission in 1857. Because of Gilbert's rigidity, in 1876 Lawes appointed Robert Warington as his personal assistant, which damaged his relationship with Gilbert. In 1889 Lawes put Rothamsted under a Lawes Agricultural Trust with endowment of 100,000 £; its work has continued to the present day.

L'Écluse (Clusius), Charles de (1526-1609), French-Low Countries botanist. He was from a wealthy Protestant family and was well educated in law. His interest in plants developed in 1551, after he went to Montellier to assist Guillaume Rondelet convert his notes on fish into a book. L'Écluse then became a translator of books, including a French edition of Junius Rembert Dodoens's *Crüjdeboeck* and several books on the medicinal plants of exotic lands. He began publishing his own botanical discoveries in 1576 with a book on Spanish plants, followed by his flora of Austria-Hungary in 1583, *Rariorum plantarum historia* (1601) and *Exoticorum* (1605)—all important contributions to botany.

Leeuwenhoek, Antoni van (1632-1723), Dutch microscopist. He was from a prosperous family, but after his father died he was apprenticed to a cloth merchant in Amsterdam. After the apprenticeship he returned to his hometown, Delft, to live. He began as a shopkeeper, but in 1660 he became a municipal official. In 1671 he made a more powerful magnifying glass than cloth merchants used, to study minute objects from nature. He soon became an expert at making single-lens microscopes, which eventually were powerful enough to study sperm (his own) and bacteria. Initially, he was enchanted by minute animals; then he wondered how similar the minute structures of plants and animals are. He showed Dutch scientists his discoveries, and Reinier de Graaf put him in touch with the Royal Society of London, which proved very receptive to publishing Leeuwenhoek's observations. He sent letters to it regularly for fifty years (1673-1723), which were translated into English and published in *Philosophical Transactions*. He also published his works in Dutch and Latin editions.

Linnaeus, Carl (1707-1778), Swedish botanist, zoologist, and physician. His father, a small-town Lutheran minister, was an enthusiastic gardener and introduced his son to botany. From the time he entered Latin School in 1716, Linnaeus was absorbed by natural history. A high school teacher insisted that he be allowed to study science and medicine, and his father reluctantly agreed. At Uppsala University Linnaeus wrote an essay defending the theory of sexuality in plants that so impressed a medical professor that he appointed Linnaeus lecturer in botany and tutor of his sons. In 1730 Linnaeus began working on a classification of plants based on the numbers of stamens and pistils, a later version of which appeared in the first edition of *Systema naturae* (1735; *A General System of Nature Through the Three Grand Kingdoms of Animals, Vegetables, and Minerals*, 1800-1801). His sexual system for flowering plants was easy to use, though artificial. In 1732 he received a grant from the Uppsala Scientific Society that supported his five-month exploration of Lapland. His discoveries were carefully recorded, though they were not published in an English translation until 1811. In 1735 he went to Holland to obtain a medical degree, to meet botanists, and to publish his manuscripts. He remained there for three very productive years. His basic ideas about classifying plants, animals, and minerals were developed and published there, with more emphasis on plants than on the other two kingdoms. He then practiced medicine in Stockholm until he became a professor of medicine at Uppsala in 1741. He soon turned it into a virtual professorship of botany. He developed a consistent system of binomial nomenclature that became widely accepted. In 1749 Linnaeus had a student defend one of his essays for a doctoral dissertation, on *œconomia naturae*. This was the first attempt to organize an ecological science. The balance of nature concept, based on the fact that predatory animals usually have fewer offspring than their prey, had come down from antiquity, but Linnaeus added environmental studies to broaden the concept. It was translated into English and impressed Charles Darwin when he was developing his theory of evolution. In 1905 botanists agreed to take Linnaeus's *Species plantarum* (1753; the species of plants) as the official starting point for scientific names, and zoologists chose the tenth edition of *Systema naturae* (1758) as the starting point for animal names.

L'Obel, Matthias (1538-1616), Flemish-English botanist. He was interested in medicinal plants by age sixteen; in 1565 he was studying medicine at Montpellier under Guillaume Rondelet, who left his botanical manuscripts to L'Obel when he died in 1566. L'Obel remained in Montpellier three more years in order to coauthor with Pierre Pena *Stirpium adversaria nova* (1570, enlarged ed. 1576) on more than twelve hundred plants that L'Obel had collected around Montpellier and elsewhere. In 1581 a Flemish translation appeared. L'Obel was interested in natural groupings of plants and was guided by the leaves.

McClintock, Barbara (1902-1992), American botanist and geneticist. She majored in botany at Cornell University, where she earned her bachelor's degree (1923), master's degree (1925), and philosophy doctorate (1927). She studied with Richard Goldschmidt in Germany in 1933, where she was shocked at Nazi behavior and left. Despite her outstanding research, Cornell would not give her faculty standing because she was a woman. In 1936-1941 she was an assistant professor at the University of Missouri but was not promoted. In 1941 she went to the Cold Spring Harbor Laboratory, where she remained. She investigated the genetics of corn (maize), especially the breakage, movement, and fusion of parts of chromosomes. She won the Nobel Prize in 1983 for research mostly conducted some forty years before.

Malpighi, Marcello (1628-1694), Italian physician and biologist. He was a native of Bologna and earned a medical degree at its university in 1653. He taught medicine at several universities until 1691, when he became chief physician to Pope Innocent XII. William Harvey's two books on the circulation of the blood were convincing, as far as they went, but Harvey had worked before the development of adequate microscopes and had not discovered the links between arteries and veins. Malpighi mastered microscopic technique and sought the links in the lungs of frogs. He published his discoveries of capillaries in 1661. The Royal Society of London was impressed and began corresponding with him. In 1671 he sent the society his first study on plant anatomy, which he accomplished without knowledge of Nehemiah Grew's first study, which the Royal Society had published a few months before. Several of Malpighi's subsequent publications were published by that society, including his *Anatome plantarum* (2 parts, 1675 and 1679; plant anatomy). For nearly 150 years there were no significant advances in plant anatomy beyond what Malpighi and Grew had accomplished.

Manton, Irene (1904-1988), English botanist and cytologist. In 1923 she won a scholarship to Cambridge University to study cytology and genetics. She graduated in 1926 and spent 1927 studying cytology in Stockholm. She earned a Ph.D. at Cambridge in 1930 with a dissertation examining chromosomes of 250 plant species. During her lectureship in botany at Manchester, 1929-1946, she continued her chromosome studies. Her effective methodology and discoveries enabled her to obtain the botany chair at Leeds, 1946-1969. She began using the electron microscope in 1950 and was first to study plant cell organelles, including chloroplasts. She studied polyploidy and hybridization in ferns, and after retirement she went on collecting expeditions to obtain nanoplankton from Denmark to South Africa and from Alaska to the Galápagos Islands, 1970-1974. She and her zoologist sister, Sidnie Milana Manton, were the first sisters to be elected to the Royal Society of London. Irene Manton won two medals from the Linnean Society and served as its president in 1973.

Mariotte, Edme (c. 1620-1684), French scientist. He was closely associated with the Académie Royale des Sciences from soon after its founding in 1666 until his death. Nothing is known of his earlier life; he might have come from Chazeuil in Burgundy, where several Mariotte families lived. He moved from Dijon to Paris in the 1670's. He was soon involved in controversy with Claude Perrault over the possible circulation of plant sap. His *De la végétation des plantes* (1679) went beyond that controversy to argue that plants take in water from their roots, but they make the different substances found in plants.

Mattioli, Pier Andrea (1501-1577), Italian physician and botanist. He was the son of a physician and earned a medical degree at the University of Padua in 1523. He had a very successful medical practice yet was also an industrious author. His books generally involved medicinal plants—at a time when virtually all species had medical uses. He began with commentaries on Pedanius Dioscorides' *De materia medica* (1544) and by republishing enlarged and revised editions, he became the leading authority on the subject. He also provided many excellent illustrations of the plants discussed—more than five hundred in early editions and finally more than twelve hundred in the last editions.

Mendel, (Johann) "Gregor" (1822-1884), Czechoslovakian experimenter in genetics. His father was a farmer, and his mother was the daughter of a village gardener. He was not robust enough to become a farmer, though he helped his father graft fruit trees. He was determined to get a good education, and he entered the Augustinian monastery in Brno because it would enable him to complete college and become a teacher; he took the name "Gregor" when he entered in 1843. There, Matthew Klácel ran an experimental garden and studied variation, heredity, and evolution in plants, later putting Mendel in charge of the garden. Mendel also became a substitute teacher in a grammar school and did well; therefore, he took an exam for science teachers but failed. He was sent to the University of Vienna, 1851-1853, to broaden his knowledge. There he learned to apply mathematics to science, and he studied botany under the controversial Franz Unger, who taught that plants evolved over time. In 1855 Mendel retook the teacher's exam and, being very nervous, failed again. In 1856 he began experiments on inheritance in peas, and the experiments he designed show that he had, in fact, mastered his science lessons. He was experimenting at a time when naturalists were not accustomed to thinking mathematically about biology. During ten years of research, he bred and tabulated at least twenty-eight thousand plants. By following the heredity of variable traits through at least three generations, he showed that traits such as height, flower color, and seed texture exhibit dominance and recessiveness and that hereditary patterns can be determined by statistical analysis of the offspring of breeding experiments. The scientific paper which he read at a meeting of the Natural Sciences Society of Brno in 1865 and published in its journal in 1866 is now judged to be clear and logical, but it was too advanced for a mathematically unsophisticated audience, and there was no response. Mendel did not give up but sought to expand his proofs to other species. In several species he did obtain the same type of results, but unfortunately he choose to study in detail the heredity of *Hieracium*, a genus that does not consistently reproduce sexually—reproducing also by apogamy. Since he never discovered this situation, his *Hieracium* results, which he reported in 1869 and published in 1870, failed to substantiate his findings of 1865. His work sank into obscurity until 1900, when three botanists—Karl Correns, Erich Tschermak, and Hugo de Vries—rediscovered and publicized it.

Michaux, André (1746-1802) and François-André (1770-1855), French botanists. At age twenty-one, André succeeded his deceased father as manager of a royal farm. However, he became more interested in botany and horticulture than in farming and went to Paris to study under Bernard de Jussieu (1777) and botanize with Jean-Baptiste Lamarck in Auvergne and the Pyrenees (1780). He also explored Iran for three years before going to America in 1785, taking along his son. They lived in New Jersey and sent back to France five thousand trees and twelve packets of seeds. In 1787 they moved to South Carolina and purchased a plantation near Charleston to use as a nursery. They collected southward into Florida. In 1789 they collected in both the Bahamas and the Appalachian Mountains. In 1792 they spent eight months on a trip to Hudson Bay, Canada, and three months in Kentucky. In 1794 they collected in the southern Appalachians again and on the Illinois prairies. In 1796 they returned to France, and André wrote *Histoire des chênes de l'Amérique* (1801), on oaks, and *Flora boreali-americana* (1803), but he did not oversee their publication because he sailed to Madagascar in 1800, where he died. In 1801 François-André, who had learned botany from his father, returned to the nursery in South Carolina and then traveled extensively in the East until 1803; he returned to the United States for more collecting and exploring in 1806-1807. He published three works on his studies: *Voyage à l'ouest des monts Alléghanys* (1804; *Travels to the Westward of the Alleghany Mountains*, 1805), *Mémoire sur la naturalisation des arbres forestiers de l'Amérique septentrionale* (1805), and *Histoire des arbres forestiers de l'Amérique septentrionale* (1810-1813, 3 vols.; *The North American Sylva: Or, A Description of the Forest Trees of the United States, Canada, and Nova Scotia*, 1819).

Mirbel, Charles François Brisseau de (1776-1854), French botanist. His education was interrupted by the French Revolution, and in 1796 he fled to the Pyrenees for two years, where he became interested in botany and mineralogy. In 1798 he obtained a post at the Muséum National d'Histoire Naturelle, where he initiated French studies on microscopic plant anatomy. He showed that seed and embryo characteristics are identical for species within natural families, laying the foundation for embryogenic classification. His numerous publications include *Traité d'anatomie et de physiologie végétales* (1802, 2 vols.) and similar, updated works in 1815 and 1832.

Mohl, Hugo von (1805-1872), German botanist. He had early interests in botany and optics and was able to combine those interests in his career. He earned a medical degree at Tübingen in 1828 with a thesis on plant pores (stomata), and in 1835 he became professor of botany there. He was a founder of *Botanische Zeitung* (1843; botanical newspaper) and published a manual on microscopy (1846). His encyclopedia memoir "Die vegetabilische Zelle" (1850; "The Vegetable Cell," 1852) was an important synthesis of his and others' researches during a crucial decade. He first used the term "protoplasm" in its modern sense.

Nägeli, Karl Wilhelm von (1817-1891), Swiss-German botanist. The son of a physician, he studied medicine in Zurich but left in 1839 to earn a Ph.D. in botany under Alphonse de Candolle in Geneva. In 1842 Nägeli went to Jena to work with Matthias Jakob Schleiden to investigate plant cells. Nägeli was influenced by German *Natur Philosophie*, and his careful research was sometimes undermined by his philosophical preconceptions. This was as true of his genetics as of his cytology. He made important discoveries, only to overinterpret them. This was unfortunate, because he achieved a position of eminence, as professor of botany at Munich. The most notorious example of his close-mindedness was his unwillingness to take seriously Gregor Mendel's genetics paper of 1866. Mendel's unfortunate choice of *Hieracium* as a subject for further hereditary studies was because of Nägeli's interest in the genus.

Oparin, Aleksandr Ivanovich (1894-1980), Russian botanist and biochemist. He studied botany at the Moscow State University and was influenced by plant physiologist K. A. Timiryazev and by the writings of Charles Darwin. Graduating in 1917, he did research in botany and biochemistry under A. N. Bakh, and in 1922 he explained at a meeting of the Russian Botanical Society his hypothesis of primordial heterotrophic organisms arising in a brew of organic compounds. He argued that because organisms receive energy and materials from outside, they are not limited by the second law of thermodynamics. In 1935 he became the deputy director of the Bakh Institute of Biochemistry in Moscow and in 1946 became director. In 1957 he organized the first international meeting on the origin of life in Moscow, and in 1970 he was elected president of the International Society for the Study of the Origin of Life. Fame came with his *The Origin of Life on Earth* (1936, 3d ed. 1957), and he also published later works on this subject.

Pasteur, Louis (1822-1895), French chemist, crystallographer, microbiologist, and immunologist. His father was a veteran of Napoleon's army and a tanner. Pasteur was only a mediocre student at the Collège Royal de Besançon, but he was able to enter the École Normale Supérieure in Paris and was inspired by chemistry professor Jean-

Baptiste Duman of the Sorbonne. He earned his Ph.D. in 1847 and remained at the École until 1848. His early research interests were in chemistry and crystallography, and in 1854 he became professor of chemistry at the new Faculty of Sciences at Lille. In 1855 he published an article showing that amyl alcohol, a by-product of industrial fermentation, is composed of two isomers, one optically active and the other not. In 1856 he began research on why a beetroot alcohol factory experienced variations in the quality of its product. He discovered that properly aged wine or beer contains spherical globules of yeast cells that produce alcohol, but sour wine or beer contains elongated yeast cells that produce lactic acid. This discovery undermined Justus von Liebig's contention that fermentation is a purely chemical process not involving living organisms, and it led, in turn, to Pasteur's opposition to the theory of spontaneous generation. Pasteur also discovered the existence of "anaerobic life" (his term). His search for ways to preserve wine led him to develop pasteurization (partial heat sterilization). In 1865 he began studying two silkworm diseases and devised ways to inhibit them. From 1877 until his death he studied anthrax, chicken cholera, swine erysipelas, and rabies. He was one of the main founders of microbiology.

Plinius (Pliny) Secundus, Gaius (c. 23-79 C.E.), Roman provincial administrator and author. He served as an army officer and naval administrator but was also a diligent compiler of a natural history encyclopedia in thirty-seven books. He drew upon both Greek and Roman authorities, and he discussed plants from agricultural. Pharmaceutical, and botanical perspectives in books 12-27. Remarkably, his *Natural History* survived the decline of Rome and was an important resource during the Middle Ages; a modern Latin-English edition is in ten volumes.

Pringsheim, Nathanael (1823-1894), German botanist. His father wanted him to study medicine at the University of Breslau, where he was influenced by the great animal physiologist and histologist Jan Evangelista Purkinje. However, Pringsheim realized his true interest was botany, and he transferred to Berlin, where he was strongly influenced by Matthias Jakob Schleiden's famous textbook on botany (1842-1843). He earned his Ph.D. in 1848 with a dissertation on the growth of cell walls. The dynamics of cell division was a thorny issue during the 1840's and 1850's, exacerbated by technical limitations in microscopy and cytology, and he challenged the explanations of both Schleiden and Hugo von Mohl. French botanist Gustave Adolphe Thuret's discovery of sexual reproduction in the marine alga *Fucus* attracted Pringsheim's interest in the study of sexual reproduction in algae. He established this as a general phenomenon in freshwater algae and corrected Thuret's account of the fusion of sperm and egg. He also became involved in a long, inconclusive debate with Anton de Bary over whether the fungus *Saprolegnia* reproduces sexually. Pringsheim also encountered opposition to his account of alternation of generations in lower cryptogams. In 1864 he became Schleiden's successor at Jena, but because of poor health and an inheritance, he resigned in 1868 and returned to a house in Berlin near the botanic garden. In 1874 he began research on photosynthesis, but his ideas on the role of chlorophyll won no converts. He was successful, however, in three organizational initiatives. In 1857 he founded *Jahrbücher für wissenschaftliche Botanik* (annals of scientific botany) and edited it until he died; in 1882 he was chief founder of the German Botanical Society and was its president until he died; and he helped establish a biological station on Helgoland island on the German coast. A museum was built there in his honor after he died.

Raunkiaer, Christen (1860-1938), Danish plant ecologist. Raunkiaer was Johannes Warming's successor.

Ray, John (1627-1705), English naturalist. He acquired an interest in plants from his mother, a herbalist-healer. At Cambridge University he earned a bachelor's degree in 1644 and a master's degree in 1651. His teaching career at Cambridge ended in 1662, when he refused to take an oath required by a new Act of Uniformity. During the 1650's Ray and his friends studied the flora of Cambridgeshire and published anonymously *Catalogus plantarum circa Cantabrigiam nascentium* (1660; *Ray's Flora of Cambridgeshire*, 1975), listing 558 species, which was not superseded until 1860. After his exclusion Ray was supported by a naturalist patron, Francis Willughby; they became close collaborators and traveled in Europe, 1663-1666. When Willughby died in 1672, Ray married and returned to live in his hometown, Black Notley. He developed his system of classification in *Methodus Plantarum Nova* (1682), and the revised edition of 1703 provided classification for nearly eighteen thousand species. His *Synopsis Stirpium Britannicarum* (1690) was the first British flora—not superseded until 1762. His most important botanical work was his *Historia Plantarum Generalis* (1689-1704, 3 vols.), which contained an introduction to plant anatomy, morphology, and physiology and a classification and description of all known species, in some three thousand folio pages. It remained a leading authority for a century.

Ruel, Jean (1474-1537), French physician and botanist. Little is known of his early years, but he received a medical degree in 1508 and in 1509 served as a physician to François I. His Latin translation of Pedanius Dioscorides' *De materia medica* was published in 1516. His main work was his *De Natura Stirpium Libri Tres* (1536), with more than nine hundred pages of text and no illustrations. Because he gave full verbal descriptions of all species, he developed both terminology and definitions that became more widely known when they were appropriated by Leonhard Fuchs (1542).

Sachs, Julius von (1832-1897), German plant physiologist. His father was an engraver, and both parents died within a year (1848-1849), which forced him to leave school, but he met the physiologist Jan Evangelista Purkinje, who took him to Prague as a draftsman. There, he finished school in 1851 and then entered the university. He found the botany and zoology lectures boring, but he did independent research, and after he had published eighteen scientific articles he received a Ph.D. in 1856. In 1859 he became assistant in plant physiology at the Agricultural and Forestry College near Dresden. In 1860 Hofmeister and Sachs began editing the *Handbuch der physiologischen Botanik* (1865). In 1861-1867 he taught at the Agricultural College in Poppelsdorf and in 1868 became professor of botany at Würzburg, where he remained. He was a brilliant lecturer and imaginative experimenter and became the foremost plant physiologist of the day. He studied metabolism, photosynthesis, mineral needs, etiolation, flower and root formation, and growth. However, his understanding of water and sugar transport was defective, and he spent his last years attacking Charles Darwin's theory of natural selection as the cause of evolution. Sachs invented numerous laboratory techniques and devices, and his textbooks—*Lehrbuch der Botanik* (1868; textbook of botany) and *Vorlesungen über Pflanzenphysiologie* (2 editions, 1882, 1887)—were authoritative. He also wrote a history of botany, 1500-1860 (1875).

Sargent, Charles Sprague (1841-1927), American botanist and arboretum administrator. He was from a prosperous Boston family and graduated from Harvard University in 1862 in classics. After serving in the Union Army during the Civil War, he toured Europe for three years. With only an amateur interest in horticulture and dendrology, he became director of the Arnold Arboretum at Harvard in 1873 and remained there. He was also appointed Arnold Professor of Arboriculture. Funds from the James Arnold estate were used to establish the arboretum on 150 acres of "worn-out farm," which Sargent increased to a 250-acre world-class resource. The annual funds from the endowment were never enough to sustain the operations which he undertook, and he raised funds from wealthy friends and from his own finances. He had the benefit of advice from Asa Gray in planning and running the arboretum. In 1879 Sachs undertook a survey of the forests of the United States, and his six-hundred-page report became Volume IX of the "Tenth Census of the United States" (1880). He was a strong supporter of U.S. national parks and national forests and chaired a committee's study and report on the latter for the National Academy of Sciences in 1896. At the urging of the Smithsonian Institution he undertook *Silva of North America* (1891-1902, 14 vols.), with 740 plates. It became the basis for his *Manual of North American Trees* (1905). He also edited the *Journal of the Arnold Arboretum* and the popular periodical, *Garden and Forest*, which encouraged forest conservation.

Sargent, Ethel (1863-1918), English plant anatomist. She graduated from Cambridge University in 1884 but never held a professional position. She next studied plant anatomy and laboratory techniques for a year at the Royal Botanic Gardens at Kew. In 1897 she visited several European laboratories, including Adolf Strasburger's at Bonn. She conducted her research in a home laboratory, and she had informal students who studied with her, most notably Agnes Arber. Her earliest research was on centrosomes in higher plants, followed by a study of oogenesis and spermatogenesis in *Lilium martagon*. She confirmed the existence of the synaptic stage in cell division at a time when some investigators dismissed it as an artifact of lab procedures. She concluded from her studies of monocots that the number and arrangement of vascular bundles (axial or lateral) are useful clues to evolution and discussed this in three important articles (1896-1902). She became a fellow of the Linnean Society of London and in 1913 was president of the Botanical Section at the meeting of the British Association for the Advancement of Science.

Saussure, Horace Bénédict de (1740-1799) and Nicolas-Théodore de (1767-1845), Swiss scientists. Horace's father was an agricultural author, and his uncle was the prominent naturalist Charles Bonnet. Horace graduated from the University of Geneva in 1759 with a dissertation on transmission of heat by sun rays. In 1760 he traveled to the Chamonix mountains to collect plants for the physician-botanist Albrecht von Haller. He also dedicated to Haller his first botanical treatise, *Observations sur l'écorce des feuilles et des pétales des plantes* (1762). In 1767 he conducted experiments at Mont Blanc on heat and cold, the weight of the atmosphere, and electricity and magnetism. In 1768 he and his wife toured France and England and met many scientists. In 1774-1776 he was rector of the University of Geneva, and in 1776 he founded the Société des Arts and was its first president. His major work is *Voyages dans les Alpes, Précédés d'un essai sur l'histoire naturelle des environs de Genève* (1779-1796, 4 vols.). Nicolas-Théodore studied science under his father and assisted in his research. They spent several weeks in the summers of 1788 and 1789 conducting research on Swiss mountains. Nicolas-Théodore became interested in the chemistry of plant physiology and after seven years of research published his *Recherches chimiques sur la végétation* in 1804. It was translated into German in 1805 and became the foundation of phytochemistry science. He continued to publish specialized studies on the subject for the rest of his life. In 1815 he was a founding member of Société Helvétique des Sciences Naturelles.

Schimper, Andreas Franz Wilhelm (1856-1901), Franco-German botanist. His father was professor of natural history at the University of Strasbourg and director of the city's museum of natural history. Schimper received a Ph.D. from the university in 1878, having studied under Anton de Bary. De Bary opposed his succeeding his father as museum director in 1880, and instead Schimper went to Johns Hopkins University to study starch formation. In 1881 he traveled in Florida and the West Indies and became interested in phytogeography. In 1883 he became lecturer in plant physiology at the University of Bonn, where he also taught phytogeography and other botany courses. In 1886 he traveled to Brazil to study salt concentration in mangroves and other littoral vegetation. He conducted similar studies in Ceylon and Java, 1889-1890. He published twenty-seven books and articles and is best remembered for his large *Pflanzengeographie auf physiologischer Grundlage* (1898; English translation, 1903).

Schleiden, Matthias Jakob (1804-1881), German botanist. The son of a prosperous physician, he earned a doctorate in law in 1827 and practiced law until 1833, when he decide to study science. He earned a Ph.D. in 1839, having worked in Johannes Müller's laboratory, where he knew Theodor Schwann. Schleiden was a popular teacher and in 1850 he became professor of botany at Jena. In 1838 he published his ideas on cell formation, "Beiträge zur Phytogenesis," which he had developed during conversations with Schwann. Schleiden accepted an idea that went back to Nehemiah Grew: that cells crystallize inside an amorphous primary substance. The clearest statement of his theory is in his *Grundzüge der wissenschaftlichen Botanik* (1842-1843, 3 vols.; *Principles of Scientific Botany: Or, Botany as an Inductive Science*, 1849). That textbook also displays his opposition to philosophical speculations that had damaged German science.

Schwann, Theodor Ambrose Hubert (1810-1882), German animal physiologist. In 1826 he entered a Jesuit college in Cologne to prepare for the priesthood but in 1829 transferred to the University of Bonn to study medicine and obtained a bachelor's degree in 1831. He had studied under the physiologist Johannes Müller and later followed him to Berlin, where Schwann earned a medical degree in 1834 with a dissertation on the importance of air for chick embryo development. He also assisted Müller with his *Handbuch der Physiologie* (1834). In 1836 Schwann concluded that yeast causes alcoholic fermentation, but Cagniard de La Tour made the same discovery and got his article published that year, whereas Schwann's appeared in 1837. Schwann explained in his *Mikroskopische Untersuchungen über die Ubereinstimmung in der Struktur und dem Wachsthum der Tiere und Pflanzen* (1839; *Microscopial Researches into the Accordance in the Structure and Growth of Animals and Plants*, 1847) his cellular theory—all cells arise from other cells—though he misunderstood cell formation. In 1839, attacks on his theory of yeast producing alcohol caused him to lose interest in research. He became a professor at Louvain and later at Liège, teaching anatomy and physiology.

Sears, Paul Bigelow (1891-1990), American botanist, ecologist, conservationist. An Ohioan, he earned a bachelor's degree in zoology from Ohio Wesleyan University (1913), a master's degree in botany from University of Nebraska (1915), and a philosophy doctorate in botany from the University of Chicago (1922). He began teaching botany at Ohio State University in 1915 but was interrupted by Army service, 1917-1919. He later taught botany at the Universities of Nebraska (1919-1927) and Oklahoma (1927-1938) and Oberlin College (1938-1950). Much of his botanical research was on the history of postglacial American vegetation, and his first book, *Deserts on the March* (1935), was a popular account of the Dust Bowl based on that research. It explained how mismanagement of agricultural lands had been a major factor in that disaster and how proper management could restore the land. That book's success reoriented his studies more toward conservation than botany, and he went to Yale University, 1950-1960, as professor and chairman of a new Master of Science Conservation Program—the first such program in the United States. His nine other books included *Life and the Environment* (1939) and *The Living Landscape* (1964). He won numerous awards, including Eminent Ecologist of the Ecological Society of America (1965), and was president of several societies, including the American Association for the Advancement of Science (1956).

Senebier, Jean (1742-1809), Swiss plant physiologist. Although he fulfilled his parents' wish and became a Calvinist pastor, his interests lay in natural history. He served as a pastor for only four years before resigning in 1773 to become librarian for his native city, Geneva. In 1777 he began publishing a French translation of Lazzaro Spallanzani's works and continued doing so until 1807. In 1779 he published *Action de la lumière sur la végétation*, the first installment on his voluminous *Traité de physiologie végétal* (1800, 5 vols.). This work displays his great experimental abilities; he also generalized upon that ability in his *Essai sur l'art d'observer et de faire des expériences* (1802).

Spallanzani, Lazzaro (1729-1799), Italian biologist. The son of a successful lawyer, he initially attended a Jesuit seminary in Reggio Emilia but left in 1749 to study law at Bologna. His cousin Laura Bassi was professor of physics and mathematics there, and she convinced him to study math and science. He received a Ph.D. in 1754 and a few years later became an ordained priest. In 1755 he began teaching languages and math at the University of Reggio Emilia, and in 1763-1769 he taught philosophy at Modena. He was professor of natural history at Pavia, 1769-1799. In 1761 he read the experiments of George Louis Leclerc Buffon and John Turberville Needham (1749) on the spontaneous generation of animalcules. In 1762 he obtained an adequate microscope and began repeating their experiments. His essay "Saggio di osservazioni microscopiche relative al sistema della generazione dei Signori Needham e Buffon" (1765; account of microscopic observations concerning Needham and Buffon's system of generation) showed that animalcules only appeared when the organic infusions were either sealed inadequately or heated inadequately. However, Needham refused to accept these results, and Spallanzani returned to the fray in 1770 and again in his *Opuscoli di fisica animale e vegetabile* (1776; *Tracts on the Nature of Animals and Vegetables*, 1799). He was one of the most brilliant experimentalists of his century, and his works were translated into English, French, and German. Spallanzani was also director of the university museum in Pavia, and the need to collect specimens for it provided a welcome excuse for his many travels.

Stopes, Marie (Charlotte Carmichael; 1880-1958), British paleobotanist and advocate of birth control and sex education. Her father was an archaeologist-anthropologist who studied early humans. She earned a chemistry scholarship to University College, London, but went on to study botany in Cambridge, earning a bachelor's degree in 1902 and a doctorate in 1905. She then went to Munich and earned a Ph.D. in 1909 with a dissertation on the morphology of cycad seeds. She published a paper on a fossil plant in 1903 and continued studying paleobotany for twenty years. She collected fossils in Japan, 1907-1909, and in 1910 published a popular book, *Ancient Plants: Being a Simple Account of the Past Vegetation of the Earth*. In 1911 she traveled in Canada and the United States to study Carboniferous fossils, and in 1913-1915 she published a *Catalogue of the Mesozoic Plants in the British Museum (Natural History)* in two volumes. Her evidence indicated the sudden rise of flowering plants early in the Cretaceous. Between 1919 and 1923 she published articles on the origins and petrography of coal; some of them were coauthored with R. V. Wheeler. In 1918 she married Humphrey Verdon-Roe, who was interested in birth control. They founded the Mother's Clinic for Birth Control in London in 1921, the first of its kind in England, and she soon turned from paleobotany to family planning.

Strasburger, Eduard Adolf (1844-1912), Polish-German botanist-cytologist. He was born and raised in Warsaw to parents of German descent. After graduating from a Warsaw gymnasium in 1862, he studied for two years at the Sorbonne in Paris and then studied botany and microscopy at Bonn. Later, he became Nathaneal Pringsheim's assistant in Jena. However, it was the enthusiasm of Jena's zoologist, Ernst Haeckel, for Charles Darwin's theory of evolution that turned Strasburger toward evolutionary research. He earned his Ph.D. in 1866, reporting on nuclear division during cell division in ferns. In 1867 he became Privatdozent at Warsaw University, but by 1869 he was back in Jena as professor of botany, and in 1873 he also became director of the botanical garden. His cytological investigations at Jena appeared in three editions of his *Über Zellbildung und Zelltheilung* (1880; on cell formation and cell division). He pioneered methods to fix and harden tissues in alcohol. In 1881 he became professor at Bonn, and his laboratory at the Botanical Institute—a former palace—became the most important center for cytological research in the world. In 1884 he in dependently concluded that hereditary material is in the filaments of the cell nucleus. He went on to study cell wall formation, the role of centrosomes, and protoplasmic connections among cells. He investigated the evolution of reproduction in plants, from algae and mosses to cryptogams and phanerogams (1894). His textbooks appeared in many editions and translations. He received two honorary degrees from universities and two medals from the Linnean Society of London.

Tansley, Arthur George (1871-1955), English plant ecologist. He studied botany at University College, London, and at Cambridge University, where he was friends with Bertram Russell. In 1902 he started the journal *The New Phytologist* as a forum for works in progress, and in 1904 he organized the British Vegetation Committee to survey the vegetation of the British Isles. He was stimulated by, but sometimes disagreed with, the publications of Frederic Clements on plant succession and climax communities. The two met in 1911 when Tansley organized an International Phytogeographical Excursion in the British Isles to bring together European and American ecologists. A reciprocal excursion was held in the United States in 1913. In 1913 Tansley also helped organize the British Ecological Society and was its first president. That society published *The Journal of Ecology*, which Tansley edited. In 1935 he attacked the Clementsian theory of a biological community being a superorganism in "The Use and Abuse of Vegetational Concepts," and proposed the "ecosystem" as an alternative concept. A synthesis of his lifetime research was his *British Isles and Their Vegetation* (1939).

Theophrastus of Eresos (c. 371-c. 287 B.C.E.), Greek educator, botanist, philosopher. He was educated under Aristotle and succeeded him as head of the Lyceum at Athens. He wrote the two earliest treatises on botany, *Historia plantarum* ("Enquiry into Plants" in *Enquiry into Plants and Minor Works on Odours and Weather Signs*, 1916) and *De causis plantarum* (*De Causis Plantarum*, 1976-1990, 3 vols.), which were comparable to similar works on animals written at the Lyceum and attributed to Aristotle. These botanical treatises discuss more than five hundred species, are comprehensive in scope, and are available in modern Greek-English editions. Theophrastus classified plants as trees, shrubs, undershrubs, and herbs, and he distinguished among annuals, biennials, and perennials. He related the distribution of species to soil, moisture, and climate.

Thunberg, Carl Peter (1743-1828), Swedish botanist. At Uppsala University, where he earned a medical degree in 1770, Carl Linnaeus influenced him to pursue botany. A friend of Linnaeus arranged for Thunberg to go to Japan on a Dutch ship, but to do so he needed to learn Dutch, and for that he spent three years in South Africa, 1772-1775, where he collected and described more than three thousand plants, about one thousand being new to science. He then spent fifteen months in Japan, 1775-1776, and before returning home he studied Englebert Kämpfer's Japanese plant collection in the British Museum. When Thunberg reached Sweden in 1779 he became botanical demonstrator at Uppsala University. His first major publication was his *Flora japonica* (1784). Linnaeus was succeeded as professor of botany by his son, but upon the son's death in 1784 Thunberg succeeded to that professorship. He published his travel memoirs in Swedish (1788-1793, 4 vols.), and they were translated into English (1793-1795, 4 vols.), French, and German. He summarized his South African findings in *Prodromus plantarum capensium* (1794-1800), and the German botanist J. A. Schultes assisted him with the more detailed *Flora capensium* (1807-1823).

Tournefort, Joseph Pitton de (1656-1708), French botanist. Although educated in Jesuit schools and destined for the priesthood, at the University of Montpellier he studied botany under Pierre Magnol and gave up a clerical career. In 1683 he became a substitute professor of botany at Jardin du Roi and presumably would have become professor there had Guy-Crescent Fagon not outlived him. Tournefort traveled in western Europe collecting plants and meeting botanists in preparation for his *Éléments de botanique: Ou, Méthode pur connoîture les plantes* (1694), which consists of one volume of his text and two volumes of Claude Aubriet's illustrations. A Latin edition appeared in 1700. Tournefort did not accept the sexuality of plants, but he depended on corolla and fruit to determine genera. He was the first botanist to study plant genera specificially, of which he distinguished 725, the majority of which are still accepted, though Carl Linnaeus changed some of the names. He also explored in the Levant, 1700-1702, and his *Relation d'un voyage du Levant* (1717, 2 vols.; *A Voyage into the Levant*, 1718) appeared posthumously.

Tschermak (von Seysenegg), Erich (1871-1962), Austrian botanist-geneticist. His father was professor of mineralogy and a museum director at the University of Vienna, and his mother was daughter of the director of the Botanical Institute and Garden at the university. He studied botany in Vienna and agriculture at the University of Halle, where he earned his Ph.D. in 1895. In 1898 he studied hybridization of vegetables at Ghent, using Charles Darwin's *The Effects of Cross and Self Fertilization in the Vegetable Kingdom* (1876) as a guide. This work led to Tschermak's rediscovery of Gregor Mendel's laws and of Mendel's article (1866). Tschermak's own article on this (1900) enabled him to become a lecturer at the Höchschule für Bodenkultur in Vienna, and in 1909 he became a full professor; he was also director of the Royal Institute for Plant Breeding. In 1909 he traveled to the United States to study Luther Burbank's methods. Tschermak bred new varieties of rye, wheat, barley, oats, legumes, pumpkins, gillyflowers, and primroses. He also studied the xenia phenomenon in several species.

Tsvet, Mikhail Semenovich (1872-1919), Swiss-Russian plant physiologist and biochemist. Although his parents were Russian, he grew up in Geneva and did not move to Russia until he earned his Ph.D. from the University of Geneva in 1896. He continued his studies of plant anatomy and physiology at the St. Petersburg Biological Laboratory. Because foreign degrees were not recognized, he earned additional master's (1901) and doctoral (1910) degrees. In 1903 he moved to Warsaw and taught in several universities. In 1915 he moved to Moscow, and in 1917 he became professor of botany and director of the botanical garden at Yuryev (now Tartu) University but died two years later from war stress, overwork, and heart disease. He produced sixty-nine publications, 1894-1916, emphasizing cytophysiology. He showed that green pigment in chloroplasts is in the chlorophyll-albumin complex, which he called "chloroglobin." He also showed that chlorophyll *a* and *b* differ in color, fluorescence, and spectral absorption. In order to separate pigments and other chemicals, in 1906 he developed "chromatography" and the law of adsorption replacement and explained how to use the technique in two articles. However, use of chromatography was rather limited until the 1930's, when its value became apparent in studies on carotene and vitamin A.

Unger, Franz (1800-1870), Austrian botanist. He studied medicine at Vienna and Prague and earned his medical degree in 1827. He then practiced medicine until 1835, when he became professor of botany and zoology at Graz and director of the botanical garden at Johanneum. Finally, he accepted the new chair of plant anatomy and physiology at Vienna, 1849-1866. His *Grundzüge der Botanik* (1843, coauthored with Stephen Endlicher), made him famous because he opposed Matthias Jakob Schleiden's erroneous ideas on cell origin; Unger argued that cells arise by division of preexisting cells. In 1851 he published a correlation between geological eras and paleobotany, and in 1852 he published newspaper articles advocating evolution; they were republished as a book, *Botanische Briefe*, which was violently attacked by the Catholic press. Calls for his resignation were drowned out, however, by student support. His *Anatomie und Physiologie der Pflanzen* (1855) synthesized his earlier writings. His teaching about cell theory and fertilization may have influenced the researches of his student Gregor Mendel.

Vavilov, Nikolai Ivanovich (1887-1943), Russian botanist-geneticist. He was from a prominent Moscow family, and his physicist brother Sergey became president of the Soviet Academy of Sciences. In 1906 Nikolai entered the Moscow Agricultural Institute and while there organized a science club that took field trips to various Russian regions. He won a prize for a thesis on garden slugs. He graduated in 1911 and taught for a year before entering the Bureau of Applied Botany at the Ministry of Agriculture. In 1913 the bureau sent him to England to study genetics. During World War I he was not drafted because of a defective eye, and he earned a master's degree with a thesis on "Plant Immunity to Infectious Diseases." In 1916 he led an expedition to Iran and the Pamir, and in 1917 he became a professor at Voronezh Agricultural Institute and at Saratov University. In 1920 he moved to Petrograd, and in 1923 he became director of the State Institute of Experimental Agronomy. In 1924 Vladimir Lenin agreed to his reorganization of the department of applied botany into the All-Union Institute of Applied Botany and New Cultures. During the 1920's and 1930's Vavilov led many botanical expeditions to many parts of the world, leading to his presidency of the U.S.S.R. Geographical Society, 1931-1940. His travel memoir, *Five Continents*, appeared posthumously in 1962. He amassed a collection of more than 250,000 specimens at the institute. His earliest research was on the genetics of plant immunity, published 1913-1919, followed by studies of variability. By 1924 he was also investigating centers of origin of cultivated plants. Alphonse de Candolle had investigated this using archaeological, historical, linguistic, and botanical evidence in 1882; Vavilov now added genetic and cytological evidence. In 1926 he identified five primary centers of origin, which coincided with early civilizations. By 1940 he had identified thirteen regions in seven centers. His main goal was to improve Soviet agriculture with new varieties of domesticates matched to particular environments. By 1931, however, he was being criticized for not achieving results fast enough. In contrast, T. D. Lysenko seemed to be making impressive achievements with his "vernalization" treatment of seeds before planting. Vavilov unwisely praised Lysenko's method in 1935; Lysenko joined the attack on Vavilov's methods. Lysenko's political power steadily increased, while Vavilov's declined. In 1939 Vavilov abandoned appeasement and criticized Lysenko for attacking Western genetics. On August 6, 1940, Vavilov was arrested and the following year was found guilty of belonging to a rightist organization, spying for England, and conducting sabotage in agriculture. He was condemned to die. Although his brother Sergey got his sentence commuted to ten years imprisonment, in only two years Nikolai died from malnutrition and unhealthy conditions. In 1955 he was rehabilitated by the Soviet Supreme Court, and in 1967 the All-Union Society of Geneticists and Selectionists was named for him.

Vries, Hugo de (1848-1935), Dutch plant physiologist, geneticist, and evolutionist. He was descended from prominent scholars and statesmen on both sides of his family. Even before he entered the University of Leiden in 1866, he was assisting Professor Willem Suringar with the herbarium of the Netherlands Botanical Society. At the university he was inspired by Julius Sachs's *Lehrbuch der Botanik* (1866) and Charles Darwin's *On the Origin of Species by Means of Natural Selection* (1859) to study plant physiology and evolution, though the university was weak in instruction in both. Suringar was hostile to Darwin's theory, and after de Vries earned a medical degree in 1870, they ceased interacting. De Vries went to Heidelberg and worked with Wilhelm Hofmeister, and in 1871 de Vries went to Würzburg and worked with Sachs. In September he began teaching at First High School in Amsterdam, but he returned to Würzburg in summers for research. In 1872 he studied tendril curling and other growth movements in plants, which Darwin praised (1876). In 1877 de Vries became instructor in botany at the new University of Amsterdam, and that summer he went to England to meet botanists, including Darwin. He became a professor in 1881. By 1885 he began changing his research from physiology to heredity and variation, as seen in his series of nineteen articles published in a Dutch agricultural journal: "Thoughts on the Improvement of the Races of Our Cultivated Plants" (1885-1887). His *Intracellulaire pangenesis* (1889; *Intracellular Pangenesis*, 1910) reviewed the hypotheses of Herbert Spencer, Darwin, Karl Nägeli, and August Friedrich Leopold Weismann before proposing his own "pangene" hypothesis. His studies during the 1890's led to the rediscovery of Gregor Mendel's laws (possibly in 1896) and discovery of mutations in *Oenotheras lamarckiana*. In 1900, while preparing to publish *Die Mutationstheorie: Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich* (1901-1903, 2 vols.; *The Mutation Theory: Experiments and Observations on the Origin of Species in the Vegetable Kingdom*, 1909-1910, 2 vols.), he surveyed the relevant literature and discovered Mendel's article of 1866. He, Karl Correns, and Erich Tschermak all published independently their rediscovery of Mendel's work. De Vries distinguished between mutations in *Oenotheras lamarckiana* which seemed "progressive" and furthering of evolution and others which seemed "retrogressive" and not contributing to evolution. His later publications pursued these findings in greater detail. Others began studying the genetics of *Oenotheras* and challenged some of his conclusions.

Wallace, Alfred Russel (1823-1913), English naturalist and evolutionist. His formal education was rudimentary, but he became a diligent reader. In 1841 he bought a botany book to aid in making a herbarium, and he was soon reading the works of Alexander von Humboldt, Charles Lyell, Charles Darwin, Robert Chambers, and other science authors. In 1847 Wallace convinced a friend, Henry Walter Bates, to go to the Amazon to seek evidence of evolution. They supported themselves by collecting biological specimens to sell. Wallace returned to England in 1852 and published a well-received *Narrative of Travels on the Amazon and Rio Negro* (1853) and a smaller book on Amazon palms. Because most of his personal materials burned on the ship to England, he lacked evidence for an elaborate defense of evolution; he published only one provocative paper (1855), which caught the attention of Lyell and Darwin. Wallace went on another extensive collecting expedition to the Malay Archipelago, 1854-1862, and on March 9, 1858, he sent to Darwin his now-famous article "On the Tendency of Varieties to Depart Indefinitely from the Original Type," which was read at a meeting of the Linnean Society along with extracts from Darwin's writings on the same subject. Both of their contributions appeared in that society's journal on August 20, 1858. After returning to England, Wallace published his highly praised travel book, *The Malay Archipelago: A Narrative of Travel with Studies of Man and Nature* (1869). Wallace became a very productive author on diverse topics; his many books included *Contributions to the Theory of Natural Selection* (1870), *Island Life* (1880), and *Darwinism* (1889). He married Annie Mitten, daughter of botanist William Mitten. Wallace received numerous medals and other honors from scientific societies.

Warming, Johannes Eugenius Bülow (1841-1924), Danish botanist. He grew up on the Jutland coast, the ecology of which he later studied. He interrupted his university training in 1863-1866 to assist the vertebrate paleontologist Peter W. Lund in his Brazilian researches. While there, Warming thoroughly investigated the flora; his findings appeared in a Danish natural history journal (1867-1893), and those articles were the basis for his important book on the phytogeography of Lagoa Santa (1892). He earned his Ph.D. at the University of Copenhagen in 1871 and taught botany there until 1882. He became botany professor at the new University of Stockholm, 1882-1886, and then botany professor and director of the botanical garden at Cophenhagen, 1886-1911. His botanical interests and publications were quite diverse, but he is best remembered for his *Plantesamfund* (1895), which was translated into English, German, and Russian. The English edition is titled *Oecology of Plants: An Introduction to the Study of Plant-Communities* (1909). He studied "Why each species has its own habit and habitat, why the species congregate to form definite communities and why these have a characteristic physiognomy." Although Warming accepted a version of Lamarckism rather than Charles Darwin's theory of natural selection, this book was nevertheless one of the main foundations for organized plant ecology.

Watson, Hewett Cottrell (1804-1881), English botanist. As a child, he became friends with the family gardener and developed a permanent interest in flowers. He studied medicine at Edinburgh, 1828-1831, but as his real interest was in botany, he left without a degree. While at Edinburgh, he became interested in phytogeography and wrote a prizewinning essay on it (1831). He was of independent means and settled near London to pursue botany and phrenology, though his interest in the latter declined about 1840. By 1834 he was a convinced transmutationist (before Charles Darwin was), and his botanical research emphasized the variability of British plants over their British distribution in hopes of documenting evolution. In 1842 William Hooker arranged for him to spend a few months collecting plants in the Azores, and he became interested in what those specimens might show about the dynamics of phytogeography and evolution. In 1845 Watson published a series of four brief articles in a popular botanical magazine on the evidence for plant evolution in Britain. A few years later, Joseph Hooker sent those and Watson's articles on the Azores flora to Darwin, who found them all interesting. Watson began synthesizing his findings in species-by-species accounts in *Cybele Britannica* (1847-1859, 4 vols.), which were useful to Darwin. However, because Watson saved his main conclusions for the last volume, and because Darwin was preparing *On the Origin of Species by Means of Natural Selection* (1859) at the same time, Darwin sent Watson a series of questions, the answers of which were very helpful, as Darwin graciously acknowledged in his book. Watson became the earliest convert to Darwin's theory, though he later had second thoughts about one aspect of it. Watson spent the rest of his life refining his species-by-species data, published in *Topographical Botany: Shewing the Distribution of British Plants* (1873-1874). In appreciation for what he accomplished, the Botanical Society of the British Isles named its journal *Watsonia*.

Watson, James Dewey (1928-   ), American molecular biologist. He entered the University of Chicago at age fifteen and majored in biology. Graduating in 1947, he went to the University of Indiana to study genetics. He chose to write his doctoral dissertation under Salvador Luria, who was a member of an informal group that studied bacteriophages in summer at Cold Spring Harbor. Upon receiving his Ph.D. in 1950, Watson went to Denmark on a National Research Council Fellowship to learn biochemistry in order to understand genes. In the spring of 1951 he attended an international biological conference in Naples, where he realized he would rather do research on DNA in London under Maurice Wilkins. He was unable to persuade Wilkins to invite him, but Luria was able to arrange for him to go to the Cavendish Laboratory at Cambridge University. There, he met Francis Crick, who was more interested in DNA as a way to understand genes than he was in X-ray diffraction of protein, on which he was to write a doctoral dissertation. Crick and Watson were congenial colleagues, and they were able to enlist the aid of many colleagues to answer various questions which they could not answer either in the laboratory or by consulting the literature. They were the only ones searching for an understanding of DNA who drew upon four areas of research—bacteriophage, biochemistry, X-ray crystallography, and stereochemical modeling—and they unraveled the mystery in spring, 1953. Their findings were published in *Nature* along with related findings by Maurice Wilkins, Rosalind Franklin, and their colleagues. In 1962 Watson, Crick, and Wilkins were jointly awarded the Nobel Prize in Physiology or Medicine for DNA discoveries. Franklin was not included because she had died. Their discovery was a major foundation for a new science, molecular biology, to which Watson continued to contribute. He taught at Harvard University, 1956-1976; later he became assistant director, then director, of the National Center for Human Genome Research, 1988-1992. His scientific memoir, *The Double Helix* (1968), was a sensation, and his *Molecular Biology of the Gene* (2d ed., 1970) has been a standard textbook.

Willdenow, Karl Ludwig (1765-1812), German botanist. He was the son of a Berlin apothecary interested in plants, who passed on that interest to his son. Willdenow studied first pharmacy, then medicine, earning his medical degree in 1789. He had already published a flora of Berlin (1787), and in addition to his medical and pharmaceutical practice, he taught botany informally; one of his students was Alexander von Humboldt, who became a friend and sometime colleague. Willdenow's *Grundriss der Kräuterkunde* (1792) was the first textbook to supersede Carl Linnaeus's *Philosophia botanica* (1751; *The Elements of Botany*, 1775), and it brought him membership in the Berlin Academy of Sciences in 1794. In 1798 he became professor of natural history at the Berlin Medical-Surgical College, and in 1801 he also became curator of the Berlin Botanical Garden. An important section of his textbook was on phytogeography, despite the fact that he had never traveled widely. This subject caught Humboldt's interest, and in 1810 Willdenow traveled to Paris to help Humboldt with a scientific account of Humboldt's vast botanical collection. However, Willdenow became sick and had to return to Berlin, where he died.

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Sources for Further Study

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PLANT CLASSIFICATION

Plants are classified, arranged, or ordered into a hierarchy of categories and ranks called *taxa* for scientific consistency, information retrieval, identification, and classification. This allows the scientist and the layperson alike to see and understand relationships between morphology and anatomy, simply and easily identify the plant they are studying, and begin to piece together the evolutionary history or *phylogeny* of plants and the groups to which they belong. The systems and methods used in plant classification historically have been either *artificial*, that is, based on any convenient trait without true regard to its connection with the biology of the plant, or *natural*, based on the present understanding of the biology, chemistry, and evolutionary history of the plant, with emphasis on those characteristics and traits that are quantitative or numerical and are thus quantifiable or mathematically described. The current trend is toward reflecting evolutionary relationships in classification systems.

Systematics

Simply naming an organism is the process of *taxonomy*, but distinguishing organisms involves *classification*. Taxonomy and classification both are included in the broad field of *systematics*. The three main schools of thought concerning systematics today are:

(1) analysis of primitive and derived characters to construct a phylogenetic branch or *clade* with a common ancestor and its derived line of organisms or species,

(2) clustering of organisms based on shared similarities without thought for any common origin or dependence, and

(3) the traditional stress on common ancestry and degree of structural difference in order to make a phylogenetic tree.

Groups

Historical work, current research, and present scientific thinking on plant classification indicate eight distinct groups, or taxa. The eight groups recognized most commonly, from largest to smallest, are *domain*, *kingdom*, *phylum* or *division*, *class*, *order*, *family*, *genus*, and *species*. These taxa and their uses are governed by rules set forth in the International Code of Botanical Nomenclature (ICBN). Scientific names for species are in Latin, and they are binomials (two names) composed of an uppercased genus name and a lowercased descriptive, or specific (species), epithet. The eighteenth century Swedish taxonomist Carolus Linnaeus is given credit for the consistent usage of this system of *binomial nomenclature* to name plant species. Historically, the nature of the organism's cell walls formed the main criterion used to list a group as plant or plantlike. (However, see *Plantae* below.)

Domains

Research that looked at nucleotide base sequences for rRNA (ribosomal RNA) conducted by Carl Woese at the University of Illinois has revealed that all life-forms (including those that are plantlike) can be divided into three major super kingdoms or domains: *Archaea*, *Bacteria*, and *Eukarya*, suggesting that all organisms evolved from a common ancestor along three distinct lines. These three lines are called domains. The first two domains, *Archaea* and *Bacteria*, are what was traditionally the kingdom *Monera*. Both domains contain *prokaryotes*, that is, organisms made of cells with no true nucleus but rather a *nucleoid* where the DNA is "naked" in the cytoplasm (not surrounded by an envelope, with smaller ribosomes, and with plasmids). The domain *Eukarya* is composed of organisms made of *eukaryotic cells*, that is organisms whose cells have nuclei, membrane-bound organelles, and a cytoskeleton. *Eukarya* contains all "higher" forms of life, including those classified in the kingdoms *Protista* (also called *Protoctista*), *Fungi*, *Plantae*, and *Animalia* (animals, including humans). The first three kingdoms are all of interest to the botanist, and typically the organisms in those kingdoms are addressed in the study of botany courses as well as in the general study of biology.

Archaea

The domain *Archaea*, sometimes referred to as the *Archaebacteria*, contains unicellular prokaryotic life-forms and has varied, branched ether-linked lipids, with cell walls made not of peptidoglycan but of glycoproteins and polysaccharides, with no membrane-bound organelles (including no nuclear membrane), with RNA polymerase similar to that found in eukaryotic organisms, with the ability to metabolize methane, and with some introns (nucleotide base sequences in the DNA that do not translate into protein products).

The domain *Archaea* is placed within the kingdom *Monera*, which includes all prokaryotic organisms and consists of a single division or phylum, *Mendosicutes* or *Archaebacteriophyta*. *Archaea* live in

Classification of Life: Domain *Eukarya*

Although there are many methods of classifying life, the system used by the *International Code of Botanical Nomenclature* is one widely accepted system. *Eukarya* is one of the three largest divisions of life, called domains. The other two, *Archaea* and *Bacteria*, consist of cells that lack a nucleus, and most of the life-forms in these two domains are unicellular. *Eukarya* consists of those life-forms made of eukaryotic cells, which possess a nucleus. Most life-forms in *Eukarya* are multicellular, although unicellular eukaryotic life-forms, some of the *Protista*, exist as well. *Eukarya* therefore comprises most life-forms, other than bacteria, that are familiar, including plants and animals. Phyla for three of the four major eukaryotic kingdoms studied by botanists are described here (*Animalia* is excluded).

Kingdom	*Category*	*Species*	*Phylum*
Fungi		33,000	*Ascomycota* (ascomycetes)
		22,500	*Basidiomycota* (basidiosporic fungi)
		800	*Chytridiomycota* (chytrids)
		1,000	*Zygomycota* (zygomycetes)
Plantae	Bryophytes	100	*Anthocerophyta* (hornworts)
		9,500	*Bryophyta* (mosses)
		6,000	*Hepatophyta* (liverworts)
	Seedless vascular plants	1,000	*Lycophyta* (lycophytes)
		2 genera	*Psilotophyta* (psilotophytes)
		11,000	*Pterophyta* (ferns)
		15	*Sphenophyta* (horsetails)
	Gymnosperms	600	*Coniferophyta* (conifers)
		150	*Cycadophyta* (cycads)
		1	*Ginkgophyta* (ginkgoes)
		70	*Gnetophyta* (gnetophytes)
	Angiosperms	235,000	*Anthophyta* (flowering plants: monocots, eudicots, magnoliids)
Protista	Slime molds	700	*Myxomycota* (plasmodial slime molds, myxomycetes)
		50	*Dictyosteliomycota* (cellular slime molds)
	Water molds	700	*Oomycota* (water molds, oomycetes)
	Algae	100,000	*Bacillariophyta* (diatoms)
		17,000	*Chlorophyta* (green algae)
		1,000	*Chrystophyta* (chrysophytes)
		200	*Cryptophyta* (cryptomonads)
		4,000	*Dinophyta* (dinoflagellates)
		1,000	*Euglenophyta* (euglenoids; photosynthetic algae)
		300	*Haptophyta* (haptophytes)
		1,500	*Phaeophyta* (brown algae)
		6,000	*Rhodophyta* (red algae; photosynthetic algae)

extreme environments thought to be similar to conditions present on the primitive earth: in extreme salinity, acidity, thermal, and anaerobic conditions.

Bacteria

The domain *Bacteria*, also placed within he kingdom *Monera* and sometimes referred to as the *Eubacteria* (or "true" bacteria), is unicellular and has unbranched lipids and phospholipids, cell walls with peptidoglycan, no membrane-bound organelles (including no nuclear membrane), and no introns (all the DNA translates into protein product).

The domain *Bacteria* includes three divisions or phyla characterized by their cell walls: division *Graciliutes* contains gram-negative bacteria, division *Firmicutes* contains gram-positive bacteria, and division *Tenericutes* contains bacteria without cell walls.

Graciliutes (prokaryotes with thin cell walls, implying a gram-negative type) is divided into three classes, one of which, *Oxyphotobacteria*, is important in plant science or botany because it contains the oxygen-producing photosynthetic bacteria. *Oxyphotobacteria* can be seen as divided into two other groups, either at the class or division level: the *Cyanobacteria* and the *Chloroxybacteria*. Both groups use chlorophyll *a* in photosynthesis, as do algae and plants proper. The cyanobacteria produce free oxygen as a by-product of photosynthesis, and forms such as *Spirulina* are commercially grown and marketed as high-protein dietary supplements. *Chloroxybacteria* also use chlorophyll *b*, which is restricted to plants and some algae otherwise.

Eukarya

The domain *Eukarya* (sometimes spelled *Eucarya*) has some unicellular and many multicellular forms, unbranched lipids and phospholipids, members both with cell walls (none of which is peptidoglycan but rather cellulose or chitin) and without cell walls, membrane-bound organelles (including the nuclear membrane), and introns. Sexual reproduction is common in this domain, and all kinds of types of life cycles are seen, including complex, haplontic, and alternation of generations.

Eukarya contains the kingdoms *Protista*, *Fungi*, and *Plantae* as well as *Animalia* (which is primarily the province of zoology). These three kingdoms are photosynthetic or heterotrophic by various means, including parasitism and saprotrophy (deriving nutrition from dead or decaying organic matter), and are of interest to the plant scientist because some members of *Protista* and all members of *Fungi* and *Plantae* have cell walls. Cell walls are the single most salient criterion distinguishing plants and plantlike organisms historically. All are nonmotile except for the *Protista*, which has members that move by flagella and cilia.

Kingdoms

In 1969 Dr. R. H. Whittaker, a plant ecologist, proposed the five-kingdom classification system followed by most scientists today. Until then—from the early Greek period and Aristotle until the mid-twentieth century—basically only two kingdoms of life were noted: animals, which were animated (that is, they moved), and plants, which were "planted" (did not move). With the development of light microscopy in the late 1600's, however, it became possible to observe unicellular organisms, and a German scientist, Ernst Haeckel, proposed a third kingdom, the protists. Whittaker put all the work together, and he placed organisms into kingdoms based on whether or not they were prokaryotic or eukaryotic, whether they were unicellular or multicellular, and the types of nutrition. The five kingdoms in Whittaker's system are the *Monera* (including the prokaryotic organisms in domains *Archaea* and *Bacteria*) and four kingdoms of eukaryotic organisms (domain *Eukarya*): *Protista*, *Fungi*, *Plantae*, and *Animalia*.

Protista

The kingdom *Protista* includes plantlike organisms of interest to the botanist: the slime molds, the water molds, and the algae. The following are divisions or phyla in *Protista*: *Myxomycota* (plasmodial slime molds), *Dictosteliomycota* or *Acrasiomycota* (dictyostelids, cellular slime molds), *Oomycota* (biflagellate water molds), *Euglenophyta* (euglenoids), *Cryptophyta* (cryptomonads), *Rhodophyta* (red algae), *Dinophyta* or *Pyrrophyta* (dinoflagellates), *Haptophya* (haptophytes), *Chrysophyta* (chrysophytes, or golden-brown algae), *Bacillariophyta* (diatoms), *Phaeophyta* (brown algae), and *Chlorophyta* (green algae).

Slime Molds. The slime molds and water molds can be classified into four divisions or phyla: *Myxomycota*, *Dictosteliomycota*, *Oomycota*, and *Chytridiomycota*. There is so much diversity within these four phyla that some taxonomists suggest seven divisions instead of the usual four. The slime molds cannot photosynthesize, and they were long considered fungi (indeed, the *Chytridiomycota* are considered fungi in most recent taxonomic treatments; see below under *Fungi*). The cellular slime molds, *Dictosteliomycota*, have about 70 species, characterized by a phagotrophic mode of nutrition, glycogen storage product, cellulosic cell walls, and amoeboid motility. The approximately 500 species of *Myxomycota*, or plasmodial slime molds, lack cell walls, and their motile cells have two whiplash flagella. Both slime molds live in terrestrial habitats.

Water Molds. Water molds, *Oomycota* and *Chytridiomycota*, absorb nutrients and have flagellated motile cells. These two phyla are distinguished by a single flagellum, as in the *Chytridiomycota*, or two flagella, as in the *Oomycota*. The uniflagellate water molds live in freshwater or marine habitats, store glycogen, and have cell walls of chitin or glucan. The biflagellate water molds prefer fresh water only, store glycogen or mycolaminarin (a glucose polymer), and have cell walls of cellulose, chitin, glucan, or a combination of any of these.

Euglenophyta. The 800 or so species of euglenoids and the 100 species of cryptomonads all lack cell walls, and instead their cells are surrounded by a flexible periplast (a plasma membrane with extra inner layers of proteins and with a grainy outer surface).

Rhodophyta. The 670 genera and 2,500 to 6,000 species of red algae, like the brown algae, are mostly marine organisms made up of microscopic filaments or macroscopic forms with complex, leafy branches. The red algae are characterized by the accessory photosynthetic proteinaceous pigments called phycobilins: phycoerythrin, phycocyanin, and allophycocyanins arranged in phycobilisomes. They have no flagella and no centrioles. Floridean starch is a storage product deposited free in the cytoplasm; cells have unstacked thylakoids in plastids and no chloroplast endoplasmic reticulum. Cell walls of red algae are cellulose and pectin mainly, but some form calcium carbonate, too. Photosynthesis in red algae depends on chlorophyll *a*; there is no chlorophyll *b*. Xanthophylls and carotenoids are also present.

Traditionally the red algae are divided into two classes, the *Bangiophyceae* and the *Florideophyceae*. Yet a single class, the *Rhodophyceae* and two subclasses, *Bangiophycidae* and *Florideophycidae*, are also used. The five orders of the red algae include the *Cyanidium*, *Porpyridiales*, *Compsopogonales*, *Bangiales*, and *Florideophyceae*. There are six families. Representative species include *Kallymenia perforata* and *Gibsmithia hawaiiensis*, both from the Philippines and members of *Florideophyceae*, and *Porphyra carolinensis*, from Masonboro Island, North Carolina, a member of the *Bangiales*. Red algae are ecologically significant as primary producers, providers of structural habitat, establishers and maintainers of coral reefs, and providers of food and gels, such as carrageenan from the *Kappaphycus* species, cultured in the Philippines.

***Dinophyta* or *Pyrrophyta*.** The 2,000 species and 130 genera of dinoflagellates also usually lack a cell wall, but most species have armorlike cellulosic plates interior to the plasma membrane. The cell-covering structure, the *theca*, clearly differentiates dinoflagellates from other algal groups, being either armored or not. Unarmored species have a membrane complex. Thecae can be smooth, simple, spiny, pored, grooved, or highly ornamental. Dinoflagellates have a distinctive flagellar arrangement among the unicellular algae, with two lateral flagella, one of which coils around the cell and undulates so the cell spins as it moves forward, and the other trailing like a rudder.

Dinoflagellates are highly varied in reproduction with primary asexual cell division, but some species reproduce sexually, and still others have complex, unusual life cycles. Nutrition is also varied, with autotrophic species (photosynthesis), heterotrophic (absorption of organic matter) species, and mixotrophic members (autotrophic cells engulf other organisms). Certain species of dinoflagellates produce neurotoxins.

Haptophyta. Haptophytes or *Prymnesiophyta* are unicellular and photosynthetic, with 500 species in 50 genera. Some are colonial. Haptophytes have a unique organelle called a haptonema (for which the phylum is named): a peglike structure where two flagella are attached. Reproductive and life histories are poorly understood. Some form toxic blooms, and some produce dimethyl sulfide (DMS). Pigments include diadinoxanthin and fucoxanthin. Genera include *Phaeocystis* and *Emiliania*.

Chrysophyta. Classes of *Chrysophyta* are *Chrysophyceae* (golden-brown algae) and *Xanthophyceae* (yellow-green algae). Chrysophytes are photosynthetic, unicellular organisms abundant in freshwater and marine environments. They have chlorophylls *a* and *c*, masked by the accessory pigment fucoxanthin, a carotenoid. Golden algae are in many ways very similar to the brown algae, storing food outside of the chloroplast in the polysaccharide laminarin or chrysolaminarin. Both brown algae and golden algae have unequal flagella of like form.

Bacillariophyta. *Bacillariophyta*, well known for their glasslike cell walls made of polymerized, opaline silica with ornate ridge patterns, are important components of the phytoplankton as primary sources of food for zooplankton in both marine and freshwater habitats. They are sometimes considered a class along with golden-brown and brown algae in a large, complex phylum called *Heterokontophyta*. Except for male gametes, diatoms lack flagella, but many can move by means of locomotion from secretions in response to outside physical and chemical stimuli. The overlapping shells, called *frustules*, can be used to identify diatom species and have accumulated over millions of years to form the fine, crumbly substance known as diatomaceous earth used in filtration and insulation.

Bacillariophytes number 250 genera and 1,500 species and have brownish plastids with chlorophylls *a* and *c* as well as fucoxanthin. Primary reproduction is asexual, by cell division. Most diatoms are autotrophic, but some must absorb organic carbon because they lack chlorophyll. Some few lack the characteristic frustules and live in symbiosis in large marine protozoa, giving organic carbon to their host.

Phaeophyta. Almost entirely marine, the almost 2,000 species of *Phaeophyta* are common along rocky shores in cold and temperate waters around the globe. The brown accessory pigment fucoxanthin gives the colors to the brown algae from pale beige to yellow-brown to very dark. Phaeophytes store mannitol and a glucose polymer called laminarin. Alginic acid is in the cellulosic cell wall, and motile cells have two lateral flagella. Brown algae are included in the class *Phaeophyceae* with four orders.

Products like ice cream are stabilized with an emulsifier from large kelps. Kelps are also used in fertilizers and are a vitamin-rich food source. *Macrocystis pyrifera*, the giant kelp, makes seaweed forests off the west coast of North America, providing habitat and shelter for many organisms. Genera such as *Sargassum* and *Turbinaria* may dominate in tropical waters, though there are fewer species of brown algae there. *Sargassum* is unique in that it is free-floating, requiring no bottom attachment. Brown algae range in size from microscopic filaments to several meters in length.

Chlorophyta. There are approximately 8,000 species of green algae, with pigments including chlorophylls *a* and *b*, carotenoids, and xanthophylls. These algae appear more than a billion years ago in the fossil record. Like plants, they store starch plants inside *plastids*, contain cellulose in their cell walls, and have motile and nonmotile cells with anywhere between one and about 120 flagella at or near the apex of the cell. *Chlorophyta* can be unicellular, multicellular, or colonial. Most chlorophytes are aquatic, but some live on the surface of snow, on tree trunks, or symbiotically with protozoans, hydras, or lichen-forming fungi.

Halimeda species (calcified green algae) are important contributors of marine sediments, and the clean white sand beaches of the Caribbean Sea and other areas around the world are made up of the calcium-carbonate remains of green algae. An interesting member of this group is the fleshy alga *Johnson-sea-linkia profunda* (Littler et al., 1985), found on bedrock at a depth of 157 meters off the Bahamas.

The class *Chlorophyceae* comprises predominantly freshwater algae that undergo mitosis in a persistent nuclear envelope. The class *Ulvophyceae* comprises predominantly marine organisms that undergo cell division by forming a phragmoplast like that of plants. The class *Charophyceae* includes mostly freshwater species whose nuclear envelopes disintegrate, as do those of plants, as mitosis proceeds.

Fungi

The kingdom *Fungi* is composed of mushrooms, rusts, smuts, puffballs, truffles, morels, molds, and yeasts. These organisms are usually filamentous, eukaryotic, and spore-producing. They generally lack chlorophyll and have a terrestrial origin. Fungi have nonmotile bodies, called *thalli*, made up of apically elongating walled filaments, *hyphae*, which as masses are referred to as *mycelia* (singular, mycelium). The life cycle includes both a sexual and an asexual component. Haploid thalli result from zygotic meiosis. The cell walls are made up of chitin with other complex carbohydrates, including cellulose. The main storage carbohydrate of the fungi (unlike plants) is glycogen, and all species of fungi are either *saprobes* (deriving nutrition from dead and decaying organic matter) or *symbionts* (living with other organisms). Symbionts may be parasitic on a host, provide a benefit to the host, or be parasitized.

The following divisions or phyla in *Fungi* are distinguished by reproductive differences: *Chytridiomycota* (uniflagellate water molds), *Zygomycota* (such as black bread mold, dung fungi, and parasites of amoebas, nematodes, and small animals), *Ascomycota* (such as bread molds, truffles, morels, and ergot), *Basidiomycota* (mushrooms, stinkhorns, puffballs, jelly fungi, smut and rust diseases of plants), *Deuteromycota*, sometimes referred to as "fungi imperfecti" (penicillin mold, root-rot fungus, vaginal yeast fungus, and athlete's foot fungus), and *Mycophycophyta*, or lichens (a division created by L. Margulis and K. V. Schwartz to separate all the organisms with a fungal body or thallus that host green algae or cyanobacteria or both). Yeasts are not a formal taxon but rather are unicellular fungi that reproduce via budding, as seen in *Zygomycota*, *Ascomycota*, or *Basidiomycota*. Lichens are assumed to be mutualistic symbionts with a fungal (mycobiont) and green-algal (photobiont) component. They may be the dominant vegetation in Nordic environments and have been placed in their own division, or phylum, by Margulis and Schwartz, called *Mycophycophyta*.

Mortality-associated human diseases caused by fungi include *Pneumocystis* (a type of pneumonia affecting those with a suppressed immune system), *Coccidioides* (valley fever in the southwestern United States), *Ajellomyces* (blastomycosis and histoplasmosis), and *Cryptococcus* (cryptococcosis). However, fungi are also vital for ecosystems, and they help to flavor and process foods such as baker's yeasts and penicillia in cheese making, as well as producing antibiotics and organic acids. Fungi produce secondary metabolites such as aflatoxin, a potent toxin and carcinogen, and coumadin, which is an anticoagulant used to treat people with heart and arterial diseases.

While at least 100,000 species of fungi are recognized, new species (more than 1,000) are described every year. It is commonly believed by biologists that more than half of all extant fungi have yet to be discovered and named, and estimates of total numbers suggest that 1.5 million species may exist. Fungi are the primary decomposers in the varied natural habitats in which they are found.

Zygomycota. The *Zygomycota*, characterized by zygospores, are in two classes, *Zygomycetes* and *Trichomycetes*, and include about 1,100 species. *Conjugation* or fusion of morphologically similar gametangia (gametangia arising from hyphae to make *zygosporangia* with a thick wall supported on either side by the former gametangia, which are then named *suspensors*) is distinctive in most members of the phylum *Zygomycota*, although by no means universal.

Class *Zygomycetes* has seven orders, thirty families, and about 900 species. Four of those orders are *Mucorales* with thirteen families, fifty-six genera, and 300 species; *Entomophthorales* (as its name implies, these fungi often prey on insects and are of interest for their obvious potential in biological control of insect pests); *Kickxellales* (named after a mycologist named Kickx); and *Glomales* (fungi living in the soil and tentatively identified with the *Zygomycota*, since most do not form the characteristic zygosporangia but have hyphae that enter about 90 percent of all living higher plant root cells, making mutualistic symbioses named mycorrhizae). Included among the zygomycetes are the species *Rhizopus stolonifer* (familiar to most biology students as the ubiquitous bread mold) and the genus *Mucor*.

Trichomycetes is a rather offbeat class of *Zygomycota* in that members of this class live attached to the inner linings of the guts of living arthropods. Though members of this class have the suspensors mentioned above, they do not otherwise resemble the zygomycetes.

Ascomycota. The *Ascomycota* have spore-containing sacs called asci with ascospores and include about 30,000 species. An example of an ascomycete human pathogen is *Coccidioides immitis*, endemic to parts of the southwestern United States. Another ascomycete, *Aspergillus flavus*, produces the aflatoxin that contaminates nuts and stored grains.

Basidiomycota. The *Basidiomycota* produce spores on basidia (club-shaped structures where nuclear fusion and meiosis occur and where the haploid basidiospores are made) and include about 25,000 species. The most conspicuous and familiar basidiomycetes are those that produce mushrooms. Basidiomycetes benefit plants by engaging in symbiotic relationships with their roots, called mycorrhizae, allowing the plant to have increased capabilities to acquire nutrients such as phosphorus. An interesting example of a basidiomycete is *Rigidioporus ulmaris*, with the largest basidiocarp in the world located at the Royal Botanic Gardens in Kew, Surrey, England.

Distinguishing characteristics of *Basidiomycota* are their unique formation of ballistospores (forcibly discharged spores), the club-shaped basidia mentioned above, their dikaryotic mycelia (two nuclei put together in mating, without fusion in the thallus but instead separate, side-by-side, in every cell), their multilayered cell walls, their clamp connections (hyphal branches made while a division of two nuclei occurs in the apical cells), and their positive diazonium blue B reactions (which cause a color change in o-dianisidine, or diazonium blue B, which is not totally unique to the *Basidiomycota* but is nevertheless noted). *Basidiomycota* is divided into three lines or classes: the *Urediniomycetes*, the *Ustilaginomycetes*, and the *Hymenomycetes*.

Deuteromycota. The *Deuteromycota*, which include about 15,000 species, are an artificial group; that is, they form a group on the basis of characteristics other than their evolutionary relationships. They all produce spores asexually or are species not yet classified by sexual reproductive features. An example of a deuteromycete of historical importance is *Penicillium chrysogenum*, known for its production of the antibiotic penicillin, and *Candida albicans*, the cause of thrush, diaper rash, and vaginal yeast infections. Recent comparison of nucleic acid sequences combined with nonsexual phenotypic characters have caused many workers to integrate the asexual fungi into the *Ascomycota*.

Plantae

The kingdom *Plantae* includes multicellular eukaryotes with cellulose-rich walls, chloroplasts with chlorophyll *a* and *b* and carotenoids, and starch as the main food reserve. Most plants reproduce sexually, with alternation of generations. Plants have sporophytes, which make haploid spores via meiosis that grow into gametophytes, which produce gametes that fuse to form the sporophyte again. This cyclic process is termed alternation of generations and is a key characteristic of plants.

The main divisions or phyla of *Plantae* are *Hepatophyta*, *Anthocerotophyta*, *Bryophyta*, *Psilophyta*, *Lycophyta*, *Sphenophyta*, *Pterophyta*, *Cycadophyta*, *Ginkgophyta*, *Coniferophyta*, *Gnetophyta*, and *Anthophyta* or *Magnoliophyta* (the angiosperms). Algae and fungi are *Thallophyta*, as opposed to *Plantae*'s nonvascular bryophytes (which include liverworts, hornworts, and mosses) and vascular plants, or *Embryophyta*. Other terms used, although not formally, are phanerogams (plants with flowers) and cryptogams (plants without flowers).

Hepatophyta. About 9,000 species of hepatophytes, or liverworts, have been named, and they range in size from tiny, leafy filaments smaller than 0.5 millimeter in diameter to plants with a thallus more than 20 centimeters wide.

Hepatophytes have unicellular rhizoids (hair-like extensions that anchor the thallus to a substrate), no cuticle, no specialized conducting tissue (no water-conducting xylem or sugar-conducting phloem), and no stomata (no epidermal pores for gas exchange). Liverworts are the simplest of all living plants, classified in one class, divided into seven orders and twenty-six families.

Anthocerotophyta. Only about 100 species of anthocerotophyes, or hornworts, exist, in six genera, divided between two families in the same class and order. The horn-shaped sporophyte of hornworts (with a diploid structure producing haploid spores via meiosis) gives the name to this division or phylum. An intercalary meristem seeming capable of indefinite growth is associated with the sporophyte, and it has stomata, too. The gametophyte (haploid thallus with sex organs) is thallose (not leafy) and has no specialized conducting tissue and stomata-like structures.

Bryophyta. The bryophytes, or mosses, comprise more than 10,000 species, and they thrive on soil, tree trunks, and shady rock walls. Some mosses have a central strand of conducting cells functionally equal to xylem and phloem, so bryophytes do have a simple type of vascular tissue. Like the hornworts and liverworts, mosses are *homosporous* (producing only one type of spore). Mosses have leafy gametophytes, multicellular rhizoids, and sporophyte stomata. Three classes are recognized: the *Sphagnopsida* (peat mosses), with one order and one family; the *Andreaeopsida* (rock mosses), with one order and one family; and the *Bryopsida* ("true" mosses), with at least twelve orders and nineteen families.

Psilotophyta. The psilotophytes (whiskferns, from the genera *Psilotum* and *Tmesipteris*, in one family, the *Psilotaceae*) are primitive. *Psilotum* has no roots or leaves, similar to the fossil genus *Rhynia*. *Tmesipteris* has aerial shoot structures that are leaflike or foliar. Both genera have compound sporangia (structures that make spores) called synangia, three-parted in *Psilotum*. Both genera have no roots, but the underground stems, the rhizomes, are infected with fungi (mycorrhizae). Dichotomous branching is obvious, especially in the aerial branches of *Psilotum*, and leaflike extensions called enations are seen.

Lycophyta. Club mosses, or lycophytes, come in three families: the *Lycopodiaceae*, the *Selaginellaceae*, and the *Isoetaceae*. They have true leaves, roots, and stems with vascular tissues. The leaves are microphylls (with one vein, not associated with a leaf gap), a defining characteristic of this group. Roots are adventitious. All members of the group are herbaceous except *Isoetes*, which has some secondary growth. Extinct *Lycophyta* are easily seen in the fossil record and apparently made up a large portion of the flora in Carboniferous swamp forests. These nonseed plants are either homosporous or heterosporous (two different types of spores).

Sphenophyta. Horsetails, or *Sphenophyta*, have only one living family, the *Equisetaceae*, and only one genus, the *Equisetum*. Fifteen living species, including *Equisetum arvense* (field horsetail), are known. Horsetails are characterized by shoots with nodes (where leaves come off) and internodes (spaces between nodes), strobili made up of a central axis with spore-bearing structures called sporangiophores, and spores with elators (strands of tissue attached to the spore itself that allow for dispersal of the spores as they spread when they dry). *Sphenophyta* is seen in the Devonian fossil record, and the order *Equisetales* can be dated from the Upper Devonian. Members of the living genus *Equisetum* and extinct members of the *Equisetales* share many anatomical features.

Pterophyta. Ferns are a group of nonseed plants with a fossil record going back to the Lower Devonian. There are about 11,000 living species. They are varied, with true leaves, roots, and stems. Leaves are macrophylls, and many members demonstrate circinate vernation, a pattern of unfolding of a crozierlike structure because of unequal growth. Both heterosporous and homosporous representatives are evident. Spore structure, sporangia, and sori (special structures on the underside of the leaf, or frond, or leaflets or pinnae containing the sporangia) are all important taxonomic features. Examples of families in the *Pterophyta* are *Adiantaceae* (the maidenhair family), *Aspleniaceae* (spleenworts), *Ophioglossaceae* (adder's-tongues), *Polypodiaceae* (the polypodium family), and *Osmundaceae* (the cinnamon fern family).

Cycadophyta. Cycads are seed plants with only three living families: the *Cycadaceae*, the *Stangeriaceae*, and the *Zamiaceae*. They are prominent among Mesozoic fossils, however. They are found in tropical or subtropical climates around the world. Their leaves are pinnately compound and palmlike. There is secondary growth, but no large amounts form. Roots enclose mutualistic cyanobacteria that fix nitrogen. Plants are dioecious (with male and female sex organs appearing on different individuals), and they bear strobili made up of megasporophylls with ovules or microsporophylls with pollen sacs. Pollen makes a pollen tube that is haustorial (parasitic), delivering flagellated sperm to an egg in an archegonium of the female gametophyte.

Ginkgophyta. The ginkgos form a phylum of seed plants represented by only one living species, *Ginkgo biloba*, whose native habitat is restricted to China, where it is probably extinct in the wild. Represented well during the Mesozoic with worldwide distribution, *Ginkgo biloba* is planted ornamentally today and seems tolerant of pollution.

The ginkgo is a deciduous tree, shedding leaves all at once in the fall in temperate zones, with fan-shaped leaves and branches that have spur shoots bearing the reproductive structures. Stems have extensive secondary xylem.

The ginkgos are dioecious trees, with the megasporangiate ("female") trees bearing two ovules at the end of a stalk. Only one ovule usually develops into a mature seed. There is an inner, stony seed coat and an outer, fleshy, fruitlike tissue. Microsporangiate ("male") trees bear reduced strobili or cones that release pollen, or microgametophytes, that are wind-borne. Pollen makes a haustorial tube that delivers flagellated sperm to an egg in an archegonium of the female gametophyte.

Coniferophyta. The conifers are seed plants that produce woody stems. The fossil record shows them from the Upper Carboniferous. There are about 550 species, arranged in seven families: *Pinacea*, *Taxodiaceae*, *Cupressaceae*, *Araucariaceae*, *Podocarpaceae*, *Cephalotaxaceae*, and *Taxaceae*. Some treatments place the conifers in the division *Pinophyta*, or gymnosperms, but as a class, *Pinatae*.

The conifers are noted for their abundant secondary xylem. They grow as trees or shrubs. Trachiary elements in the xylem of conifers include only tracheids, and sieve elements in the phloem include only sieve cells. The leaves of conifers are macrophylls but in most species are reduced as needles or scales.

Conifers are either dioecious or monoecious plants. Microgametophytes (pollen) are produced in microsporangiate strobili (pollen cones), with pollen sacs located on the lower surface. Sperm are not flagellated and are carried directly to egg via pollen tube. All species are wind-pollinated.

Gnetophyta. This phylum has three extant families—the *Ephedraceae*, the *Gnetaceae*, and the *Welwitschiaceae*—and four genera, such as *Ephedra* (Mormon tea). The plants grow as trees, shrubs, lianas, or stumps. Leaves are simple, opposite or whorled, straplike in the genus *Welwitschia*, angiosperm-like in the *Gnetaceae*, or scalelike in the genus *Ephedra*. Flowers are normally dioecious with compound stobili. Female flowers have an erect ovule, a nucellus of two or three coats, and a micropyle projecting as a long tube. The male cone is associated with bracts. Fertilization occurs through pollen tubes with two male nuclei. Some double fertilization is recorded, as in the angiosperms, but this double fertilization is not exactly homologous. Insect pollination is encouraged as a result of cone exudations.

Anthopyta* or *Magnoliophyta. The phylum or division *Anthophyta*, also referred to as the *Magnoliophyta* and commonly as the angiosperms, comprises the flowering plants and consists of about a quarter of a million species. The angiosperms constitute by far the largest phylum of plants and have traditionally been divided into two main classes. The class *Magnoliopsida*, the dicots, consists of about 180,000 species with two seed leaves, or cotyledons; netted venation in the leaves; flower parts in fours and fives and multiples thereof; primary vascular bundles in a ring in the stem; and a vascular cambium to produce true secondary growth in many species. The class *Liliopsida*, the monocots, consist of about 80,000 species with one seed leaf, or cotyledon, parallel venation, flower parts in threes, primary vascular bundles scattered in the stem, and no vascular cambium to produce true secondary growth. However, this division into two classes, monocots and dicots, is challenged now. Recently, the angiosperms have been divided into the eudicots ("true" dicots, or *Dicotyledones*) and the monocots (or *Monocotyledones*), with a small number of species (about 3 percent) relegated to the category of magnoliids.

Land plants date back in the fossil record only to the early Cretaceous period, and *Magnoliophyta* is now the dominant plant group in most biomes (biogeographic groups shaped by climate, topography, and soils). This dominance is due to vegetative and reproductive structures and functions uniquely adapted to a terrestrial existence.

Vegetative Characteristics. Members of the *Magnoliophyta*, or *Anthophyta*, vary in size from tiny aquatic duckweed to extremely large forest trees. Flowering plants have many *habits* (forms) and *niches* (lifestyles) and are annuals, biennials, perennials, woody trees and shrubs, herbaceous plants, vines, carnivorous plants, parasites, epiphytes, succulents, and saprophytes. Vessel elements making up the xylem are common in this phylum, and leaves are broad and have complex venation patterns.

Reproduction. True flowers are interpreted as a modified shoot or a reduced compound strobilus. Floral elements are sepals, petals, stamens, pistils, and carpels. Ovules within megasporophylls are fused into an ovary (carpels). Pollination (movement of microgametophyte or pollen to a receptive surface of pistil or stigma) can be effected by wind, water, gravity, animal vectors (such as insects, birds, and bats), but self-pollination and asparthenogenesis (fruit production without fertilization) are also common. Double fertilization is evident in all members of this group: Two sperm nuclei are present in the pollen, one fusing with the egg to form the new embryo and the other fusing with the embryo sac nuclei to form the endosperm. The endosperm is the stored food tissue for the embryonic plant until it can photosynthesize or obtain food on its own through saprophytic or parasitic (haustorial) means. Seeds are distributed by all sorts of fruits (developed ovary tissue), such as follicles, berries, drupes, capsules, and legumes.

F. Christopher Sowers

See also: *Plantae*; Systematics and taxonomy; Systematics: overview.

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PLANT NAMES: COMMON-TO-SCIENTIFIC

Most people use common names for plants. Common names are usually easier to spell, pronounce, and remember than are the more precise and standardized binomial scientific genus and species names. However, there are no rules for the use of common plant names, and that leads to some problems. Many plants have more than one common name in different parts of the country, in different parts of the world, and sometimes between next-door neighbors. Another problem with common plant names is that some are so convenient, they are used inaccurately to describe more than one type of plant. The third problem with common plant names is that they are given to plants that people find interesting, useful, or familiar; many unfamiliar plants therefore do not receive common names. Therefore, some plants have too many common names, and some common names are used too often, whereas some plants do not have common names.

The following table lists, in alphabetical order by common name (left-hand column), some of the more common organisms studied by scientists, including not only plants (kingdom *Plantae*) but also some of the more important members of the kingdoms *Archaea*, *Bacteria*, *Fungi*, and *Protista*. Where more than one very common name exists, the organisms below are listed under both or all common names. To learn more about the taxonomy and special characteristics of a plant, please look it up under its scientific name in the appendix that follows this one, titled "Plant Names: Scientific-to-Common." Those interested in the taxonomic arrangement of organisms may also wish to consult the appendix in this volume headed "Plant Classification."

William B. Cook

Common Name	Scientific Name
Acacia, catclaw	*Acacia greggii*
Acetobacter	*Acetobacter* spp.
Acne pathogen	*Propionibacterium acnes*
Actinomycete	*Frankia* spp.
Aflatoxin fungus	*Aspergillus flavus*
African violet	*Saintpaulia ionantha*
Agaric, red-gilled	*Melanophyllum echinatum*
Agave, tequila	*Agave tequilana*
Agrobacterium	*Agrobacterium tumefaciens*
Alaska cedar	*Chamaecyparis nootkatensis*
Alder, red	*Alnus rubra*
Alder, Sitka	*Alnus sinuata*
Alfalfa	*Medicago sativa*
Algae, brown	*Elachista* spp.
Algae, brown	*Laminaria* spp.
Algae, brown	*Padina* spp.
Algae, brown	*Streblonema* spp.
Algae, coralline red	*Porolithon craspedium*
Algae, golden brown	*Chrysamoeba* spp.
Algae, golden brown	*Dinobryon* spp.
Algae, golden brown	*Paraphysomonas* spp.
Algae, golden brown	*Uroglenopsis* spp.
Algae, green	*Phycopeltis* spp.
Algae, green	*Ulothrix* spp.
Algae, green	*Ulva* spp.
Algae, green	*Ulvaria* spp.
Algae, red	*Bangia* spp.
Algae, red	*Cyanidium* spp.
Algae, red	*Dasya* spp.
Algae, red	*Gelidium* spp.
Algae, red	*Gracilaria* spp.
Algae, red	*Porphyra* spp.
Algae, red tide	*Gonyaulax tamarensis*
Allegheny serviceberry	*Amelanchier laevis*
Allspice	*Pimenta dioica*
Almond	*Prunus dulcis*
Aloe vera	*Aloe vera*
Alum root	*Heuchera sanguinea*
Aluminum plant	*Pilea cadierei*
Amaranth, globe	*Gomphrena globosa*
American basswood	*Tilia americana*
American beautyberry	*Callicarpa americana*
American beech	*Fagus grandifolia*
American chestnut	*Castanea dentata*
American elder	*Sambucus canadensis*
American elm	*Ulmus americana*
American ginseng	*Panax quinquefolius*
American holly	*Ilex opaca*
American hornbeam	*Carpinus caroliniana*
American pasque flower	*Pusatilla hirsutissima*
American plum	*Prunus americana*
American sycamore	*Platanus occidentalis*

Common Name	Scientific Name
American wild rice	*Zizania aquatica*
Anemone smut	*Urocystis anemones*
Angelica	*Angelica archangelica*
Anise	*Pimpinella anisum*
Anise, star	*Illicium verum*
Anthrax pathogen	*Bacillus anthracis*
Anthurium	*Anthurium andraeanum*
Apache plume	*Fallugia paradoxa*
Appendaged bacterium	*Caulobacter crescentus*
Apple	*Malus x domesticus*
Apple, custard	*Annona reticulata*
Apple, may	*Podophyllum peltatum*
Apple, star	*Chrysophyllum cainito*
Apple scab pathogen	*Enturia inaequalis*
Applemint	*Mentha suaveolens*
Apricot	*Prunus armeniaca*
Apricot jelly	*Phlogiotis helvelloides*
Aquatic moss	*Hygrohypnum bestii*
Arabian jasmine	*Jasminum sambac*
Arbor-vitae, Chinese	*Thuja orientalis*
Arbutus, trailing	*Epigaea repens*
Arizona cypress	*Cupressus arizonica*
Artichoke, globe	*Cynara scolymus*
Artichoke, Jerusalem	*Helianthus tuberosus*
Ash, common prickly	*Zanthoxylum americana*
Ash, European mountain	*Sorbus aucuparia*
Ash, green	*Fraxinus pennsylvanica*
Ash, white	*Fraxinus americana*
Ashy coral mushroom	*Clavulina cinerea*
Asparagus	*Asparagus officinalis*
Aspen, quaking	*Populus tremuloides*
Atlas cedar	*Cedrus atlantica*
Australian tree fern	*Cyathea cooperi*
Austrian pine	*Pinus nigra*
Avocado	*Persea americana*
Azalea	*Rhododendron* spp.
Azospirillum	*Azospirillum* spp.
Baby blue-eyes	*Nemophila menziesii*
Baby's breath	*Gypsophila paniculata*
Bachelor's button	*Centaurea cyanus*
Bacteria: acne pathogen	*Propionibacterium acnes*
Bacteria: agrobacterium	*Agrobacterium tumefaciens*
Bacteria: appendaged	*Caulobacter crescentus*
Bacteria: cyanobacterium	*Anabaena cylindrica*
Bacteria: extreme halophile	*Halobacterium halobium*
Bacteria: gliding	*Cytophaga hutchinsonii*
Bacteria: iron	*Thiobacillus ferrooxidans*
Bacteria: lactic acid	*Lactobacillus* spp.
Bacteria: leprosy pathogen	*Mycobacterium leprae*
Bacteria: purple nonsulfur	*Rhodospirillum rubrum*
Bacteria: sulfur	*Desulfovibrio* spp.
Bakers' yeast	*Saccharomyces cerevisiae*
Bald cypress	*Taxodium distichum*
Balloon flower	*Platycodon grandiflorus*
Balsa	*Ochroma pyrmidale*
Banana	*Musa x paradisiaca*
Banana, finger	*Musa acuminata*
Baobab	*Adansonia digitata*
Barberry, common	*Berberis vulgaris*
Basswood, American	*Tilia americana*
Bay laurel	*Laurus nobilis*
Bdellovibrio	*Bdellovibrio bacteriovorus*
Bean, castor	*Ricinus communis*
Bean, fava	*Vicia faba*
Bean, kidney	*Phaseolus vulgaris*
Bean, lima	*Phaseolus lunatus*
Bean, mung	*Vigna radiata*
Bean, scarlet runner	*Phaseolus coccineus*
Bean, string	*Phaseolus vulgaris*
Bearberry	*Arctostaphylos uva-ursi*
Beard tongues	*Penstemon* spp.
Beautyberry, American	*Callicarpa americana*
Bedstraw	*Galium aparine*
Beech, American	*Fagus grandifolia*
Beech, European	*Fagus sylvatica*
Beet	*Beta vulgaris*
Beet, sugar	*Beta vulgaris*
Begonia, smooth-leaf	*Begonia semperflorens*
Begonia, tuberous	*Begonia tuberhybrida*
Belladonna lily	*Amaryllis belladonna*
Bells of Ireland	*Moluccella laevis*
Bent grass, creeping	*Agrostis stolonifera*
Betel	*Piper betel*
Betel nut palm	*Areca catechu*
Big laurel	*Rhododendron maximum*
Big sagebrush	*Artemisia tridentata*
Bigleaf maple	*Acer macrophyllum*
Birch, paper	*Betula papyrifiera*
Birch, river	*Betula nigra*
Birch, yellow	*Betula alleghaniensis*
Birch rust	*Melampsoridium betulinum*
Bird of paradise	*Caesalpinia gilliesii*
Bird of paradise	*Strelitzia reginae*
Bird's eyes	*Gilia tricolor*
Bird's foot violet	*Viola pedata*
Bird's-nest fern	*Asplenium nidus-avis*
Bird's-nest fungus	*Crucibulum laeve*
Bitternut hickory	*Carya cordiformis*
Bitterroot	*Lewisia rediviva*
Black bread mold	*Rhizopus stolonifer*
Black cherry	*Prunus serotina*
Black cottonwood	*Populus trichocarpa*
Black currant	*Ribes nigrum*
Black-eyed pea	*Vigna unguiculata*
Black-eyed Susan	*Rudbeckia hirta*
Black-eyed Susan vine	*Thunbergia alata*

Common Name	Scientific Name
Black hawthorn	*Crataegus douglasii*
Black Hills spruce	*Picea glauca*
Black locust	*Robinia pseudoacacia*
Black mangrove	*Avicennia nitida*
Black oak	*Quercus velutina*
Black raspberry	*Rubus occidentalis*
Black spruce	*Picea mariana*
Black stem rust	*Puccinia graminis*
Black tupelo	*Nyssa sylvatica*
Black walnut	*Juglans nigra*
Black willow	*Salix nigra*
Blackberry	*Rubus* spp.
Blackfoot daisy	*Melampodium leucanthum*
Blackjack oak	*Quercus marilandica*
Blanket flower	*Gaillardia pulchella*
Blazing star	*Mentzelia decapetala*
Bleeding heart	*Dicentra spectabilis*
Blight, potato	*Phytophthora infestans*
Bloodleaf	*Iresine herbstii*
Bloodroot	*Sanguinaria canadensis*
Blue-eyed grass	*Sisyrinchium bellum*
Blue grass, Kentucky	*Poa pratensis*
Blue spruce	*Picea pungens*
Blue thimble flower	*Gilia capitata*
Blueberry, highbush	*Vaccinium corymbosum*
Blueberry, lowbush	*Vaccinium angustifolium*
Bluebonnet	*Lupinus texensis*
Bolete, king	*Boletus edulis*
Boston fern	*Nephrolepis exaltata*
Botulism pathogen	*Clostridium botulinum*
Bougainvillea	*Bougainvillea spectabilis*
Box elder	*Acer negundo*
Bracken fern	*Pteridium aquilinum*
Brazil nut	*Bertholletia excelsa*
Breadfruit	*Artocarpus altilis*
Brewers' yeast	*Saccharomyces cerevisiae*
Bristlecone pine	*Pinus aristata*
British soldiers	*Cladonia cristatella*
Broccoli	*Brassica oleracea*
Broom, Scotch	*Cytisus scoparius*
Broomrape	*Orobanche* spp.
Broomweed	*Gutierrezia dracunculoides*
Brown algae	*Elachista* spp.
Brown algae	*Laminaria* spp.
Brown algae	*Padina* spp.
Brown algae	*Streblonema* spp.
Brown rot pathogen	*Monilinia fructicola*
Brussels sprouts	*Brassica oleracea*
Buckeye, Ohio	*Aesculus glabra*
Buckthorn, Carolina	*Rhamnus caroliniana*
Buckthorn, cascara	*Rhamnus purshiana*
Buckwheat	*Fagopyrum esculentum*
Buddhist pine	*Podocarpus macrophyllus*
Buffalo grass	*Buchloe dactyloides*

Common Name	Scientific Name
Bull kelp	*Nereocystis leutkeana*
Bull thistle	*Cirsium vulgare*
Bulrush, low	*Scirpus cernuus*
Bunt fungus	*Tilletia caries*
Bur oak	*Quercus marcocarpa*
Burmuda grass	*Cynodon dactylon*
Butterfly bush	*Buddleja davidii*
Butterfly weed	*Asclepias tuberosa*
Buttonbush, common	*Cephalanthus occidentalis*
Cabbage	*Brassica oleracea*
Cabbage palmetto	*Sabal palmetto*
Cactus, saguaro	*Carnegiea gigantea*
California hazel	*Corylus cornuta*
California nutmeg	*Torreya californica*
California pitcher plant	*Darlingtonia californica*
California poppy	*Eschscholzia californica*
Calliopsis	*Coreopsis tinctoria*
Camas	*Camassia quamash*
Camellia	*Camellia japonica*
Camphor tree	*Cinnamomum camphora*
Canada thistle	*Cirsium arvense*
Candle snuffer mosses	*Encalypta* spp.
Candlenut tree	*Aleurites moluccana*
Canna lily	*Canna indica*
Cannonball tree	*Couroupita guianensis*
Canteloupe	*Cucumis melo*
Canterbury bell	*Campanula medium*
Cape primrose	*Streptocarpus* spp.
Caper	*Capparis spinosa*
Carambola	*Averrhoa carambola*
Caraway	*Carum carvi*
Carbon antlers	*Xylaria hypoxylon*
Carbon balls	*Daldina concentrica*
Cardamom	*Elettaria cardamomum*
Cardinal flower	*Lobelia cardinalis*
Carnation	*Dianthus caryophyllus*
Carob	*Ceratonia siliqua*
Carolina buckthorn	*Rhamnus caroliniana*
Carpetweed	*Mollugo verticillata*
Carrion flower	*Stapelia variegata*
Carrot	*Daucus carota*
Cascara buckthorn	*Rhamnus purshiana*
Cashew	*Anacardium occidentale*
Cassava	*Manihot esculenta*
Cast-iron plant	*Aspidistra elatior*
Castor bean	*Ricinus communis*
Catalpa, southern	*Catalpa bignonioides*
Catbrier	*Smilax bona-nox*
Catclaw acacia	*Acacia greggii*
Catnip	*Nepeta cataria*
Cattail	*Typha latifolia*
Cauliflower	*Brassica oleracea*
Cecropia	*Cecropia peltata*

Common Name	Scientific Name
Cedar, Alaska	*Chamaecyparis nootkatensis*
Cedar, atlas	*Cedrus atlantica*
Cedar, deodar	*Cedrus deodara*
Cedar, ground	*Lycopodium complanatum*
Cedar, incense	*Libocedrus decurrens*
Cedar, northern white	*Thuja occidentalis*
Cedar, Port-Orford	*Chamaecyparis lawsoniana*
Cedar, western red	*Thuja plicata*
Cedar elm	*Ulmus crassifolia*
Celeriac	*Apium graveolens*
Celery	*Apium graveolens*
Cellular slime mold	*Dictyostelium discoideum*
Century plant	*Agave americana*
Chain tree, golden	*Laburnum anagyroides*
Chamomile	*Anthemis nobilis*
Chanterelle	*Cantharellus cibarius*
Chard	*Beta vulgaris*
Chaste tree	*Vitex agnus-castus*
Cheese mold	*Penicillium roqueforti*
Chenille plant	*Acalpha hispida*
Cherimoya	*Annona cherimola*
Cherokee rose	*Rosa sinica*
Cherry, black	*Prunus serotina*
Cherry, common choke	*Prunus virginiana*
Cherry, sweet	*Prunus avium*
Chervil	*Anthricus cerefolium*
Chestnut, American	*Castanea dentata*
Chestnut, horse	*Aesculus hippocastanum*
Chestnut, water	*Eleocharis dulcis*
Chickasaw plum	*Prunus angustifolia*
Chicken mushroom	*Laetiporus sulphureus*
Chickory	*Cichorium intybus*
Chickpea	*Cicer arietinum*
Chickweed	*Stellaria media*
China berry	*Melia azedarach*
Chinese arbor-vitae	*Thuja orientalis*
Chinese lotus	*Nelumbo nucifera*
Chinese photinia	*Photinia serrulata*
Chinkapin oak	*Quercus muehlenbergii*
Chives	*Allium schoenoprasum*
Chlamydomonas	*Chlamydomonas* spp.
Christmas fern	*Polystichum acrostichoides*
Chytrid	*Allomyces macrogynus*
Chytrid	*Olpidium brassicae*
Chytrid	*Physoderma alfalfae*
Chytrid	*Rozella allomycis*
Cilantro	*Coriander sativum*
Cinnamon	*Cinnamomum zeylanicum*
Cinnamon fern	*Osmunda cinnamomea*
Cleavers	*Galium aparine*
Cliff brake	*Pellaea* spp.
Climbing fern	*Lygodium japonicum*
Clove	*Syzygium aromaticum*
Clover, crimson	*Trifolium incarnatum*

Common Name	Scientific Name
Clover, red	*Trifolium pratense*
Clover, white	*Trifolium repens*
Clover, white sweet	*Melilotus albus*
Clover-leaf ferns	*Marsilea* spp.
Coast redwood	*Sequoia sempervirens*
Coca	*Erythroxylum coca*
Cocklebur	*Xanthium strumarium*
Cocoa	*Theobroma cacao*
Coconut palm	*Cocos nucifera*
Coffee	*Coffea arabica*
Coffee	*Coffea canephora*
Coffee tree, Kentucky	*Gymnocladus dioica*
Coleus	*Coleus hybridus*
Collards	*Brassica oleracea*
Columbine, Rocky Mountain	*Aquilegia caerulea*
Columbine, western	*Aquilegia formosa*
Comb tooth	*Hericium ramosum*
Comfrey	*Symphytum officinale*
Common barberry	*Berberis vulgaris*
Common buttonbush	*Cephalanthus occidentalis*
Common choke cherry	*Prunus virginiana*
Common daylily	*Hemerocallis fulva*
Common fig	*Ficus carica*
Common hop tree	*Ptelea trifoliata*
Common horsetail	*Equisetum arvense*
Common juniper	*Juniperus communis*
Common persimmon	*Diospyros virginiana*
Common prickly ash	*Zanthoxylum americana*
Common scouring rush	*Equisetum hyemale*
Compact spike moss	*Selaginella densa*
Coneflower, purple	*Echinacea purpurea*
Coral bells	*Heuchera sanguinea*
Coralbean, eastern	*Erythrina herbacea*
Coralline red algae	*Porolithon craspedium*
Coriander	*Coriander sativum*
Corn	*Zea mays*
Corn smut	*Ustilago maydis*
Cotton	*Gossypium hirsutum*
Cottonwood, black	*Populus trichocarpa*
Cottonwood, eastern	*Populus deltoides*
Cottonwood, plains	*Populus sargentii*
Coulter pine	*Pinus coulteri*
Cowpea	*Vigna unguiculata*
Crabapple, southern	*Malus angustifolia*
Cramp balls	*Daldina concentrica*
Cranberry	*Vaccinium macrocarpon*
Crape myrtle	*Lagerstroemia indica*
Creeping bent grass	*Agrostis stolonifera*
Creeping thyme	*Thymus serpyllum*
Creosote bush	*Larrea tridentata*
Cress	*Lepidium sativum*
Crimped gill	*Plicaturopsis crispa*
Crimson clover	*Trifolium incarnatum*

Common Name	Scientific Name
Crocus, saffron	*Crocus sativus*
Crown of thorns	*Euphorbia splendens*
Cryptomonads	*Chilomonas* spp.
Cryptomonads	*Chroomonas* spp.
Cryptomonads	*Chroomonas lacustris*
Cryptomonads	*Cryptomonas* spp.
Cryptomonads	*Cryptomonas undulata*
Cryptomonads	*Goniomonas* spp.
Cryptomonads	*Rhodomonas* spp.
Cucumber	*Cucumis sativus*
Cumin	*Cuminum cyminum*
Currant, black	*Ribes nigrum*
Currant, golden	*Ribes aureum*
Custard apple	*Annona reticulata*
Cyanobacteria	*Anabaena cylindrica*
Cycad	*Zamia floridana*
Cypress, Arizona	*Cupressus arizonica*
Cypress, bald	*Taxodium distichum*
Cypress, Monterey	*Cupressus macrocarpa*
Daisy, blackfoot	*Melampodium leucanthum*
Daisy, Transvaal	*Gerbera jamesonii*
Damping-off pathogen	*Pythium* spp.
Dandelion	*Taraxacum officinale*
Dark leaf spot pathogen	*Alternaria brassicicola*
Date palm	*Phoenix dactylifera*
Dawn redwood	*Metasequoia glyptostroboides*
Day flower	*Commelina communis*
Daylily, common	*Hemerocallis fulva*
Dead man's fingers	*Xylaria polymorpha*
Death camas	*Zigadenus venenosus*
Death cap	*Amanita phalloides*
Deer fern	*Blechnum spicant*
Deodar cedar	*Cedrus deodara*
Desertwillow	*Chilopsis linearis*
Desmid	*Xanthidium armatum*
Devil's backbone	*Pedilanthes tithymaloides*
Devil's walking stick	*Aralia spinosa*
Diatoms	*Chaetoceros* spp.
Diatoms	*Navicula* spp.
Diatoms	*Nitzschia* spp.
Diatoms	*Thalassiosira pseudonana*
Diatoms	*Triceratium* spp.
Dill	*Anethum graveolens*
Dinoflagellates	*Dinophysis* spp.
Dinoflagellates	*Gymnodinium* spp.
Dinoflagellates	*Ornithocercus* spp.
Dinoflagellates	*Symbiodinium* spp.
Dodder	*Cuscuta* spp.
Dogwood, flowering	*Cornus florida*
Dogwood, red-osier	*Cornus stolonifera*
Douglas fir	*Pseudotsuga menziesii*
Downy hawthorn	*Crataegus mollis*
Dracaena	*Dracaena marginata*

Common Name	Scientific Name
Dragon tree	*Dracaena draco*
Duckweed	*Lemna gibba*
Dulse	*Palmaria palmata*
Dumbcane	*Dieffenbachia amoena*
Dunaliella	*Dunaliella* spp.
Dung mosses	*Splachnum* spp.
Durian	*Durio zibethinus*
Dusty miller	*Senecio cineraria*
Dutch elm disease pathogen	*Ophiostoma ulmi*
Dutchman's pipe	*Aristolochia durior*
E. coli	*Escherichia coli*
Earth tongue, velvety	*Trichoglossom hirsutum*
Earthball	*Scleroderma aurantium*
Earthstar, rounded	*Geastrum saccatum*
East Indian pitcher plant	*Nepenthes reinwardtiana*
Eastern coralbean	*Erythrina herbacea*
Eastern cottonwood	*Populus deltoides*
Eastern hemlock	*Tsuga canadensis*
Eastern red cedar	*Juniperus virginiana*
Eastern wahoo	*Euonymus atropurpureus*
Eastern white pine	*Pinus strobus*
Ebony spleenwort	*Asplenium platyneuron*
Eelgrass	*Zostera maritima*
Eggplant	*Solanum melanogena*
Elder, American	*Sambucus canadensis*
Elder, box	*Acer negundo*
Elephant's ear	*Alocasia macrorrhiza*
Elf cup	*Tarzetta cupularis*
Elm, American	*Ulmus americana*
Elm, cedar	*Ulmus crassifolia*
Elm, slippery	*Ulmus rubra*
Elodea	*Elodea canadensis*
Endive	*Chicorium endiva*
Engelmann spruce	*Picea engelmannii*
English ivy	*Hedera helix*
English walnut	*Juglans regia*
Entoloma, salmon unicorn	*Entoloma salmoneum*
Ergot	*Claviceps purpurea*
Eucalyptus	*Eucalyptus regnans*
Euglenoids	*Euglena* spp.
Euglenoids	*Eutreptia pertyi*
Euglenoids	*Phacus helikoides*
Euglenoids	*Trachelomonas grandis*
Euonymus, winged	*Euonymus elata*
European beech	*Fagus sylvatica*
European mountain ash	*Sorbus aucuparia*
Evening primrose	*Oenothera biennis*
Extreme halophile	*Halobacterium halobium*
Fairy ring mushroom	*Marasmius oreades*
Fava bean	*Vicia faba*
Feather mosses	*Thuidium* spp.

Common Name	Scientific Name
Fennel, florentine	*Foeniculum vulgare*
Fenugreek	*Trigonella foenum-graecum*
Fern, Australian tree	*Cyathea cooperi*
Fern, bird's-nest	*Asplenium nidus-avis*
Fern, Boston	*Nephrolepis exaltata*
Fern, bracken	*Pteridium aquilinum*
Fern, Christmas	*Polystichum acrostichoides*
Fern, cinnamon	*Osmunda cinnamomea*
Fern, climbing	*Lygodium japonicum*
Fern, clover-leaf	*Marsilea* spp.
Fern, deer	*Blechnum spicant*
Fern, grape	*Botrychium* spp.
Fern, Hawaiian tree	*Cibotium glaucum*
Fern, lady	*Athyrium filix-femina*
Fern, licorice	*Polypodium glycyrrhiza*
Fern, lip	*Cheilanthes* spp.
Fern, maidenhair	*Adiantum capillus-veneris*
Fern, mosquito	*Azolla* spp.
Fern, ostrich	*Matteuccia struthiopteris*
Fern, resurrection	*Polypodium polypodioides*
Fern, royal	*Osmunda regalis*
Fern, sensitive	*Onoclea sensibilis*
Fern, staghorn	*Platycerium bifurcatum*
Fern, Tasmanian tree	*Dicksonia antarctica*
Fern, walking	*Asplenium rhizophyllum*
Fern, wood	*Dryopteris* spp.
Fescue, tall	*Festuca arundinacea*
Feverfew	*Tanacetum parthenium*
Fiddle-leaf fig	*Ficus lyrata*
Field bindweed	*Convolvulus arvensis*
Fig, common	*Ficus carica*
Fig, fiddle-leaf	*Ficus lyrata*
Fig, Florida strangler	*Ficus aurea*
Fig, weeping	*Ficus benjamina*
Filbert	*Corylus maxima*
Finger banana	*Musa acuminata*
Fir, Douglas	*Pseudotsuga menziesii*
Fir, grand	*Abies grandis*
Fir, noble	*Abies procera*
Fir, subalpine	*Abies lasiocarpa*
Fir, white	*Abies concolor*
Fir moss	*Huperzia lucidula*
Fireweed	*Epilobium angustifolium*
Fishtail palm	*Caryota urens*
Flamboyant tree	*Delonix regia*
False Solomon's seal	*Smilacina racemosa*
Flax	*Linum usitatissimum*
Florentine fennel	*Foeniculum vulgare*
Florida silverpalm	*Coccothrinax argentata*
Florida strangler fig	*Ficus aurea*
Flowering dogwood	*Cornus florida*
Flowering maple	*Abutilon hybridum*
Fly agaric	*Amanita muscaria*
Flytrap, Venus's	*Dionaea muscipula*

Common Name	Scientific Name
Foolish seedling pathogen	*Gibberella fujikuroi*
Forget-me-not	*Myosotis alpestris*
Forsythia, weeping	*Forsythia suspensa*
Four-o'clock	*Mirabilis jalapa*
Foxglove	*Digitalis purpurea*
Foxtail millet	*Setaria italica*
Frankincense	*Boswellia carteri*
Fuchsia	*Fuchsia hybrida*
Fungus, aflatoxin	*Aspergillus flavus*
Fungus, bird's-nest	*Crucibulum laeve*
Fungus, bunt	*Tilletia caries*
Fungus, hemlock varnish shelf	*Ganoderma tsugae*
Fungus, lasso	*Arthrobotrys anchonia*
Fungus, mycorrhizal	*Glomus pansihalos*
Fungus, nematicidal	*Dactylaria candida*
Fungus, stinking smut	*Tilletia caries*
Garden geranium	*Pelargonium hortorum*
Garden pea	*Pisum sativum*
Garden verbena	*Verbena hybrida*
Garlic	*Allium sativum*
Gaura	*Gaura lindheimeri*
Gayfeather	*Liatris spicata*
Gentian, prairie	*Eustoma exaltatum*
Geranium, garden	*Pelargonium hortorum*
Gherkin	*Cucumis anguria*
Giant blue iris	*Iris giganticaerulea*
Giant kelp	*Macrocystis pyrifera*
Giant protea	*Protea cynaroides*
Giant pumpkin	*Cucurbita maxima*
Giant sequoia	*Sequoiadendron giganteum*
Gilia	*Ipomopsis rubra*
Ginger	*Zingiber officinale*
Ginkgo	*Ginkgo biloba*
Ginseng, American	*Panax quinquefolius*
Gliding bacterium	*Cytophaga hutchinsonii*
Globe amaranth	*Gomphrena globosa*
Globe artichoke	*Cynara scolymus*
Gloriosa lily	*Gloriosa rothschildiana*
Gloxinia	*Sinningia speciosa*
Goathead	*Tribulus terrestris*
Goat's beard	*Tragopogon dubius*
Golden brown algae	*Chrysamoeba* spp.
Golden brown algae	*Dinobryon* spp.
Golden brown algae	*Paraphysomonas* spp.
Golden brown algae	*Uroglenopsis* spp.
Golden chain tree	*Laburnum anagyroides*
Golden waxy cap	*Hygrophorus flavescens*
Goldenseal	*Hydrastis canadensis*
Golden currant	*Ribes aureum*
Gooseberry	*Ribes grossularia*
Grand fir	*Abies grandis*
Granite mosses	*Andreaea* spp.

Common Name	Scientific Name
Grape	*Vitis vinifera*
Grape, Oregon	*Mahonia aquifolium*
Grape fern	*Botrychium* spp.
Grape hyacinth	*Muscari neglectum*
Grape ivy	*Cissus rhombifolia*
Grapefruit	*Citrus paradisi*
Green algae	*Phycopeltis* spp.
Green algae	*Ulothrix* spp.
Green algae	*Ulva* spp.
Green algae	*Ulvaria* spp.
Green ash	*Fraxinus pennsylvanica*
Ground cedar	*Lycopodium complanatum*
Guava	*Psidium guajava*
Gumbo-limbo	*Bursera simarouba*
Hackberry	*Celtis occidentalis*
Hairy corn salad	*Valerianella amarella*
Hairy vetch	*Vicia villosa*
Halophile, extreme	*Halobacterium halobium*
Haptophytes	*Chrysochromulina* spp.
Haptophytes	*Emiliania huxleyi*
Haptophytes	*Pavlova* spp.
Haptophytes	*Phaeocystis* spp.
Haptophytes	*Pleurochrysis* spp.
Hart's tongue	*Phyllitis scolopendrium*
Hawaiian tree fern	*Cibotium glaucum*
Hawthorn, black	*Crataegus douglasii*
Hawthorn, downy	*Crataegus mollis*
Hawthorn, littlehip	*Crataegus spathulata*
Hawthorn, red	*Crataegus* spp.
Hazel, California	*Corylus cornuta*
Helicobacterium	*Helicobacter pylori*
Hemlock, eastern	*Tsuga canadensis*
Hemlock, poison	*Conium maculata*
Hemlock, water	*Cicuta maculata*
Hemlock varnish shelf fungus	*Ganoderma tsugae*
Hemp	*Cannabis sativa*
Hemp, Manila	*Musa textilis*
Hen and chickens	*Sempervivum tectorum*
Hen-of-the-woods	*Grifola frondosa*
Henbit	*Lamium amplexicaule*
Hibiscus	*Hibiscus rosa-sinensis*
Hickory, bitternut	*Carya cordiformis*
Hickory, shagbark	*Carya ovata*
Highbush blueberry	*Vaccinium corymbosum*
Hog plum	*Ximenia americana*
Holly, American	*Ilex opaca*
Hollyhock	*Althaea rosea*
Honey locust	*Gleditsia triacanthos*
Honeysuckle	*Lonicera japonica*
Hop tree, common	*Ptelea trifoliata*
Hophornbeam	*Ostrya virginiana*
Hops	*Humulus lupulus*

Common Name	Scientific Name
Horehound	*Marrubium vulgare*
Hornbeam, American	*Carpinus caroliniana*
Hornworts	*Anthoceros* spp.
Hornworts	*Dendroceros* spp.
Horse chestnut	*Aesculus hippocastanum*
Horseradish	*Armoracia rusticana*
Horsetail, common	*Equisetum arvense*
Horsetail, wood	*Equisetum sylvaticum*
Hyacinth, grape	*Muscari neglectum*
Hyacinth, water	*Eichhornia crassipes*
Hydrangea	*Hydrangea macrophylla*
Hydrilla	*Hydrilla verticillata*
Hyperthermophile	*Pyrobaculum aerophilum*
Ice plant	*Mesembryanthemum crystallinum*
Incense cedar	*Libocedrus decurrens*
India rubber plant	*Ficus elastica*
Indian mock strawberry	*Duchesnea indica*
Indian mustard	*Brassica juncea*
Indian paintbrush	*Castilleja* spp.
Indian pipe	*Monotropa uniflora*
Indigo milky	*Lactarius indigo*
Ipecac	*Cephaelis ipecacuanha*
Iris	*Iris* spp.
Iris, giant blue	*Iris giganticaerulea*
Irish moss	*Chondrus crispus*
Iron bacterium	*Thiobacillus ferrooxidans*
Ironwood	*Ostrya virginiana*
Ivy, grape	*Cissus rhombifolia*
Jacaranda	*Jacaranda mimosifolia*
Jack-in-the-pulpit	*Arisaema triphyllum*
Jacob's ladder	*Polemonium caeruleum*
Japanese maple	*Acer palmatum*
Jasmine, Arabian	*Jasminum sambac*
Jelly, apricot	*Phlogiotis helvelloides*
Jerusalem artichoke	*Helianthus tuberosus*
Jessamine, yellow	*Gelsemium sempervirens*
Jicama	*Pachyrhizus erosus*
Jimson weed	*Datura stromonium*
Johnny-jump-up	*Viola tricolor*
Johnson grass	*Sorghum halapense*
Jojoba	*Simmondsia californica*
Jonquil	*Narcissus jonquilla*
Joshua tree	*Yucca brevifolia*
Juniper, common	*Juniperus communis*
Juniper, one seed	*Juniperus monosperma*
Juniper, Rocky Mountain	*Juniperus scopulorum*
Kaffir lily	*Clivia miniata*
Kangaroo paw	*Anigozythos manglesii*
Kapok	*Ceiba pentandra*
Kava	*Piper methysticum*

Common Name	Scientific Name
Kelp	*Sargassum* spp.
Kelp, bull	*Nereocystis leutkeana*
Kelp, giant	*Macrocystis pyrifera*
Kelp, winged	*Alaria esculenta*
Kentucky blue grass	*Poa pratensis*
Kentucky coffee tree	*Gymnocladus dioica*
Kidney bean	*Phaseolus vulgaris*
King bolete	*Boletus edulis*
Kinnikinnick	*Arctostaphylos uva-ursi*
Kiwi	*Actinidia chinensis*
Kohlrabi	*Brassica oleracea*
Kola nut	*Cola nitida*
Kudzu	*Pueraria lobata*
Kumquat	*Fortunella margarita*
Lace lichen	*Ramalina menziesii*
Lactic acid bacteria	*Lactobacillus* spp.
Lady fern	*Athyrium filix-femina*
Lamb's ears	*Stachys byzantina*
Lamb's quarters	*Chenopodium album*
Lantana	*Lantana camara*
Larch, western	*Larix occidentalis*
Larkspur	*Consolida ajacis*
Lasso fungus	*Arthrobotrys anchonia*
Laurel	*Laurus nobilis*
Laurel, mountain	*Kalmia latifolia*
Leafy liverwort	*Barbilophozia lycopodioides*
Lemon	*Citrus limon*
Lemon balm	*Melissa officinalis*
Lentil	*Lens culinaris*
Leprosy pathogen	*Mycobacterium leprae*
Lettuce	*Lactuca sativa*
Lettuce, miner's	*Montia parviflora*
Lichen, lace	*Ramalina menziesii*
Lichen, litmus	*Roccella tinctoria*
Lichen, lung	*Lobaria pulmonaria*
Lichen, map	*Rhizocarpon geographicum*
Lichen, old man's beard	*Usnea alpina*
Lichen, pencil marks	*Graphis scripta*
Lichen, powder puff	*Cladonia stellaris*
Lichen, reindeer	*Cladonia rangiferina*
Lichen, studded leather	*Peltigera aphthosa*
Licorice fern	*Polypodium glycyrrhiza*
Lignum vitae	*Guaiacum sanctum*
Lilac	*Syringa vulgaris*
Lily, belladonna	*Amaryllis belladonna*
Lily, canna	*Canna indica*
Lily, gloriosa	*Gloriosa rothschildiana*
Lily, kaffir	*Clivia miniata*
Lily, plantain	*Hosta ventricosa*
Lily, royal water	*Victoria amazonica*
Lily, sego	*Calochortus nuttallii*
Lily, tiger	*Lily lancifolium*
Lily of the valley	*Convallaria majalis*
Lima bean	*Phaseolus lunatus*
Limber pine	*Pinus flexilis*
Lime	*Citrus aurantifolia*
Lime, Spanish	*Meliococcus bijugatus*
Ling chih	*Ganoderma lucidum*
Lip ferns	*Cheilanthes* spp.
Litmus lichen	*Roccella tinctoria*
Littlehip hawthorn	*Crataegus spathulata*
Live oak	*Quercus virginiana*
Liverworts, leafy	*Barbilophozia lycopodioides*
Liverworts, leafy	*Lophozia* spp.
Liverworts, leafy	*Mylia taylorii*
Liverworts, leafy	*Porella cordaeana*
Liverworts, leafy	*Ptilidium pulcherimum*
Liverworts, leafy	*Scapania cuspiduligera*
Liverworts, thalloid	*Conocephalum conicum*
Liverworts, thalloid	*Marchantia polymorpha*
Liverworts, thalloid	*Pellia neesiana*
Living stones	*Lithops* spp.
Loblolly pine	*Pinus taeda*
Lobster mushroom	*Hypomyces lactifluorum*
Locust, black	*Robinia pseudoacacia*
Lodgepole pine	*Pinus contorta*
Lombardy poplar	*Populus nigra*
London plane tree	*Platanus acerifolia*
Loofa sponge plant	*Luffa cylindrica*
Lotus, Chinese	*Nelumbo nucifera*
Lovage	*Levisticum officinale*
Low bulrush	*Scirpus cernuus*
Lowbush blueberry	*Vaccinium angustifolium*
Lung lichen	*Lobaria pulmonaria*
Lychee	*Litchi chinenesis*
Lyme disease pathogen	*Borrelia burgdorferi*
Macadamia, rough-shelled	*Macadamia tetraphylla*
Macadamia, smooth-shelled	*Macadamia integrifolia*
Mace	*Myristica fragrans*
Madagascar periwinkle	*Catharanthus roseus*
Madrone, Pacific	*Arbutus menziesii*
Magnolia, southern	*Magnolia grandiflora*
Mahogany, West Indies	*Swietenia mahogani*
Maidenhair fern	*Adiantum capillus-veneris*
Maidenhair tree	*Ginkgo biloba*
Maize	*Zea mays*
Mamey sapote	*Pouteria sapota*
Mamoncillo	*Meliococcus bijugatus*
Mandrake	*Mandragora officinarum*
Mangel	*Beta vulgaris*
Mango	*Mangifera indica*
Mangosteen	*Garcinia mangostana*
Mangrove, black	*Avicennia nitida*
Mangrove, red	*Rhizophora mangle*

Common Name	Scientific Name
Mangrove, white	*Laguncularia racemosa*
Manila hemp	*Musa textilis*
Manioc	*Manihot esculenta*
Map lichen	*Rhizocarpon geographicum*
Maple, bigleaf	*Acer macrophyllum*
Maple, flowering	*Abutilon hybridum*
Maple, Japanese	*Acer palmatum*
Maple, red	*Acer rubrum*
Maple, silver	*Acer saccharinum*
Maple, sugar	*Acer saccharum*
Marigold	*Tagetes patula*
Marijuana	*Cannabis sativa*
Marjoram, sweet	*Origanum hortensis*
Marshmarigold	*Caltha palustris*
Maternity plant	*Kalanchoe daigremontiana*
Maximillian sunflower	*Helianthus maximilianii*
May apple	*Podophyllum peltatum*
Maypop	*Passiflora incarnata*
Meadow violet	*Viola sororia*
Meningococcus	*Neisseria meningitidis*
Mermaid's wine glass	*Acetabularia* spp.
Merman's shaving brush	*Penicillus dumetosus*
Mesquite	*Prosopis glandulosa*
Methanogens	*Methanococcus* spp.
Methanogens	*Methanosarcina* spp.
Mexican hat	*Ratibida columnifera*
Mexican sarsaparilla	*Smilax aristolochiaefolia*
Mignonette tree	*Lawsonia inermis*
Mildew pathogen, powdery	*Plasmopara viticola*
Milfoil	*Myriophyllum aquaticum*
Milfoil	*Myriophyllum spicatum*
Milkweed	*Asclepias speciosa*
Millet, foxtail	*Setaria italica*
Mimosa tree	*Albizia julibrissin*
Miner's lettuce	*Montia parviflora*
Miniature pumpkin	*Cucurbita pepo*
Mistletoe	*Phoradendron sertinum*
Mock orange	*Philadelphus coronarius*
Mold, black bread	*Rhizopus stolonifer*
Mold, cheese	*Penicillium roqueforti*
Mold, mushroom	*Sporodinia grandis*
Mold, penicillin	*Penicillium notatum*
Mold, pink	*Neurospora crassa*
Money plant	*Lunaria annua*
Monkey flowers	*Mimulus* spp.
Monkey puzzle tree	*Araucaria imbricata*
Monk's hood	*Aconitum napellus*
Monterey cypress	*Cupressus macrocarpa*
Moonwort	*Botrychium lunaria*
Morel, yellow	*Morchella esculenta*
Mormon tea	*Ephedra nevadensis*
Morning glory	*Ipomoea tricolor*
Moses-in-the-cradle	*Rhoeo spathacea*
Mosquito fern	*Azolla* spp.
Moss, aquatic	*Hygrohypnum bestii*
Moss, candle snuffer	*Encalypta* spp.
Moss, compact spike	*Selaginella densa*
Moss, dung	*Splachnum* spp.
Moss, feather	*Thuidium* spp.
Moss, fir	*Huperzia lucidula*
Moss, granite	*Andreaea* spp.
Moss, Irish	*Chondrus crispus*
Moss, peat	*Sphagnum* spp.
Moss, reindeer	*Cladonia subtenuis*
Moss, rose	*Portulaca grandiflora*
Moss, wolf	*Letharia vulpina*
Mosses	*Atrichum* spp.
Mosses	*Brachythecium* spp.
Mosses	*Campylium* spp.
Mosses	*Mnium* spp.
Mosses	*Plagiomnium*
Mosses	*Polytrichum* spp.
Mosses	*Timmia* spp.
Mother-in-law's tongue	*Sansevieria trifasciata*
Mother of thousands	*Kalanchoe daigremontiana*
Mountain garland	*Clarkia unguiculata*
Mountain laurel	*Kalmia latifolia*
Mulberry, red	*Morus rubra*
Mullein	*Verbascum thapsus*
Mung bean	*Vigna radiata*
Mushroom, ashy coral	*Clavulina cinerea*
Mushroom, chicken	*Laetiporus sulphureus*
Mushroom, commercial	*Agaricus bisporus*
Mushroom, fairy ring	*Marasmius oreades*
Mushroom, lobster	*Hypomyces lactifluorum*
Mushroom, oyster	*Pleurotus ostreatus*
Mushroom, shiitake	*Lentinula edodes*
Mushroom, slippery jack	*Suillus luteus*
Mushroom, velvet foot	*Flammulina velutipes*
Mushroom mold	*Sporodinia grandis*
Muskmelon	*Cucumis melo*
Mustard, Indian	*Brassica juncea*
Mustard, white	*Sinapis alba*
Mycoplasma	*Mycoplasma* spp.
Mycorrhizal fungus	*Glomus pansihalos*
Myrrh	*Commiphora myrrha*
Myrtle, crape	*Lagerstroemia indica*
Nasturtium	*Tropaeolum majus*
Native violet	*Viola* spp.
Navel orange	*Citrus sinensis*
Neem tree	*Azadirachta indica*
Nematicidal fungus	*Dactylaria candida*
Netted stinkhorn	*Dictyophora duplicata*
Nettle, stinging	*Urtica dioica*
New Zealand spinach	*Tetragonia expansa*
Noble fir	*Abies procera*

Common Name	Scientific Name
Norfolk Island pine	*Araucaria heterophylla*
Northern white cedar	*Thuja occidentalis*
Norway spruce	*Picea abies*
Nut grass	*Cyperus esculentus*
Nut sedge	*Cyperus esculentus*
Nutmeg	*Myristica fragrans*
Nutmeg, California	*Torreya californica*
Oak	*Quercus* spp.
Oak, black	*Quercus velutina*
Oak, blackjack	*Quercus marilandica*
Oak, bur	*Quercus marcocarpa*
Oak, chinkapin	*Quercus muehlenbergii*
Oak, live	*Quercus virginiana*
Oak, pin	*Quercus palustris*
Oak, post	*Quercus stellata*
Oak, red	*Quercus rubra*
Oak, scarlet	*Quercus coccinea*
Oak, shingle	*Quercus imbricaria*
Oak, shumard	*Quercus shumardii*
Oak, white	*Quercus alba*
Oat	*Avena sativa*
Obedience plant	*Physostegia virginiana*
Ocotillo	*Fouquieria splendens*
Oedogonium	*Oedogonium* spp.
Ohio buckeye	*Aesculus glabra*
Oil palm	*Elaeis guineensis*
Okra	*Hibiscus esculentus*
Old man's beard lichen	*Usnea alpina*
Oleander	*Nerium oleander*
Olive	*Olea europea*
Olive, Russian	*Elaeagnus angustifolia*
One seed juniper	*Juniperus monosperma*
Onion	*Allium cepa*
Opium poppy	*Papaver somniferum*
Orange, mock	*Philadelphus coronarius*
Orange, navel	*Citrus sinensis*
Orange, osage	*Maclura pomifera*
Orange, sweet	*Citrus sinensis*
Orchard grass	*Dactylis glomerata*
Orchid	*Cattleya* spp.
Orchid	*Cymbidium* spp.
Orchid	*Dendrobium* spp.
Orchid, vanilla	*Vanilla planifolia*
Oregon grape	*Mahonia aquifolium*
Oriental sycamore	*Platanus orientalis*
Osage orange	*Maclura pomifera*
Ostrich fern	*Matteuccia struthiopteris*
Oyster mushroom	*Pleurotus ostreatus*
Pacific madrone	*Arbutus menziesii*
Pacific willow	*Salix lasiandra*
Pacific yew	*Taxus brevifolia*
Paintbrush, Indian	*Castilleja* spp.

Common Name	Scientific Name
Palm, betel nut	*Areca catechu*
Palm, coconut	*Cocos nucifera*
Palm, date	*Phoenix dactylifera*
Palm, fishtail	*Caryota urens*
Palm, oil	*Elaeis guineensis*
Palm, Panama hat	*Carludovica palmata*
Palm, ponytail	*Beaucarnea recurvata*
Palm, royal	*Roystonea regia*
Palm, sago	*Cycas revoluta*
Palm, sea	*Postelsia palmaeformis*
Palm, Seychelles	*Lodoicea maldivica*
Palm, travelers	*Ravenala madagascariensis*
Palmetto, cabbage	*Sabal palmetto*
Palmetto, saw	*Serenoa repens*
Palms, rattan	*Calamus* spp.
Palo verde	*Cercidium torreyanum*
Pampas grass	*Cortaderia selloana*
Panama hat palm	*Carludovica palmata*
Papaya	*Carica papaya*
Paper birch	*Betula papyrifiera*
Paper rush	*Cyperus papyrus*
Paradise tree	*Simarouba glauca*
Parrot fever pathogen	*Chlamydia psittaci*
Parsley	*Petroselinum crispum*
Parsnip	*Pastinaca sativa*
Pasque flower, American	*Pusatilla hirsutissima*
Passion flower	*Passiflora caerulea*
Passionfruit	*Passiflora edulis*
Pathogen, acne	*Propionibacterium acnes*
Pathogen, anthrax	*Bacillus anthracis*
Pathogen, apple scab	*Enturia inaequalis*
Pathogen, botulism	*Clostridium botulinum*
Pathogen, brown rot	*Monilinia fructicola*
Pathogen, damping-off	*Pythium* spp.
Pathogen, dark leaf spot	*Alternaria brassicicola*
Pathogen, Dutch elm disease	*Ophiostoma ulmi*
Pathogen, foolish seedling	*Gibberella fujikuroi*
Pathogen, leprosy	*Mycobacterium leprae*
Pathogen, lyme disease	*Borrelia burgdorferi*
Pathogen, parrot fever	*Chlamydia psittaci*
Pathogen, plague	*Yersinia pestis*
Pathogen, potato blight	*Phytophthora infestans*
Pathogen, powdery mildew	*Plasmopara viticola*
Pathogen, thrush	*Candida albicans*
Paulownia, royal	*Paulownia tomentosa*
Pawpaw	*Asimina triloba*
Pea, black-eyed	*Vigna unguiculata*
Pea, garden	*Pisum sativum*
Peach	*Prunus persica*
Peacock's tail	*Padina pavonia*
Peanut	*Arachis hypogaea*
Pear	*Pyrus communis*

Common Name	Scientific Name
Peat mosses	*Sphagnum* spp.
Pecan	*Carya illinoensis*
Pencil marks lichen	*Graphis scripta*
Pencil tree	*Euphorbia tirucalli*
Penicillin mold	*Penicillium notatum*
Peony	*Paeonia* spp.
Peperomia	*Peperomia* spp.
Pepper	*Capsicum annuum*
Pepper	*Piper nigrum*
Peppermint	*Mentha piperita*
Periwinkle	*Vinca major*
Periwinkle, Madagascar	*Catharanthus roseus*
Persimmon, common	*Diospyros virginiana*
Petunia	*Petunia hybrida*
Philodendron, split leaf	*Monstera deliciosa*
Photinia, Chinese	*Photinia serrulata*
Pickerel weed	*Pontederia cordata*
Pigweed	*Amaranthus retroflexus*
Pimpernel, scarlet	*Anagallis arvensis*
Pin oak	*Quercus palustris*
Pincushion flower	*Scabiosa atropurpurea*
Pine, Austrian	*Pinus nigra*
Pine, bristlecone	*Pinus aristata*
Pine, Buddhist	*Podocarpus macrophyllus*
Pine, coulter	*Pinus coulteri*
Pine, eastern white	*Pinus strobus*
Pine, limber	*Pinus flexilis*
Pine, loblolly	*Pinus taeda*
Pine, lodgepole	*Pinus contorta*
Pine, Norfolk Island	*Araucaria heterophylla*
Pine, pinyon	*Pinus edulis*
Pine, ponderosa	*Pinus ponderosa*
Pine, red	*Pinus resinosa*
Pine, running	*Lycopodium clavatum*
Pine, Scotch	*Pinus sylvestris*
Pine, screw	*Pandanus amaryllifolius*
Pine, slash	*Pinus elliottii*
Pine, southern	*Pinus palustris*
Pine, sugar	*Pinus lambertiana*
Pine, western white	*Pinus monticola*
Pine, wollemi	*Wollemia nobilis*
Pineapple	*Ananas comosus*
Pink lady's slipper	*Cypripedium acaule*
Pink mold	*Neurospora crassa*
Pinyon, single-leaf	*Pinus monophylla*
Pinyon pine	*Pinus edulis*
Pistachio	*Pistacia vera*
Pitcher plant, California	*Darlingtonia californica*
Pitcher plant, East Indian	*Nepenthes reinwardtiana*
Plague pathogen	*Yersinia pestis*
Plains cottonwood	*Populus sargentii*
Plantain	*Musa x paradisiaca*
Plantain	*Plantago lanceolata*
Plantain	*Plantago major*
Plantain lily	*Hosta ventricosa*
Plasmodial slime mold	*Physarum polycephalum*
Plum, American	*Prunus americana*
Plum, chickasaw	*Prunus angustifolia*
Plum, hog	*Ximenia americana*
Poinsettia	*Euphorbia pulcherrima*
Poison hemlock	*Conium maculata*
Poison sumac	*Toxicodendron vernix*
Pokeweed	*Phytolacca americana*
Polyanthus daffodil	*Narcissus tazetta*
Polypore, resinous	*Ischnoderma resinosum*
Pomegranate	*Punica granatum*
Ponderosa pine	*Pinus ponderosa*
Pondweed	*Potamogeton* spp.
Ponytail palm	*Beaucarnea recurvata*
Poplar, lombardy	*Populus nigra*
Poplar, white	*Populus alba*
Poplar, yellow	*Liriodendron tulipifera*
Poppy, California	*Eschscholzia californica*
Poppy, opium	*Papaver somniferum*
Port-Orford cedar	*Chamaecyparis lawsoniana*
Post oak	*Quercus stellata*
Potato	*Solanum tuberosum*
Potato, sea	*Leathesia difformis*
Potato, sweet	*Ipomoea batatas*
Potato blight pathogen	*Phytophthora infestans*
Powder puff lichen	*Cladonia stellaris*
Powdery mildew pathogen	*Plasmopara viticola*
Prairie gentian	*Eustoma exaltatum*
Prairie rose	*Rosa pranticola*
Prayer plant	*Maranta leuconeura*
Prickly pear	*Opuntia polyacantha*
Primrose	*Primula vulgaris*
Primrose, cape	*Streptocarpus* spp.
Primrose, evening	*Oenothera biennis*
Privet	*Ligustrum vulgare*
Protea, giant	*Protea cynaroides*
Psathyrella, ringed	*Psathyrella longistriata*
Puffball, western giant	*Calvatia booniana*
Pumpkin	*Cucurbita moschata*
Pumpkin, giant	*Cucurbita maxima*
Pumpkin, miniature	*Cucurbita pepo*
Puncture vine	*Tribulus terrestris*
Purple coneflower	*Echinacea purpurea*
Purple heart	*Setcreasea pallida*
Purple nonsulfur bacterium	*Rhodospirillum rubrum*
Purslane	*Portulaca oleracea*
Pussy willow	*Salix discolor*
Quaking aspen	*Populus tremuloides*
Queen Anne's lace	*Daucus carota*
Quillwort	*Isoetes melanopoda*

Common Name	Scientific Name
Quince	*Cydonia oblonga*
Quinine	*Cinchona* spp.
Radish	*Raphanus sativus*
Rafflesia	*Rafflesia arnoldii*
Ragweed	*Ambrosia artemisiifolia*
Rambutan	*Nephelium lapaceum*
Raspberry	*Rubus idaeus*
Raspberry, black	*Rubus occidentalis*
Rattan palms	*Calamus* spp.
Red alder	*Alnus rubra*
Red algae	*Bangia* spp.
Red algae	*Cyanidium* spp.
Red algae	*Dasya* spp.
Red algae	*Gelidium* spp.
Red algae	*Gracilaria* spp.
Red algae	*Porphyra* spp.
Red algae, coralline	*Porolithon craspedium*
Red cedar, eastern	*Juniperus virginiana*
Red clover	*Trifolium pratense*
Red-gilled agaric	*Melanophyllum echinatum*
Red hawthorn	*Crataegus* spp.
Red mangrove	*Rhizophora mangle*
Red maple	*Acer rubrum*
Red mulberry	*Morus rubra*
Red oak	*Quercus rubra*
Red-osier dogwood	*Cornus stolonifera*
Red pine	*Pinus resinosa*
Red tide algae	*Gonyaulax tamarensis*
Red top	*Agrostis gigantea*
Redbud	*Cercis canadensis*
Redwood, coast	*Sequoia sempervirens*
Redwood, dawn	*Metasequoia glyptostroboides*
Reindeer lichen	*Cladonia rangiferina*
Reindeer moss	*Cladonia subtenuis*
Resinous polypore	*Ischnoderma resinosum*
Resurrection fern	*Polypodium polypodioides*
Resurrection plant	*Selaginella lepidophylla*
Rhizobium	*Rhizobium* spp.
Rhododendron	*Rhododendron* spp.
Rhubarb	*Rheum rhaponticum*
Rice	*Oryza sativa*
Rice, American wild	*Zizania aquatica*
Ringed psathyrella	*Psathyrella longistriata*
River birch	*Betula nigra*
Rock weed	*Fucus* spp.
Rocky Mountain columbine	*Aquilegia caerulea*
Rocky Mountain juniper	*Juniperus scopulorum*
Rose, Cherokee	*Rosa sinica*
Rose, prairie	*Rosa pranticola*
Rose, wild prairie	*Rosa arkansana*
Rose-colored yeast	*Sporobolomyces roseus*
Rose moss	*Portulaca grandiflora*

Common Name	Scientific Name
Rose of Sharon	*Hibiscus syriacus*
Rosemary	*Rosmarinus officinalis*
Roses	*Rosa* spp.
Rounded earthstar	*Geastrum saccatum*
Rowan	*Sorbus aucuparia*
Royal fern	*Osmunda regalis*
Royal palm	*Roystonea regia*
Royal paulownia	*Paulownia tomentosa*
Royal water lily	*Victoria amazonica*
Rubber plant, India	*Ficus elastica*
Rue	*Ruta graveolens*
Ruellia	*Ruellia peninsularis*
Running pine	*Lycopodium clavatum*
Rush	*Juncus effusus*
Russian olive	*Elaeagnus angustifolia*
Russian thistle	*Salsola kali*
Rust	*Coleosporium tussilaginis*
Rust	*Gymnosporangium clavariiforme*
Rust, birch	*Melampsoridium betulinum*
Rust, black stem	*Puccinia graminis*
Rust, violet	*Phragmidium violaceum*
Rutabaga	*Brassica napus*
Rye	*Secale cereale*
Sacred bamboo	*Nandina domestica*
Safflower	*Carthamus tinctorius*
Saffron crocus	*Crocus sativus*
Sage	*Salvia officinalis*
Sagebrush, big	*Artemisia tridentata*
Sago palm	*Cycas revoluta*
Saguaro cactus	*Carnegiea gigantea*
St. John's wort	*Hypericum perforatum*
Salmon unicorn entoloma	*Entoloma salmoneum*
Salmonberry	*Rubus spectabilis*
Salsify	*Tragopogon porrifolius*
Sand verbena	*Abronia fragrans*
Sandalwood tree	*Santalum album*
Sandbar willow	*Salix interior*
Sapodilla	*Manilkara zapota*
Sapote, mamey	*Pouteria sapota*
Sapote, white	*Casimiroa edulis*
Sarsaparilla, Mexican	*Smilax aristolochiaefolia*
Sassafras	*Sassafras albidum*
Sausage fruit	*Kigelia africana*
Savory, summer	*Satureia hortensis*
Savory, winter	*Satureia montana*
Saw palmetto	*Serenoa repens*
Scaevola	*Scaevola* spp.
Scarlet cup	*Sarcoscypha coccinea*
Scarlet oak	*Quercus coccinea*
Scarlet pimpernel	*Anagallis arvensis*
Scarlet runner bean	*Phaseolus coccineus*
Scenedesmus	*Scenedesmus* spp.

Common Name	Scientific Name
Schefflera	*Schefflera actinophylla*
Scotch broom	*Cytisus scoparius*
Scots pine	*Pinus sylvestris*
Scouring rush, common	*Equisetum hyemale*
Scrambled-egg slime	*Fuligo septica*
Scrambled eggs	*Corydalis aurea*
Screw pine	*Pandanus amaryllifolius*
Sea grape	*Coccoloba uvifera*
Sea lace	*Chorda filum*
Sea palm	*Postelsia palmaeformis*
Sea potato	*Leathesia difformis*
Sedge, nut	*Cyperus esculentus*
Sego lily	*Calochortus nuttallii*
Sensitive fern	*Onoclea sensibilis*
Sensitive plant	*Mimosa pudica*
Sequoia, giant	*Sequoiadendron giganteum*
Service tree	*Sorbus domestica*
Serviceberry, Allegheny	*Amelanchier laevis*
Sesame seed	*Sesamum indicum*
Seychelles palm	*Lodoicea maldivica*
Shagbark hickory	*Carya ovata*
Shaving brush, merman's	*Penicillus dumetosus*
Shiitake mushroom	*Lentinula edodes*
Shingle oak	*Quercus imbricaria*
Shooting star	*Dodecatheon meadia*
Showy lady's slipper	*Cypripedium reginae*
Shumard oak	*Quercus shumardii*
Sideoats grama	*Bouteloua curtipendula*
Silk-tassel bush	*Garrya elliptica*
Silk tree	*Albizia julibrissin*
Silver maple	*Acer saccharinum*
Silverpalm, Florida	*Coccothrinax argentata*
Single-leaf pinyon	*Pinus monophylla*
Sitka alder	*Alnus sinuata*
Sitka spruce	*Picea sitchensis*
Skullcap	*Scutellaria lateriflora*
Slash pine	*Pinus elliottii*
Slime, scrambled-egg	*Fuligo septica*
Slime mold, cellular	*Dictyostelium discoideum*
Slime mold, plasmodial	*Physarum polycephalum*
Slippery elm	*Ulmus rubra*
Slippery jack mushroom	*Suillus luteus*
Sloe	*Prunus spinosa*
Smoke tree	*Dalea spinosa*
Smooth-leaf begonia	*Begonia semperflorens*
Smut, anemone	*Urocystis anemones*
Smut, corn	*Ustilago maydis*
Smut fungus, stinking	*Tilletia caries*
Snake plant	*Sansevieria trifasciata*
Snapdragon	*Antirrhinum majus*
Snow-on-the-mountain	*Euphorbia marginata*
Snowberry	*Symphoricarpus albus*
Snowdrop	*Galanthus nivalis*
Soapberry	*Sapindus saponaria*

Common Name	Scientific Name
Solomon's seal, false	*Smilacina racemosa*
Sorghum	*Sorghum bicolor*
Sorrel	*Rumex acetosa*
Soursop	*Annona muricata*
Sourwood	*Oxydendrum arboreum*
Southern catalpa	*Catalpa bignonioides*
Southern crabapple	*Malus angustifolia*
Southern magnolia	*Magnolia grandiflora*
Southern pine	*Pinus palustris*
Soybean	*Glycine max*
Spanish lime	*Meliococcus bijugatus*
Spearmint	*Mentha spicant*
Speedwell	*Veronica* spp.
Spider flower	*Cleome spinosa*
Spider plant	*Chlorophytum comosum*
Spiderwort	*Tradescantia virginiana*
Spike moss, compact	*Selaginella densa*
Spinach	*Spinacea oleracea*
Spinach, New Zealand	*Tetragonia expansa*
Spiraea	*Spiraea* spp.
Spirogyra	*Spirogyra* spp.
Spleenwort, ebony	*Asplenium platyneuron*
Split leaf philodendron	*Monstera deliciosa*
Spring beauty	*Claytonia virginica*
Spruce, black	*Picea mariana*
Spruce, Black Hills	*Picea glauca*
Spruce, Engelmann	*Picea engelmannii*
Spruce, Norway	*Picea abies*
Spruce, Sitka	*Picea sitchensis*
Squash	*Cucurbita maxima*
Squash	*Cucurbita moschata*
Squash	*Cucurbita pepo*
Staghorn fern	*Platycerium bifurcatum*
Staghorn sumac	*Rhus typina*
Star anise	*Illicium verum*
Star apple	*Chrysophyllum cainito*
Star fruit	*Averrhoa carambola*
Star of Bethlehem	*Campanula isophylla*
Stinging nettle	*Urtica dioica*
Stinkhorn, netted	*Dictyophora duplicata*
Stinking smut fungus	*Tilletia caries*
Stonewort	*Chara* spp.
Stonewort	*Nitella* spp.
Strawberry, Indian mock	*Duchesnea indica*
Strawberry, wild	*Fragaria virginiana*
Strawberry tree	*Arbutus unedo*
Strep mutans	*Streptococcus mutans*
String bean	*Phaseolus vulgaris*
String of beads	*Senecio rowleyanus*
Studded leather lichen	*Peltigera aphthosa*
Subalpine fir	*Abies lasiocarpa*
Sudan grass	*Sorghum sudanese*
Sugar beet	*Beta vulgaris*
Sugar maple	*Acer saccharum*

Common Name	Scientific Name
Sugar pine	*Pinus lambertiana*
Sugarcane	*Saccharum officinarum*
Sulfur bacteria	*Desulfovibrio* spp.
Sumac, poison	*Toxicodendron vernix*
Sumac, staghorn	*Rhus typina*
Summer savory	*Satureia hortensis*
Sunchoke	*Helianthus tuberosus*
Sundew	*Drosera rotundifolia*
Sunflower	*Helianthus annuus*
Sunflower, Maximillian	*Helianthus maximilianii*
Sweet basil	*Ocimum basilicum*
Sweet cherry	*Prunus avium*
Sweet marjoram	*Origanum hortensis*
Sweet orange	*Citrus sinensis*
Sweet potato	*Ipomoea batatas*
Sweet William	*Dianthus barbatus*
Sweetgum	*Liquidambar styraciflua*
Sweetsop	*Annona squamosa*
Sycamore, American	*Platanus occidentalis*
Sycamore, Oriental	*Platanus orientalis*
Syringa	*Philadelphus lewisii*
Tall fescue	*Festuca arundinacea*
Tallowwood	*Ximenia americana*
Tamarack	*Larix laricina*
Tamarisk	*Tamarix parviflora*
Tangerine	*Citrus reticulata*
Tansy	*Tanacetum vulgare*
Tapioca	*Manihot esculenta*
Taq	*Thermus aquaticus*
Tasmanian tree fern	*Dicksonia antarctica*
Tea	*Camellia sinensis*
Teak	*Tectona grandis*
Teasel	*Dipsacus sylvestris*
Tequila agave	*Agave tequilana*
Thalloid liverwort	*Conocephalum conicum*
Thermoacidophile	*Sulfolobus sulfataricus*
Thermoplasma	*Thermoplasma acidophilum*
Thimbleberry	*Rubus parviflorus*
Thistle, bull	*Cirsium vulgare*
Thistle, Canada	*Cirsium arvense*
Thistle, Russian	*Salsola kali*
Thrush pathogen	*Candida albicans*
Thyme, creeping	*Thymus serpyllum*
Tiger lily	*Lily lancifolium*
Timothy	*Phleum pratense*
Tobacco	*Nicotiana tobacum*
Tomatillo	*Physalis ixocarpa*
Tomato	*Lycopersicon esculentum*
Trailing arbutus	*Epigaea repens*
Transvaal daisy	*Gerbera jamesonii*
Travelers palm	*Ravenala madagascariensis*
Tree ear	*Auricularia auricula*
Tree of heaven	*Ailanthus altissima*
Truffle, black	*Tuber melanosporum*
Trumpet vine	*Campsis radicans*
Tuberous begonia	*Begonia tuberhybrida*
Tulip	*Tulipa* spp.
Tulip tree	*Liriodendron tulipifera*
Tumbleweed	*Salsola kali*
Tung oil tree	*Aleurites fordii*
Tupelo, black	*Nyssa sylvatica*
Turkey tail	*Trametes versicolor*
Turmeric	*Curcuma domestica*
Turnip	*Brassica rapa*
Umbrella tree	*Schefflera actinophylla*
Vanilla orchid	*Vanilla planifolia*
Velvet foot mushroom	*Flammulina velutipes*
Velvety earth tongue	*Trichoglossom hirsutum*
Venus's flytrap	*Dionaea muscipula*
Verbena, garden	*Verbena hybrida*
Verbena, sand	*Abronia fragrans*
Vetch, hairy	*Vicia villosa*
Vibrio	*Vibrio fisheri*
Violet	*Viola palmata*
Violet, African	*Saintpaulia ionantha*
Violet, bird's foot	*Viola pedata*
Violet, meadow	*Viola sororia*
Violet, native	*Viola* spp.
Violet, wood	*Viola papilionacea*
Violet rust	*Phragmidium violaceum*
Volvox	*Volvox* spp.
Wahoo, eastern	*Euonymus atropurpureus*
Wake robin	*Trillium grandiflorum*
Walking fern	*Asplenium rhizophyllum*
Walnut, black	*Juglans nigra*
Walnut, English	*Juglans regia*
Wandering jew	*Zebrina pendula*
Water chestnut	*Eleocharis dulcis*
Water hemlock	*Cicuta maculata*
Water hyacinth	*Eichhornia crassipes*
Water net	*Hydrodictyon* spp.
Watermelon	*Citrullus lanatus*
Wax flower	*Hoya carnosa*
Weeping fig	*Ficus benjamina*
Weeping forsythia	*Forsythia suspensa*
Weeping willow	*Salix babylonica*
Weigelia	*Weigelia florida*
West Indies mahogany	*Swietenia mahogani*
Western columbine	*Aquilegia formosa*
Western giant puffball	*Calvatia booniana*
Western hemlock	*Tsuga heterophylla*
Western larch	*Larix occidentalis*
Western red cedar	*Thuja plicata*
Western wheatgrass	*Agropyron smithii*

Common Name	Scientific Name
Western white pine	*Pinus monticola*
Wheat	*Triticum aestivum*
Wheatgrass, western	*Agropyron smithii*
Whiskfern	*Psilotum nudum*
White ash	*Fraxinus americana*
White clover	*Trifolium repens*
White fir	*Abies concolor*
White mangrove	*Laguncularia racemosa*
White mustard	*Sinapis alba*
White oak	*Quercus alba*
White poplar	*Populus alba*
White sapote	*Casimiroa edulis*
White sweet clover	*Melilotus albus*
White willow	*Salix alba*
Wild prairie rose	*Rosa arkansana*
Wild rice, American	*Zizania aquatica*
Wild strawberry	*Fragaria virginiana*
Willow, black	*Salix nigra*
Willow, Pacific	*Salix lasiandra*
Willow, pussy	*Salix discolor*
Willow, sandbar	*Salix interior*
Willow, weeping	*Salix babylonica*
Willow, white	*Salix alba*
Wine cup	*Callirhoe involucrata*
Winged euonymus	*Euonymus elata*
Winged kelp	*Alaria esculenta*
Winter savory	*Satureia montana*
Wintergreen	*Gaultheria procumbens*
Wisteria	*Wisteria sinensis*

Common Name	Scientific Name
Witch hazel	*Hamamelis virginiana*
Witches' hair	*Alectoria sarmentosa*
Wolf moss	*Letharia vulpina*
Wollemi pine	*Wollemia nobilis*
Wood ferns	*Dryopteris* spp.
Wood horsetail	*Equisetum sylvaticum*
Wood violet	*Viola papilionacea*
Woodsia	*Woodsia* spp.
Wormwood	*Artemisia absinthium*
Xanthomonas	*Xanthomonas campestris*
Yam	*Dioscorea alata*
Yarrow	*Achillea millefolium*
Yaupon	*Ilex vomitoria*
Yeast, bakers'	*Saccharomyces cerevisiae*
Yeast, brewers'	*Saccharomyces cerevisiae*
Yeast, rose-colored	*Sporobolomyces roseus*
Yellow birch	*Betula alleghaniensis*
Yellow-eyed grass	*Xyris* spp.
Yellow jessamine	*Gelsemium sempervirens*
Yellow morel	*Morchella esculenta*
Yellow poplar	*Liriodendron tulipifera*
Yew, Pacific	*Taxus brevifolia*
Yucca	*Yucca* spp.
Zebra wood	*Connarus guianensis*
Zuchini	*Cucurbita pepo*

PLANT NAMES: SCIENTIFIC-TO-COMMON

The following table lists, in alphabetical order by genus and species name (far-left column), some of the more common organisms studied by scientists, including not only plants (kingdom *Plantae*) but also some of the more important members of the kingdoms *Archaea*, *Bacteria*, *Fungi*, and *Protista*. Arranged alphabetically by genus, organisms from these different kingdoms are intermixed in this table. Those interested in the taxonomic arrangement of organisms should refer to the appendix in this volume headed "Plant Classification." Useful articles, also in these volumes, are "Cladistics," "Molecular Systematics," "Systematics and Classification," "Systematics: Overview," and the various articles filed under "evolution." To find the scientific name for a common plant name, consult the appendix titled "Plant Names: Common-to-Scientific."

Scientific names for plants are created according to rules set forth in the International Code of Botanical Nomenclature (ICBN). The ICBN describes how names are to be constructed, but it does not indicate which names are correct, or best. The ICBN specifies a two-word naming system called binomial nomenclature. Each plant is given a two-word name (a binomial), and all scientists agree to use this name exclusively. As a result of this naming system, the confusion caused by the common plant names that most people use (such as "bluebells") is avoided. Occasionally, a scientific name must be changed, usually because the rules for naming a plant were not followed correctly. Normally, however, the scientific name is very stable.

In addition to the binomial, which names a plant's species, each plant has a name for each higher-level group to which it belongs. Each plant belongs to a genus, each genus to a family, each family to an order, each order to a class, each class to a phylum, each phylum to a kingdom, and each kingdom to one of the three domains of life: *Archaea*, *Bacteria* (both made up of microorganisms formed by prokaryotic, or nucleus-free, cells), and *Eukarya*. The domain *Eukarya*, made up of organisms with cells that have nuclei, contains four kingdoms of life: *Protista* (protists, mainly molds and algae), *Fungi* (mainly nonphotosynthetic organisms), *Plantae* (plants, both nonvascular and vascular), and *Animalia* (animals).

Names for the higher-level plant groups, or taxa, are all created according to rules of the ICBN. The rules for naming higher-level groups do not indicate which names are best or most correct. Unlike the binomial genus-species names, on which scientists generally agree, the best name for the higher-level groups to which these genera belong can sometimes be controversial. Therefore, some of the higher-level groups have more than one proposed name. Neither of the names is necessarily more correct than the other. Usually the different names reflect different ideas about how the higher-level groups are related to each other. In some cases, the higher-level names that are listed were selected from several proposed names. Other sources may classify some of these genera under slightly different higher-level group names, as a result of the ongoing studies, discussions, and controversies over classification. The binomial genus-species name, however, will nearly always be the same. The existence of more than one name for some of the higher levels of plant classification is simply a reminder that botanists are constantly learning new things about plants and occasionally change their ideas about how plants should be named.

Each of the organisms (bacteria, fungi, and plants) listed in this appendix is alphabetized by its binomial scientific name (far left-hand column); the most often used common name appears in the middle column. Finally, the far-right column identifies the kingdom (k.), phylum (p.), class (c.), order (o.), and family (f.) in which the species is commonly classified, along with some notable characteristics. All organisms can be assumed to belong to the domain *Eukarya* unless one of the other domains (either *Archaea* or *Bacteria*) is identified. The abbreviation g., for "group," indicates a group name that is "artificial"—that is, not based on evolutionary relationships but rather on some common characteristics that have made it convenient for researchers to regard these organisms as a group. The abbreviation spp. stands for "species" (plural).

William B. Cook

Scientific Name	Common Name	Taxonomy and Characteristics
Abies concolor	White fir	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with upright, disintegrating cones.
Abies grandis	Grand fir	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with upright, disintegrating cones.
Abies lasiocarpa	Subalpine fir	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with upright, disintegrating cones.
Abies procera	Noble fir	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with upright, disintegrating cones.
Abronia fragrans	Sand verbena	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Nyctaginaceae*. Tubular, fragrant flowers in dense clusters; found in coastal or desert sands.
Abutilon hybridum	Flowering maple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Small trees with shallow-lobed leaves producing pastel, cup-shaped, hibiscus-like flowers.
Acacia greggii	Catclaw acacia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree with short, curved spines on branches.
Acalpha hispida	Chenille plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Amaranthaceae*. Small, inconspicuous flowers that hang in long, ropelike, crimson clusters from near leaf bases.
Acer macrophyllum	Bigleaf maple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Aceraceae*. Tree with large, lobed, fanlike leaves; paired, winged fruits.
Acer negundo	Box elder	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Aceraceae*. Tree with leaves divided into three leaflets; fruit a pair of winged seeds.
Acer palmatum	Japanese maple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Aceraceae*. Shrub or tree with narrow-lobed, fan-shaped leaves; purple flowers produce paired, winged fruits.
Acer rubrum	Red maple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Aceraceae*. Tree with lobed, fanlike leaves turning scarlet in fall; paired, winged fruits; Rhode Island state tree.
Acer saccharinum	Silver maple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Aceraceae*. Tree with fanlike leaves, silvery beneath; paired, winged fruits.
Acer saccharum	Sugar maple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Aceraceae*. Tree with lobed, fanlike leaves; paired, winged fruits; sap collected to make maple syrup and sugar; state tree of New York, Vermont, Wisconsin, West Virginia.

Scientific Name	Common Name	Taxonomy and Characteristics
Acetabularia spp.	Mermaid's wine glass	k. *Protista*, p. *Chlorophyta*, c. *Ulvophyceae*, o. *Dasycladales*, f. *Dasycladaceae*. Clumps or lawns of single cells with holdfast, flexible stalk, and umbrella-like top.
Acetobacter spp.	Acetobacter	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Alphaproteobacteria*, o. *Rhodospirillales*, f. *Rhodospirillaceae*. Gram-negative cell producing acetic acid; one species is used to make vinegar; others spoil alcoholic beverages.
Achillea millefolium	Yarrow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Gray fernlike leaves and flat-topped flower clusters.
Aconitum napellus	Monk's hood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Tender plant with dark blue flowers, one petal forming a hood over the others; seeds and roots are poisonous.
Actinidia chinensis	Kiwi	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Theales*, f. *Actinidiaceae*. Woody vine; fruit a hairy berry with light green flesh surrounding many small, black seeds; eaten fresh.
Adansonia digitata	Baobab	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Bombacaceae*. African tree with massive trunk; produces a fruit called monkey bread.
Adiantum capillus-veneris	Maidenhair fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Adiantaceae*. Stems black, scaly; leafstalk shiny purple-brown.
Aesculus glabra	Ohio buckeye	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones,* o. *Sapindales*, f. *Hippocastenaceae*. Tree with large, divided fan-shaped leaves; glossy seeds in spiny husks; Ohio state tree.
Aesculus hippocastanum	Horse chestnut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Hippocastenaceae*. Tree with large lobed leaves; upright clusters of ivory flowers marked with yellow; glossy red-brown seeds in soft-spiny husks.
Agaricus bisporus	Mushroom, commercial	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Agaricaceae*. Most common commercial edible mushroom.
Agave americana	Century plant	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Long, fleshy, sword-shaped leaves with hooked spines on edges and tip; tall sturdy flower stalk appears before death.
Agave tequilana	Tequila agave	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Stiff fleshy leaves; tall, stout flowering stalk produced before plant dies; used to make tequila.
Agrobacterium tumefaciens	Agrobacterium	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Alphaproteobacteria*, o. *Rhizobiales*, f. *Rhizobiaceae*. Gram-negative cell causes cancerlike crown gall disease on plants; used in genetic engineering of plants.
Agropyron smithii	Western wheatgrass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. South Dakota state grass.

Scientific Name	Common Name	Taxonomy and Characteristics
Agrostis gigantea	Red top	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Quick-sprouting grass planted with slower-sprouting lawn grasses as a "nurse" crop.
Agrostis stolonifera	Creeping bent grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Quality lawn grass; requires intensive care.
Ailanthus altissima	Tree of heaven	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Simaroubaceae*. Tree with divided leaves; fruit a twisted wing with seed in its center, produced in dense clusters; invasive weedy plant.
Alaria esculenta	Winged kelp	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Laminariales*, f. *Alariaceae*. Single long, thin blade; lateral yellow-brown branches of spore-bearing blades near base.
Albizia julibrissin	Mimosa tree, silk tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree with umbrella-like profile; fluffy pink flower clusters.
Alectoria sarmentosa	Witches' hair	k. *Fungi*, g. lichen, f. *Alectoriaceae*. A dangling, stringy form of lichen found on tree branches.
Aleurites fordii	Tung oil tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Tree whose fruits are pressed to collect oil used in paints and varnishes.
Aleurites moluccana	Candlenut tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Shrubby tree producing clusters of fragrant white flowers; fruits burn due to high oil content; Hawaii state tree.
Allium cepa	Onion	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Hollow leaves from a swelling bulb harvested for pungent flavor in cooking.
Allium sativum	Garlic	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. V-shaped leaves from a bulb; segments of bulb (cloves) used for seasoning.
Allium schoenoprasum	Chives	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Small clump-forming onion; leaves chopped as garnish.
Allomyces macrogynus	Chytrid	k. *Fungi*, p. *Chytridiomycota*, c. *Chytridiomycetes*, o. *Blastocladiales*, f. *Blastocladiaceae*. Fungus that has a life cycle with alternation of generations, typical of plants.
Alnus rubra	Red alder	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Tree whose roots are associated with soil microorganisms that convert (fix) nitrogen from the air to a form used by plants.
Alnus sinuata	Sitka alder	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Spreading shrub or small tree found in alpine or subarctic areas.
Alocasia macrorrhiza	Elephant's ear	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arales*, f. *Araceae*. Clusters of large arrow-shaped leaves on tall stalks.

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Aloe vera	Aloe vera	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Aloaceae*. Clusters of soft, fleshy leaves patterned with dark and light green; slimy leaf contents used to treat ailments of the skin and other organs.
Alternaria brassicicola	Dark leaf spot pathogen	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Dematiaceae*. Causes disease on members of the cabbage family; carried by seeds.
Althaea rosea	Hollyhock	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Tall hairy plants with coarse leaves and hibiscus-like flowers.
Amanita muscaria	Fly agaric	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Amanitaceae*. Mushroom with blood-red cap marked by white patches; stalk with ring of tissue and swollen base.
Amanita phalloides	Death cap	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Amanitaceae*. Mushroom with greenish cap, skirtlike tissue ring, and saclike cup on stalk; deadly.
Amaranthus retroflexus	Pigweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Amaranthaceae*. Coarse, weedy plant with long taproot.
Amaryllis belladonna	Belladonna lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Amaryllidaceae*. Showy clusters of trumpet-shaped flowers on bare stalk.
Ambrosia artemisiifolia	Ragweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Pollen from yellow flowers is associated with hay fever in many; obnoxious farm weed.
Amelanchier laevis	Allegheny serviceberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree producing loose clusters of white flowers followed by edible purple berries.
Anabaena cylindrica	Cyanobacteria	d. *Bacteria*, k. *Eubacteria*, p. *Cyanobacteria*, c. *Cyanobacteria* (ICBN subsection *IV*, f. *I*). Uses a type of photosynthesis that produces oxygen and resembles plant photosynthesis.
Anacardium occidentale	Cashew	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Anacardiaceae*. Tropical tree; fruit (nut) produced at end of fleshy stalk (“apple”), both eaten.
Anagallis arvensis	Scarlet pimpernel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Primulales*, f. *Primulaceae*. Spreading plant that resembles common chickweed but with brick-red flowers.
Ananas comosus	Pineapple	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Bromeliales*, f. *Bromeliaceae*. Tropical plant with stiff, swordlike clustered leaves; each fruit is formed from the bases of entire flower cluster on stout stalk.
Andreaea spp.	Granite mosses	k. *Plantae*, p. *Bryophyta*, c. *Andreaeidae*, o. *Andreaeales*, f. *Andreaeaceae*. Small, tufted reddish to black plants encrusted on rock surfaces.

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Anethum graveolens	Dill	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Seeds, dried leaves, and stems used in cooking, pickling.
Angelica archangelica	Angelica	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Hollow stems candied; leaves used to flavor wines.
Anigozythos manglesii	Kangaroo paw	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Haemodoraceae*. Sword-shaped leaves from thick woody roots; tubular flowers in various colors attract hummingbirds; state emblem of Western Australia.
Annona cherimola	Cherimoya	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Annonaceae*. Tropical tree with large, oval, scaly fruits containing custardlike white flesh and dark seeds.
Annona muricata	Soursop	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Annonaceae*. Small tropical tree; dark green fruit covered with lines of soft spines and filled with custardlike white flesh.
Annona reticulata	Custard apple	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Annonaceae*. Tropical tree; heart-shaped fruits with custardlike white flesh.
Annona squamosa	Sweetsop	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Annonaceae*. Tropical tree; thick fruit with custardlike white flesh.
Anthemis nobilis	Chamomile	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Small flower heads used to make tea.
Anthoceros spp.	Hornworts	k. *Plantae*, p. *Anthocerophyta*, c. *Anthoceropsida*, o. *Anthocerotales*, f. *Anthocerotaceae*. Green body with hornlike reproductive form.
Anthricus cerefolium	Chervil	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Long seeds used in French cooking.
Anthurium andraeanum	Anthurium	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arales*, f. *Araceae*. Tropical plant with dark, glossy leaves and glossy, heart-shaped, bright-colored flower bracts.
Antirrhinum majus	Snapdragon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Tall plant with long flower stalk bearing many two-lipped flowers; commonly used as cut flowers.
Apium graveolens	Celeriac, celery	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Variety of celery grown for its swollen stem, which is chopped into soups and salads.
Aquilegia caerulea	Rocky Mountain columbine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Tall, bold plant with lacy divided leaves; flowers, held above leaves, are large, blue and white, with five prominent spurs; Colorado state flower.

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Aquilegia formosa	Western columbine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Tender plant with fernlike leaves and drooping, scarlet-spurred flowers.
Arachis hypogaea	Peanut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tender plant; seed pods mature underground after flowering; seeds are processed for many foods; stems and leaves are used as fodder, pods for industrial energy production.
Aralia spinosa	Devil's walking stick	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Araliaceae*. Small tree with spiny stems, branches.
Araucaria heterophylla	Norfolk Island pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Araucariaceae*. Evergreen tree with overlapping, sharp-tipped needlelike leaves and roughly spherical cones.
Araucaria imbricata	Monkey puzzle tree	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Araucariaceae*. Evergreen tree with stiff, leathery, sharp-tipped, scalelike leaves on trunk and branches; spherical cone of pointed scales disintegrates at maturity.
Arbutus menziesii	Pacific madrone	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Tree with evergreen, leathery leaves; red bark peels from trunk and branches; flowers are urn-shaped.
Arbutus unedo	Strawberry tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Shrub or small tree producing red, warty, spherical fruits sometimes used in jams.
Arctostaphylos uva-ursi	Bearberry, kinnikinnick	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Low-growing shrub used as a ground cover.
Areca catechu	Betel nut palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tall tree with featherlike leaves and orange or scarlet fruit; seed chewed with leaves of *Piper betel* for stimulant and narcotic effects.
Arisaema triphyllum	Jack-in-the-pulpit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Arales*, f. *Araceae*. Small woodland plant with one or two leaves divided into three segments; tubular sheath surrounds fingerlike flower spike and covers it with a hood.
Aristolochia durior	Dutchman's pipe	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Aristolochiales*, f. *Aristolochiaceae*. Oddly shaped yellow-green flowers like curved pipes with dull purple, flared bowl.
Armoracia rusticana	Horseradish	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Pale yellow fleshy taproot harvested to make horseradish sauce.
Artemisia absinthium	Wormwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Rangy shrub with sharp aroma, bitter taste.

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Artemisia tridentata	Big sagebrush	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Shrub producing leaves with three-lobed tips; pungently fragrant; Nevada state flower.
Arthrobotrys anchonia	Lasso fungus	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Moniliaceae*. Traps roundworms (nematodes) with loops that tighten around them.
Artocarpus altilis	Breadfruit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Tree producing each spherical or cylindrical, yellow-green, starchy fruit from an entire flower cluster; fruit is roasted, boiled, or fried and eaten and is a staple crop on Pacific islands.
Asclepias speciosa	Milkweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Asclepiadaceae*. Small, sturdy plant with elaborate flowers; wounds bleed milky sap; hairy parachutes on seeds.
Asclepias tuberosa	Butterfly weed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Asclepiadaceae*. Milkweed with clusters of bright orange flowers.
Asimina triloba	Pawpaw	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Annonaceae*. Deciduous tree; flowers purple; edible fruit yellow to brown, lumpy.
Asparagus officinalis	Asparagus	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Tall, branched plants with fernlike leaves and red berries; young, sprouting stems eaten raw or cooked.
Aspergillus flavus	Aflatoxin fungus	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Moniliaceae*. Produces aflatoxin, a potent cancer-causing chemical, on stored grains.
Aspidistra elatior	Cast-iron plant	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Tough, glossy leaves with parallel veins.
Asplenium nidus-avis	Bird's-nest fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Aspleniaceae*. Clustered upright, glossy, pale green leaves with undivided blades.
Asplenium platyneuron	Ebony spleenwort	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Aspleniaceae*. Wiry leafstalk lined with paired rounded leaflets.
Asplenium rhizophyllum	Walking fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Aspleniaceae*. Long, tapering leaf blade bears complete young plant.
Athyrium filix-femina	Lady fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Woodsiaceae*. Large, delicately divided leaves.
Atrichum spp.	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Polytrichales*, f. *Polytrichaceae*. Plants form cushionlike mats.
Auricularia auricula	Tree ear	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Auriculariales*, f. *Auriculariaceae*. Brown, rubbery, ear-shaped mushrooms clustered on dead wood.

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Avena sativa	Oat	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Cereal grass cultivated for edible grain.
Averrhoa carambola	Carambola, star fruit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Geraniales*, f. *Oxalidaceae*. Tropical tree producing fleshy fruit with a star-shaped outline when cut in half.
Avicennia nitida	Black mangrove	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Avicenniaceae*. Tree with broad evergreen leaves found in marine tidal zones.
Azadirachta indica	Neem tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Meliaceae*. Tropical evergreen producing fragrant white flowers and edible fruits; extracts used in insecticides, folk remedies.
Azolla spp.	Mosquito fern	k. *Plantae*, p. *Pterophyta*, c. *Salviniopsida*, o. *Salviniales*, f. *Azollaceae*. Free floating, often in dense mats; leaves small, lobed, green to red.
Azospirillum spp.	Azospirillum	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Alphaproteobacteria*, o. *Rhodospirillales*, f. *Rhodospirillaceae*. Gram-negative curved cells convert (fix) nitrogen from the air into a form used by plants.
Bacillus anthracis	Anthrax pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Firmicutes*, c. *Bacilli*, o. *Bacillales*, f. *Bacillaceae*. Gram-positive rod producing the anthrax toxin, which has been produced as a biological weapon.
Bangia spp.	Red algae	k. *Protista*, p. *Rhodophyta*, c. *Rhodophyceae*, o. *Bangiales*, f. *Bangiaceae*. Bodies formed by dark red or purple filaments; includes edible species.
Barbilophozia lycopodioides	Liverwort, leafy	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Jungermanniales*, f. *Jungermanniaceae*. Frilly-looking four-lobed leaves produce large, showy display.
Bdellovibrio bacteriovorus	Bdellovibrio	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Deltaproteobacteria*, o. *Bdellovibrionales*, f. *Bdellovibrionaceae*. Gram-negative curved cell; preys on other bacteria.
Beaucarnea recurvata	Ponytail palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Long, narrow drooping leaves clustered on top of stem; base of stem dramatically swollen.
Begonia semperflorens	Smooth-leaf begonia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Begoniaceae*. Popular bedding plant with smooth, glossy leaves from green to bronze or red; bright flowers from white to red-orange.
Begonia tuberhybrida	Tuberous begonia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Begoniaceae*. Tender plant with asymmetrical leaves; large showy flowers in all colors except blue; from short underground stems (tubers).
Berberis vulgaris	Common barberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Berberidaceae*. Spiny shrub producing yellow flowers and drooping clusters of red berries; used for jelly, candy, or pickling; winter host of wheat rust pathogen.

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Bertholletia excelsa	Brazil nut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lecythidales*, f. *Lecythidaceae*. Tall tropical tree producing large, round, rock-hard fruit containing many seeds (nuts).
Beta vulgaris	Beets, chard, mangel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Chenopodiaceae*. Swollen red roots boiled and eaten hot or cold.
Betula alleghaniensis	Yellow birch	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Tree; bark yellow to copper-colored.
Betula nigra	River birch	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Tree found along river banks; bark on mature trees is dark and scaly.
Betula papyrifiera	Paper birch	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Tree; bark of mature trees white and peeling horizontally; New Hampshire state tree.
Blechnum spicant	Deer fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Blechnaceae*. Green leaves shorter than darker, spore-bearing leaves.
Boletus edulis	King bolete	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Boletales*, f. *Boletaceae*. Large mushroom with red-brown caps; spores located in pores rather than gills.
Borrelia burgdorferi	Lyme disease pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Spirochaetes*, c. *Spirochaetes*, o. *Spirochaetales*, f. *Spirochaetaceae*. Gram-negative spiral-shaped cell that causes Lyme disease.
Boswellia carteri	Frankincense	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Burseraceae*. One of several *Boswellia* species producing an aromatic gum resin used in incense.
Botrychium spp.	Grape fern	k. *Plantae*, p. *Pterophyta*, c. *Ophioglossopsida*, o. *Ophioglossales*, f. *Ophioglossaceae*. One leaf per season; green lower portion divided into half-moon segments; upper portion without blade bears spores.
Botrychium lunaria	Moonwort	k. *Plantae*, p. *Pterophyta*, c. *Ophioglossopsida*, o. *Ophioglossales*, f. *Ophioglossaceae*. One leaf per season; green lower portion divided, upper portion without blade bears spores.
Bougainvillea spectabilis	Bougainvillea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Nyctaginaceae*. Vine with showy bracts surrounding flowers.
Bouteloua curtipendula	Sideoats grama	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Texas state grass.
Brachythecium spp.	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Brachytheciaceae*. Leaves folded along prominent midrib.
Brassica juncea	Indian mustard	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Flour from ground seeds included in table mustard.

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Brassica napus	Rutabaga	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Turniplike plant producing a yellowish, flavorful root.
Brassica oleracea	Cabbage family	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Green flowering stalk harvested while flowers are in bud, eaten raw or cooked; includes broccoli, brussels sprouts, cabbage, cauliflower, collards, kohlrabi.
Brassica rapa	Turnip	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Grown for swollen root used in soups and salads; young leaves eaten as greens.
Buchloe dactyloides	Buffalo grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Bunch grass used for drought-tolerant, low-maintenance lawns.
Buddleja davidii	Butterfly bush	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Buddlejaceae*. Shrub producing small, fragrant flowers in dense, slender clusters; attracts butterflies.
Bursera simarouba	Gumbo-limbo	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Burseraceae*. Tree with leaves divided into leathery leaflets; red leathery fruits single-seeded; light wood used for fishing floats.
Caesalpinia gilliesii	Bird of paradise	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Shrubby plant with showy, clustered red and yellow flowers.
Calamus spp.	Rattan palms	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Spiny vines grow into tops of neighboring trees and produce large crowns of leaves.
Callicarpa americana	American beautyberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Verbenaceae*. Shrub producing long stalks of red-purple berries.
Callirhoe involucrata	Wine cup	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Trailing plant with tall flower stalks bearing deep wine-colored, cup-shaped flowers.
Calochortus nuttallii	Sego lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Tall, graceful, early summer flowers from bulbs; Utah state flower.
Caltha palustris	Marshmarigold	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Bog or marsh plant with glossy, heart-shaped leaves and vivid yellow flowers.
Calvatia booniana	Western giant puffball	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Lycoperales*, f. *Lycoperdaceae*. Volleyball-sized sphere filled with dark spores.
Camassia quamash	Camas	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Grasslike leaves surround bare flower stalk with loose cluster of deep blue flowers.
Camellia japonica	Camellia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Theales*, f. *Theaceae*. Shrub or small tree producing glossy leaves and large showy flowers; Alabama state flower.

Scientific Name	Common Name	Taxonomy and Characteristics
Camellia sinensis	Tea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Theales*, f. *Theaceae*. Dense shrub with leathery leaves harvested and processed to make tea.
Campanula isophylla	Star of bethlehem	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Campanulales*, f. *Campanulaceae*. Hanging plant with pale blue, star-shaped flowers.
Campanula medium	Canterbury bell	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Campanulales*, f. *Campanulaceae*. Pink, blue, purple or white flowers are bell- or urn-shaped.
Campsis radicans	Trumpet vine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Bignoniaceae*. Vigorous climbing vine producing clusters of bold orange or red tubular flowers.
Campylium spp.	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Amblystegiaceae*. Plants star-shaped from above; clusters of plants with a bristly look.
Candida albicans	Thrush pathogen	k. *Fungi*, g. deuteromycetes, c. *Blastomycetes*, o. *Cryptococcales*, f. *Cryptococcaceae*. Causes human infections when the immune system is weak or normal bacteria are depleted.
Canna indica	Canna lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Cannaceae*. Leafy, banana-like plant with bright flower clusters on tall stalks.
Cannabis sativa	Hemp, marijuana	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Cannabaceae*. Shrub with fanlike divided leaves; stem fibers used for rope, rough cloth; leaves and flowers contain a psychoactive compound.
Cantharellus cibarius	Chanterelle	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Cantharellales*, f. *Cantharellaceae*. Mushroom with bright yellow to orange wavy-edged cap, thick ridges merge with the stalk; available commercially.
Capparis spinosa	Caper	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Capparaceae*. Unopened flower buds pickled to make capers.
Capsicum annuum	Pepper	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Produces a hollow berry; varieties differ in fruit size, shape, color, flavor; includes sweet and chili peppers.
Carica papaya	Papaya	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Caricaceae*. Treelike plant with large, deeply lobed leaves; many thick, fleshy fruits grow from stem (trunk); seeds in center in a slimy envelope.
Carludovica palmata	Panama hat palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyclanthales*, f. *Cyclanthaceae*. Segments of large, palmlike leaves woven into Panama hats.
Carnegiea gigantea	Saguaro cactus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Cactaceae*. Massive upright cylindrical stem with a few stout upright branches; blossom is Arizona state flower.

Scientific Name	Common Name	Taxonomy and Characteristics
Carpinus caroliniana	American hornbeam	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree whose fruit is a cluster of leaflike bracts.
Carthamus tinctorius	Safflower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Yellow-green flower heads nestled in leaflike bracts; used in arrangements; dried flowers resemble saffron in color and flavor.
Carum carvi	Caraway	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Umbrella-like flower cluster producing seeds used to flavor cheeses, breads.
Carya cordiformis	Bitternut hickory	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Juglanales*, f. *Juglandaceae*. Tree; fruit a thin, scaly husk enclosing a thin-shelled, four-ribbed nut with a bitter seed.
Carya illinoensis	Pecan	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Juglanales*, f. *Juglandaceae*. Tree whose fruit is a dark brown husk enclosing thin-shelled red-brown nut; Texas state tree.
Carya ovata	Shagbark hickory	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Juglanales*, f. *Juglandaceae*. Tree whose fruit is a four-parted brown to black husk enclosing a light brown nut; bark shaggy on mature trees.
Caryota urens	Fishtail palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tree with leaf blades divided into segments narrow at the base and wider at the tips, resembling fish tail fins.
Casimiroa edulis	White sapote	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Tropical tree producing masses of lime-sized, yellow-green fruits with juicy, sweet flesh and large seeds.
Castanea dentata	American chestnut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; fruits have prickly husks containing two or three flattened nuts.
Castilleja spp.	Indian paintbrush	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Tender plant with bright yellow, red or purple flower bracts; *C. linariaefolia* is Wyoming state flower.
Catalpa bignonioides	Southern catalpa	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Bignoniaceae*. Tree producing clusters of tubular white, yellow, or purple flowers followed by long beanlike fruits.
Catharanthus roseus	Madagascar periwinkle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Apocynaceae*. Tender plant with flowers twisted in bud; popular bedding plant and source of drug used to treat childhood leukemia.
Cattleya spp.	Orchid	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Orchidales*, f. *Orchidaceae*. Plants with large, showy flowers that grow perched on other plants; most popular cultured orchids.
Caulobacter crescentus	Appendaged bacterium	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Alphaproteobacteria*, o. *Caulobacterales*, f. *Caulobacteraceae*. Goes through a complex life cycle.

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Cecropia peltata	Cecropia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Fast-growing tropical tree; preferred food source of sloths.
Cedrus atlantica	Atlas cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with upright, disintegrating cone.
Cedrus deodara	Deodar cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with upright, disintegrating cone.
Ceiba pentandra	Kapok	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Bombacaceae*. Tall tropical tree; silky, cottonlike fibers surrounding seeds are used to make mattresses, life preservers.
Celtis occidentalis	Hackberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Ulmaceae*. Small tree with slightly curved leaf tips, red to purple berries.
Centaurea cyanus	Bachelor's button	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Flower heads have lobed segments in shades of pink, blue, or white.
Cephaelis ipecacuanha	Ipecac	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rubiales*, f. *Rubiaceae*. Plants produce a mixture of alkaloids used in treatment of amoebic dysentery.
Cephalanthus occidentalis	Common buttonbush	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rubiales*, f. *Rubiaceae*. Shrub with spherical white flower heads that appear bristly from stamens sticking out beyond the small flowers.
Ceratonia siliqua	Carob	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tree with pulpy pods used to make bread, cake, and chocolate substitute.
Cercidium torreyanum	Palo verde	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree producing masses of small, bright yellow, spring flowers; bluish-green spiny branches bear leaves divided into tiny leaflets; Arizona state tree.
Cercis canadensis	Redbud	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree; showy pink-purple flowers appear in spring before glossy leaves; Oklahoma state tree.
Chaetoceros spp.	Diatoms	k. *Protista*, p. *Bacillariophyta*, c. *Bacillariophyceae*, o. *Chaetocerotales*, f. *Chaetocerotaceae*. Cells grow in chains. Source of diatomaceous earth, used as abrasives and in filters.
Chamaecyparis lawsoniana	Port-orford cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with flat twigs of scalelike leaves; cone has shield-shaped scales.
Chamaecyparis nootkatensis	Alaska cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with flat twigs of scalelike leaves; cone scales are shield-shaped.
Chara spp.	Stonewort	k. *Protista*, p. *Chlorophyta*, c. *Charophyceae*, o. *Charales*, f. *Characeae*. Filaments with several branches per node and single-celled internodes.

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Cheilanthes spp.	Lip ferns	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Adiantaceae*. Stem short with orange scales; leaves tufted, evergreen.
Chenopodium album	Lamb's quarters	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Portulacaceae*. Leaves gray-green and sometimes cooked like spinach.
Chicorium endiva	Endive	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Leaves eaten fresh or blanched to reduce bitterness.
Chilomonas spp.	Cryptomonads	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Cryptomonadaceae*. Cells with colorless plastids; thought to have a photosynthetic ancestor. *Chilomonas paramecium* produces low levels of a fish-killing toxin.
Chilopsis linearis	Desertwillow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Bignoniaceae*. Shrub or small tree with narrow, willowlike leaves and tubular white, yellow, and purple flowers followed by broad beanlike fruit; adapted to severe desert conditions.
Chlamydia psittaci	Parrot fever pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Chlamydiae*, c. *Chlamydiae*, o. *Chlamydiales*, f. *Chlamydiaceae*. Very small gram-negative cell causes parrot fever; can cause pneumonia in humans.
Chlamydomonas spp.	Chlamydomonas	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*, o. *Volvocales*, f. *Chylamydomoniaceae*. Single cells grow in fresh water, moist soils, and snow; *C. reinhardtii* widely used for laboratory research.
Chlorophytum comosum	Spider plant	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Popular houseplant forms clumps of broad, grasslike leaves and plantlets on wiry hanging branches.
Chondrus crispus	Irish moss	k. *Protista*, p. *Rhodophyta*, c. *Rhodophyceae*, o. *Gigartinales*, f. *Gigartinaceae*. Marine red alga; source of carrageenan, used as a thickener in paints, cosmetics, dairy products.
Chorda filum	Sea lace	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Chordariales*, f. *Chordariaceae*. Noted for its long, cordlike blade from a disclike holdfast.
Chroomonas spp.	Cryptomonads	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Cryptomonadaceae*. Cells with single blue-green, H-shaped chloroplasts.
Chroomonas lacustris	Cryptomonad	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Cryptomonadaceae*. Grows in ice-covered Antarctic lakes during summer.
Chrysamoeba spp.	Golden brown algae	k. *Protista*, p. *Chrysophyta*, c. *Chrysophyceae*, o. *Chrysamoebales*, f. *Chrysamoebaceae*. Amoeba-like cells may produce a single flagellum.

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Chrysochromulina spp.	Haptophytes	k. *Protista*, p. *Haptophyta*, c. *Prymnesiaceae*, o. *Prymnesiales*, f. *Prymnesiaceae*. Marine cells that obtain food by photosynthesis and by consuming bacteria; some cause toxic blooms.
Chrysophyllum cainito	Star apple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ebenales*, f. *Sapotaceae*. Evergreen broadleaf tropical tree with edible pulpy fruit.
Cibotium glaucum	Hawaiian tree fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Dicksoniaceae*. Broad plant with short, treelike trunk topped by many feathery, golden-green leaves.
Cicer arietinum	Chickpea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Pea relative producing pods with one or two seeds; main ingredient in hummus.
Cichorium intybus	Chickory	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Roots used as coffee substitute; leaves eaten in salads or cooked.
Cicuta maculata	Water hemlock	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Reported to be the most poisonous North American plant; easily confused with angelica.
Cinchona spp.	Quinine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rubiales*, f. *Rubiaceae*. Plants produce an alkaloid, quinine, that is effective in treating malaria.
Cinnamomum camphora	Camphor tree	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Laurales*, f. *Lauraceae*. Tree with shiny yellow-green leaves and many clusters of tiny yellow flowers; source of commercial camphor.
Cinnamomum zeylanicum	Cinnamon	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Laurales*, f. *Lauraceae*. Tall tree; grown for its bark, which is scraped off and used whole or ground to powder for use as a cooking spice.
Cirsium arvense	Canada thistle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Stiff plants with spines on stems and leaves; fluffy; pink to purple flowers.
Cirsium vulgare	Bull thistle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Rigid upright plants with spines on stems, leaves, and flower heads; flowers deep purple in dense clusters, followed by seeds with hairy parachutes.
Cissus rhombifolia	Grape ivy	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rhamnales*, f. *Vitaceae*. Trailing or climbing vine grown as a houseplant.
Citrullus lanatus	Watermelon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Hairy trailing or climbing vine; solid fruits with seedy, red or yellow, juicy flesh.
Citrus aurantifolia	Lime	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Small tree with glossy leaves producing green lemonlike fruit used for juice or flavoring.

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Citrus limon	Lemon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Small tree with glossy leaves producing a very acidic yellow fruit used for juice or candied rind.
Citrus paradisi	Grapefruit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Evergreen tree with glossy leaves producing large yellow, orangelike fruits; eaten fresh, canned, or pressed for juice.
Citrus reticulata	Tangerine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Small tree with glossy leaves; small orangelike fruits eaten fresh or canned.
Citrus sinensis	Navel orange, sweet orange	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Evergreen tree with glossy leaves; fruit has juicy segments and peelable rind; eaten fresh or pressed for juice; blossom is Florida state tree.
Cladonia cristatella	British soldiers	k. *Fungi*, g. lichen, f. *Cladoniaceae*. Small, erect, light-colored stalks with red knobs on top.
Cladonia rangiferina	Reindeer lichen	k. *Fungi*, g. lichen, f. *Cladoniaceae*. Gray-green and darkening with age; grows in thick cushions in tundra.
Cladonia stellaris	Powder puff lichen	k. *Fungi*, g. lichen, f. *Cladoniaceae*. Resembles pale green cauliflower heads.
Cladonia subtenuis	Reindeer moss	k. *Fungi*, g. lichen, f. *Cladoniaceae*. One of several lichens in the diets of reindeer and other Arctic mammals.
Clarkia unguiculata	Mountain garland	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Onagraceae*. Tender upright plant with reddish stems and rose, purple, or white flowers.
Claviceps purpurea	Ergot	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Clavicepitales*, f. *Clavicepitaceae*. Infects grain crops, producing toxins that cause ergotism or St. Anthony's fire.
Clavulina cinerea	Ashy coral mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales*, f. *Polyporaceae*. Gray, highly branched fungus resembling coral.
Claytonia virginica	Spring beauty	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Portulacaceae*. Wiry stem with pair of narrow succulent leaves; flowers white with or without pink stripes.
Cleome spinosa	Spider flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Capparaceae*. Shrub with spiny stem; clusters of white or pink flowers with fluffy exposed stamens.
Clivia miniata	Kaffir lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Amaryllidaceae*. Shiny, dark green leaves with bare flower stalks bearing clusters of orange, funnel-shaped flowers.

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Clostridium botulinum	Botulism pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Firmicutes*, c. *Clostridia*, o. *Clostridiales*, f. *Clostridiaceae*. Gram-positive rod producing the powerful toxin that causes botulism.
Coccoloba uvifera	Sea grape	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Polygonales*, f. *Polygonaceae*. Shrub with leathery evergreen leaves producing long clusters of grapelike berries; found on sandy marine shores.
Coccothrinax argentata	Florida silverpalm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tree; fan-shaped leaves; one-seeded black fruits.
Cocos nucifera	Coconut palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tree with large, featherlike leaves; fruit is three-sided and one-seeded, with a fibrous husk; seed contains white solid "meat" and thin white liquid "milk."
Coffea arabica	Coffee	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rubiales*, f. *Rubiaceae*. Shrub or small tree producing crimson fruits containing seeds (beans) processed for coffee.
Coffea canephora	Coffee	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rubiales*, f. *Rubiaceae*. Tree producing small fruits harvested for seeds (beans) inside husk; ground seeds are used for coffee.
Cola nitida	Kola nut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Sterculiaceae*. Tree; fruit contains caffeine; extract used in carbonated beverages and phamaceuticals.
Coleosporium tussilaginis	Rust	k. *Fungi*, p. *Basidiomycota*, c. *Uredinomycetes*, o. *Uredinales*, f. *Coliosporiaceae*. Infects several hosts, including pine needles.
Coleus hybridus	Coleus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Popular bedding plant; many varieties have boldly colored leaves.
Commelina communis	Day flower	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Commelinales*, f. *Commelinaceae*. Trailing or climbing plant with brilliant blue flowers that fade in late morning.
Commiphora myrrha	Myrrh	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Burseraceae*. One of several *Commiphora*. Species producing aromatic gum resin used in perfumes and incense.
Conium maculata	Poison hemlock	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Presumed to be the source of the poison used by Socrates to commit suicide.
Connarus guianensis	Zebra wood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Connaraceae*. Small tree or shrub harvested for wood, striped black, brown, and whitish.
Conocephalum conicum	Liverwort, thalloid	k. *Plantae*, p. *Hepatophyta*, c. *Marchantiopsida*, o. *Marchantiales*, f. *Conocephalaceae*. Found on moist sand or acidic rock surfaces; pores on lobes are surrounded by distinct hexagonal pattern.

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Consolida ajacis	Larkspur	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Tall plant with fernlike leaves; flowers white, pink, or purple on tall stalks.
Convallaria majalis	Lily of the valley	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Small, fragrant, waxy, white, drooping, bell-shaped flowers on a stalk with two broad leaves; all parts are poisonous.
Convolvulus arvensis	Field bindweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Convolvulaceae*. Trailing, climbing vine; aggressive noxious pest of grain and other crops; white funnel-shaped flowers showy for their size.
Coreopsis tinctoria	Calliopsis	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Wiry stems; flower heads with yellow segments, maroon bases, maroon centers.
Coriander sativum	Cilantro, coriander	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Spherical fruits and young leaves used in cooking.
Cornus florida	Flowering dogwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Cornales*, f. *Cornaceae*. Small tree; small flowers surrounded by four showy, petal-like white or pink bracts; fruits bright red; state tree of Virginia, Missouri; state flower of Virginia, North Carolina.
Cornus stolonifera	Red-osier dogwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Cornales*, f. *Cornaceae*. Shrub; blue-black fruit in flat-topped clusters.
Cortaderia selloana	Pampas grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Giant evergreen grass with saw-toothed leaves and long, fluffy plumes of flowers.
Corydalis aurea	Scrambled eggs	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Papaverales*, f. *Fumariaceae*. Tender plant with blue-green, fernlike leaves and clusters of oddly shaped yellow flowers.
Corylus cornuta	California hazel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Shrub or small tree; fruit a round nut surrounded by leafy, hairy bracts.
Corylus maxima	Filbert	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Shrub or small tree; fruit a short, round, tapering nut surrounded by leafy, hairy bracts.
Couroupita guianensis	Cannonball tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lecythidales*, f. *Lecythidaceae*. Tropical tree producing large, hard spherical fruits.
Crataegus spp.	Red hawthorn	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree; dense flower clusters produce scarlet fruits; blossom is Missouri state flower.
Crataegus douglasii	Black hawthorn	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Thorny tree; broad flower clusters produce shiny black fruits.

Scientific Name	Common Name	Taxonomy and Characteristics
Crataegus mollis	Downy hawthorn	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree with long spines; dense flower clusters produce scarlet fruits.
Crataegus spathulata	Littlehip hawthorn	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree; leaves with three lobes at tip; white flowers in dense clusters followed by small scarlet fruits.
Crocus sativus	Saffron crocus	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Iridaceae*. Cluster of small grasslike leaves from underground stems (corms); dried orange-red stigmas of flowers are the source of the spice saffron.
Crucibulum laeve	Bird's-nest fungus	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Nidulariales*, f. *Nidulariaceae*. Cup-shaped cap resembles nest containing round spore-bearing "eggs."
Cryptomonas spp.	Cryptomonads	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Cryptomonadaceae*. Small cells found in cold or deep waters; chloroplasts, when present, surrounded by four-layered envelope.
Cryptomonas undulata	Cryptomonad	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Cryptomonadaceae*. Grows deep in lakes where light is very low.
Cucumis anguria	Gherkin	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Hairy climbing or trailing vine; small cucumber-like fruit used mostly for pickles.
Cucumis melo	Canteloupe, muskmelon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Climbing or trailing vine; hollow fruits with thick, fleshy rind; skin hard, warty.
Cucumis sativus	Cucumber	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Hairy climbing or trailing vine; solid fruits with seedy centers; eaten fresh, cooked, or pickled.
Cucurbita maxima	Giant pumpkin, squash	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Trailing vine with bristly-hairy stem and leaves; yellow, funnel-shaped flowers produce hollow, seedy fruit with thick, fleshy rind.
Cucurbita moschata	Pumpkin, squash	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Trailing vine with soft-hairy stem and leaves; yellow, funnel-shaped flowers produce hollow, seedy fruit with thick, fleshy rind.
Cucurbita pepo	Zucchini	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Trailing stem or bushy plant; cylindrical or spherical fruit harvested when immature and used fresh, cooked, or in baking.
Cuminum cyminum	Cumin	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Small seeds used for pungent caraway-like scent and flavor.

Scientific Name	Common Name	Taxonomy and Characteristics
Cupressus arizonica	Arizona cypress	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Trees with scalelike leaves; cone scales shield-shaped.
Cupressus macrocarpa	Monterey cypress	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with scalelike leaves; cone scales shield-shaped.
Curcuma domestica	Turmeric	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Zingiberaceae*. Tender plant with broad, fanlike leaves; thick underground stems used as spice in curries and as yellow dye.
Cuscuta spp.	Dodder	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Cuscutaceae*. Yellow or orange wiry vines parasitic on series of host plants; grows into dense colonies in infested areas.
Cyanidium spp.	Red algae	k. *Protista*, p. *Rhodophyta*, c. *Bangiophyceae*, o. *Porphyridiales*, f. *Cyanidium* single cells; most grow in acidic hot springs.
Cyathea cooperi	Australian tree fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Cyatheaceae*. Narrow, treelike trunk bears large, finely divided leaves with irritating brown hairs.
Cycas revoluta	Sago palm	k. *Plantae*, p. *Cycadophyta*, c. *Cycadopsida*, o. *Cycadales*, f. *Cycadaceae*. Palmlike shrub with seeds borne on stalks of specialized leaves.
Cydonia oblonga	Quince	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Shrub producing a hard, distasteful, pearlike fruit; used in jams, jellies after cooking.
Cymbidium spp.	Orchid	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Orchidales*. Grows rooted in soil at high altitudes; popular ornamental.
Cynara scolymus	Globe artichoke	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Large, scaly flower head is boiled and eaten.
Cynodon dactylon	Burmuda grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Fine-textured lawn grass; spreads vigorously by runners.
Cyperus esculentus	Nut grass, nut sedge	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Cyperaceae*. Persistent lawn weed regrowing from deep tubers (“nuts”) after leaves are pulled off.
Cyperus papyrus	Paper rush	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Cyperaceae*. Tall stems topped by clusters of threadlike green stringers; found in standing water; ancient form of writing paper was made from pith and stems.
Cypripedium acaule	Pink lady’s slipper	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Orchiales*, f. *Orchidaceae*. Small, delicate plants rooted in soil; pink flowers with bowl-shaped segment; New Hampshire state wildflower.
Cypripedium reginae	Showy lady’s slipper	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Orchiales*, f. *Orchidaceae*. Small, delicate plants rooted in soil; pink flowers with bowl-shaped segment; Minnesota state flower.

Scientific Name	Common Name	Taxonomy and Characteristics
Cytisus scoparius	Scotch broom	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Bushy blue-green shrub producing masses of bright yellow flowers.
Cytophaga hutchinsonii	Gliding bacterium	d. *Bacteria*, k. *Eubacteria*, p. *Bacteroidetes*, c. *Sphingobacteria*, o. *Sphingobacteriales*, f. *Flexibacteraceae*. Moves rapidly by an unknown method; breaks down cellulose in plant cell walls.
Dactylaria candida	Nematicidal fungus	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Moniliaceae*. Captures very small worms (nematodes) with sticky knobs or loops.
Dactylis glomerata	Orchard grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Tall grass with dense flower clusters on leafy stalks.
Daldina concentrica	Carbon balls, cramp balls	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Xylariales*, f. *Xylariaceae*. Small, hard, black balls clustered on wood.
Dalea spinosa	Smoke tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree with spiny twigs; purple flower clusters.
Darlingtonia californica	California pitcher plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Nepenthales*, f. *Sarraceniaceae*. "Carnivorous" plant; clusters of hollow, water-filled, tubular leafstalks trap and digest insects.
Dasya spp.	Red algae	k. *Protista*, p. *Rhodophyta*, c. *Florideophyceae*, o. *Ceramiales*, f. *Dasyaceae*. Develop branched, feathery bodies.
Datura stromonium	Jimson weed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Coarse shrub with long, trumpet-shaped, white or pale purple flower; produces poisonous and narcotic chemicals.
Daucus carota	Carrot, Queen Anne's lace	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Root varies by variety from short to long, always swollen; eaten raw, cooked, or juiced.
Delonix regia	Flamboyant tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tall broad tree with large masses of red and white flowers.
Dendrobium spp.	Orchid	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Orchidales*, f. *Orchidaceae*. Grows perched on other plants; popular ornamental.
Dendroceros spp.	Hornworts	k. *Plantae*, p. *Anthocerophyta*, c. *Anthoceropsida*, o. *Anthocerotales*, f. *Dendrocerotaceae*. Ribbonlike body lives on leaves of other plants.
Desulfovibrio spp.	Sulfur bacteria	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Deltaproteobacteria*, o. *Desulfovibrionales*, f. *Desulfovibrionaceae*. Grows without oxygen; produces rotten-egg odor and black color of mudflats such as those on the Black Sea.
Dianthus barbatus	Sweet William	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Caryophyllaceae*. Small, frilly, white, pink, or two-colored flowers with leafy bracts.

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Dianthus caryophyllus	Carnation	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Caryophyllaceae*. Fragrant, showy, frilled, white, pink, or red flowers; Scarlet carnation is Ohio state flower.
Dicentra spectabilis	Bleeding heart	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Papaverales*, f. *Fumariaceae*. Tender woodland plant with fernlike leaves producing pale purple, drooping, heart-shaped flowers.
Dicksonia antarctica	Tasmanian tree fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Dicksoniaceae*. Thick, red-brown, treelike trunk bears many large, arching, divided leaves.
Dictyophora duplicata	Netted stinkhorn	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Phallales*, f. *Phallaceae*. Pitted head covered with green spore slime; white netted skirt on stalk; foul odor.
Dictyostelium discoideum	Cellular slime mold	k. *Protista*, p. *Dictyosteliomycota*, c. *Dictyosteliomycetes*, o. *Dictyosteliales*, f. *Dictyosteliaceae*. Single amoeba-like cells join to form a sluglike mass for reproduction.
Dieffenbachia amoena	Dumbcane	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Arales*, f. *Araceae*. Ornamental plant with broad green and white leaves; all parts contain sap that numbs skin on contact.
Digitalis purpurea	Foxglove	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Tall plant with hairy gray-green leaves clustered at base and tubular, white or purple, dangling flowers along mature stem; source of digitalis used as heart medicine.
Dinobryon spp.	Golden brown algae	k. *Protista*, p. *Chrysophyta*, c. *Chrysophyceae*, o. *Ochromonadales*, f. *Dinobryaceae*. Tree-shaped colonies made up of cells in vaselike chambers; obtain food by photosynthesis and consuming bacteria.
Dinophysis spp.	Dinoflagellates	k. *Protista*, p. *Dinophyta*, c. *Dinophyceae*, o. *Dinophysiales*, f. *Dinophysiaceae*. Armored marine cells with or without chloroplasts.
Dionaea muscipula	Venus's flytrap	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Nepenthales*, f. *Droseraceae*. "Carnivorous" plant; grows in nutrient-poor soils in the southeastern U.S.; traps insects with leaves modified into "snap-traps."
Dioscorea alata	Yam	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Dioscoreaceae*. Climbing vines with heart-shaped leaves; one of several species grown in tropics for the starchy tuber; not related to sweet potato (which is sold as both "yams" and "sweet potatoes" in the U.S.).
Diospyros virginiana	Common persimmon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ebenales*, f. *Ebenaceae*. Tree producing edible fleshy fruit.
Dipsacus sylvestris	Teasel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales*, f. *Dipsacaceae*. Prickly plant with large, spiny flowering head; used in dried arrangements.

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Dodecatheon meadia	Shooting star	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Primulales*, f. *Primulaceae*. Tender plant; bare stalk with several drooping flowers; pale blue petals bent back, other flower parts pointed forward.
Dracaena draco	Dragon tree	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Stout treelike trunk with upright branches bearing clusters of long, sword-shaped leaves.
Dracaena marginata	Dracaena	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Small, palmlike tree; slender, smooth, gray stems bear clusters of narrow, leathery leaves; leaves sprout from cut stems.
Drosera rotundifolia	Sundew	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Nepenthales*, f. *Droseraceae*. "Carnivorous" plant; one of many species of sundews that capture insects with sticky droplets on sturdy hairs covering leaves.
Dryopteris spp.	Wood ferns	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Adiantaceae*. Stems short, thick, scaly; leaves clustered, often evergreen.
Duchesnea indica	Indian mock strawberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small spreading plant producing dry, insipid, seedy fruit resembling a strawberry.
Dunaliella spp.	Dunaliella	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*, o. *Volvocales*, f. *Dunaliellaceae*. Grows in extremely salty waters; used commercially to produce glycerol and beta-carotene.
Durio zibethinus	Durian	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Bombacaceae*. Tropical tree producing seeds in flavorful sacs within a sharp-spiny stinking husks.
Echinacea purpurea	Purple coneflower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Coarse upright stems; showy purple flower heads with spiny centers.
Eichhornia crassipes	Water hyacinth	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Pontederiaceae*. Noxious imported weed that grows vigorously in fresh water.
Elachista spp.	Brown algae	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Chordariales*, f. *Elachistaceae*. Grows as tufts of filaments on large brown algae.
Elaeagnus angustifolia	Russian olive	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Proteales*, f. *Elaeagnaceae*. Small tree with shredding bark, silver-gray willowlike leaves, and fragrant flowers; berrylike fruits resemble small olives.
Elaeis guineensis	Oil palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tall tree with feather-shaped leaves and large clusters of small coconut-like fruits; palm oil and palm kernel oil are extracted for commercial uses.

Scientific Name	Common Name	Taxonomy and Characteristics
Eleocharis dulcis	Water chestnut	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Cyperaceae*. Upright tubular stems from compressed firm-fleshed underground stems (corms); found in standing water.
Elettaria cardamomum	Cardamom	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Zingiberaceae*. Tall, leafy, grasslike relative of ginger; seeds used as cooking spice, as flavoring, and in perfumes.
Elodea canadensis	Elodea	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Hydrocharitales*, f. *Hydrocharitaceae*. Freshwater aquatic with many translucent leaves; often used in aquaria.
Emiliania huxleyi	Haptophyte	k. *Protista*, p. *Haptophyta*, c. *Prymnesiophyceae*, o. *Coccolithophorales*, f. *Coccolithaceae*. Tolerates high salt concentrations; forms extensive marine blooms; contributes large amounts of sulfur to acid rain formation.
Encalypta spp.	Candle snuffer mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Encalyptaceae*. Conspicuous cover (calyptra) over the spore-bearing capsule.
Entoloma salmoneum	Salmon unicorn entoloma	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Entolomataceae*. Salmon-colored mushroom; found in forest litter and decaying logs.
Enturia inaequalis	Apple scab pathogen	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Pleosporales*, f. *Venturaceae*. Disfigures skin of apple fruit.
Ephedra nevadensis	Mormon tea	k. *Plantae*, p. *Gnetophyta*, c. *Gnetopsida*, o. *Gnetales*, f. *Ephedraceae*. One of many species of *Ephedra*; some used as source of ephedrine.
Epigaea repens	Trailing arbutus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Small, low shrub producing clusters of waxy pink or white fragrant flowers at branch tips; Massachusetts state flower.
Epilobium angustifolium	Fireweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Onagraceae*. Tall, graceful plant found on recently disturbed land.
Equisetum arvense	Common horsetail	k. *Plantae*, p. *Sphenophyta*, c. *Sphenopsida*, o. *Equisetales*, f. *Equisetaceae*. Rough green stems with branches; cone-bearing stems unbranched.
Equisetum hyemale	Common scouring rush	k. *Plantae*, p. *Sphenophyta*, c. *Sphenopsida*, o. *Equisetales*, f. *Equisetaceae*. Gray-green, rough, unbranched stem.
Equisetum sylvaticum	Wood horsetail	k. *Plantae*, p. *Sphenophyta*, c. *Sphenopsida*, o. *Equisetales*, f. *Equisetaceae*. Rough green stems produce branched branches, giving a shaggy look; cone-bearing stems branch after cones drop off.
Erythrina herbacea	Eastern coralbean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree producing long cluster of scarlet flowers; seeds scarlet.
Erythroxylum coca	Coca	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Linales*, f. *Erythroxylaceae*. Shrub or small tree; leaves harvested for narcotic alkaloid, cocaine.

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Escherichia coli	E. coli	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Gammaproteobacteria*, o. *Enterobacteriales*, f. *Enterobacteriaceae*. Gram-negative rod living in the intestines of mammals; some forms can cause disease.
Eschscholzia californica	California poppy	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Papaverales*, f. *Papaveraceae*. Clusters of fernlike leaves and bright yellow-orange flowers; common ornamental; California state flower.
Eucalyptus regnans	Eucalyptus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Myrtaceae*. Tall tree with resinous leaves and fruits; includes tallest flowering plant.
Euglena spp.	Euglena	k. *Protista*, p. *Euglenophyta*, c. *Euglenophyceae*, o. *Euglenales*, f. *Euglenaceae*. Cylindrical cells with red, green, or colorless plastids.
Euonymus atropurpureus	Eastern wahoo	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Celastrales*, f. *Celastraceae*. Small tree; clustered, dark purple flowers; fruit four-lobed, deep red-purple.
Euonymus elata	Winged euonymus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Celastrales*, f. *Celastraceae*. Shrub; twigs with corky wings along sides; leaves bright red in fall.
Euphorbia marginata	Snow-on-the-mountain	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Succulent plant with white stripes on upper leaves.
Euphorbia pulcherrima	Poinsettia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Shrub or pot plant with bright, leafy bracts; popular winter holiday plant.
Euphorbia splendens	Crown of thorns	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Shrubby plant with long sharp thorns along stem; bright red or yellow, leafy bracts surround flowers.
Euphorbia tirucalli	Pencil tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Shrub or small tree with tangle of pale green, pencil-thick fleshy branches.
Eustoma exaltatum	Prairie gentian	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Gentianaceae*. Small clumped plant with large, purple, cup-shaped flowers.
Eutreptia pertyi	Euglenoid	k. *Protista*, p. *Euglenophyta*, c. *Euglenophyceae*, o. *Eutreptiales* , f. *Eutreptiaceae*. Fresh or marine cells arranged in star-shaped groups.
Fagopyrum esculentum	Buckwheat	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Polygonales*, f. *Polygonaceae*. Seeds ground to a high-lysine flower, used in baking and soups.
Fagus grandifolia	American beech	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; fruit a spiny husk containing two or three nuts.
Fagus sylvatica	European beech	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; fruit a spiny husk containing two or three nuts.

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Fallugia paradoxa	Apache plume	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Shrub with flaky bark producing flowers like single white roses followed by feathery fruits.
Festuca arundinacea	Tall fescue	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Coarse bunchgrass used for pasture, drought-resistant lawns, and erosion control.
Ficus aurea	Florida strangler fig	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Tree-sized plant; seedlings grow on trunk of host tree and eventually surround it with stems and roots.
Ficus benjamina	Weeping fig	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Evergreen tree; small, thin, leathery, glossy leaves on drooping branches; popular houseplant.
Ficus carica	Common fig	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Tree or shrub with deeply lobed leaves; purple-red flowers in a flask-shaped chamber; each fruit is a ripened chamber and flower cluster.
Ficus elastica	India rubber plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Shrub or small tree; leaves large, leathery, glossy; wounds weep white latex; popular houseplant.
Ficus lyrata	Fiddle-leaf fig	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Tree with large, rigid, glossy leaves shaped like violins.
Flammulina velutipes	Velvet foot mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Xerulaceae*. Sticky tan cap, pale gills, velvety-brown stalk; grows in clusters.
Foeniculum vulgare	Florentine fennel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Swollen, enlarged leaf bases eaten raw or cooked for aniselike flavor.
Forsythia suspensa	Weeping forsythia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Oleaceae*. Graceful, drooping branches produce bright yellow spring flowers.
Fortunella margarita	Kumquat	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Produces small fruits with edible rinds and tart flesh; candied or used in jelly.
Fouquieria splendens	Ocotillo	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Fouquieriaceae*. Tall, stiff, whiplike stems covered with stout thorns; small, fleshy leaves appear only after heavy rain.
Fragaria virginiana	Wild strawberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small mound of divided leaves producing creeping stems; fruits are swollen red flower bases with tiny, scattered, crunchy seeds.

Scientific Name	Common Name	Taxonomy and Characteristics
Frankia spp.	Actinomycete	d. Bacteria, k. *Eubacteria*, p. *Actinobacteria*, c. *Actinobacteria*, o. *Actinomycetales*, f. *Actinomycetaceae*. Grows as a branching filament, resembling fungal growth; converts (fixes) nitrogen from the air to a form used by plants; forms nodules on roots of several plant species, including alder.
Fraxinus americana	White ash	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scropulariales*, f. *Oleaceae*. Tree with divided leaves; fruit a single-winged seed, produced in large numbers.
Fraxinus pennsylvanica	Green ash	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scropulariales*, f. *Oleaceae*. Tree with divided leaves; fruit a single-winged seed, produced in large numbers.
Fuchsia hybrida	Fuchsia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Onagraceae*. Popular ornamental viney shrub with colorful, showy, dangling flowers.
Fucus spp.	Rock weed	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Fucales*, f. *Fucaceae*. Common brown algae on tidal rocks.
Fuligo septica	Scrambled-egg slime	k. *Protista*, p. *Myxomycota*, c. *Myxomycetes*, o. *Physarales*, f. *Physaraceae*. Soft, fluffy, yellowish mass becomes crusty inside with age.
Gaillardia pulchella	Blanket flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Flower heads of red, yellow; popular bedding plant.
Galanthus nivalis	Snowdrop	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Amaryllidaceae*. Early spring plant with one white, nodding flower per stalk.
Galium aparine	Bedstraw, cleavers	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rubiales*, f. *Rubiaceae*. Rangy plant with rings of several leaves; stems and leaves stick to clothing with sticky hairs.
Ganoderma lucidum	Ling chih	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales*, f. *Polyporaceae*. Bracketlike, shiny, red striped cap.
Ganoderma tsugae	Hemlock varnish shelf fungus	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales*, f. *Polyporaceae*. Soft, firm bracket with shiny finish.
Garcinia mangostana	Mangosteen	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Theales*, f. *Clusiaceae*. Tropical evergreen tree; dark purple shell of fruit contains seeds, each enclosed in a fleshy, edible sac.
Garrya elliptica	Silk-tassel bush	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Cornales*, f. *Garryaceae*. Shrub producing clusters of purple, grapelike fruits.
Gaultheria procumbens	Wintergreen	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Low-growing shrubs; leaves and berries taste like wintergreen.
Gaura lindheimeri	Gaura	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Onagraceae*. Tall, narrow plant with small, honeysuckle-like flowers.

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Geastrum saccatum	Rounded earthstar	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Lycoperdales*, f. *Geastraceae*. Sac of spores sitting on a ring of fleshy, triangular rays.
Gelidium spp.	Red algae	k. *Protista*, p. *Rhodophyta*, c. *Florideophyceae*, o. *Gelidiales*, f. *Gelidiaceae*. Highly branched body; includes red algae, which provide agar, used in microbiology and commercially as a thickener.
Gelsemium sempervirens	Yellow jessamine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Loganiaceae*. Fine, woody vine producing many bright yellow flowers in early spring; South Carolina state flower.
Gerbera jamesonii	Transvaal daisy	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Popular bedding plants with colorful flower heads.
Gibberella fujikuroi	Foolish seedling pathogen	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Hypocreales*, f. *Nectriaceae*. Played an important role in the discovery of the plant growth hormones, gibberellins.
Gilia capitata	Blue thimble flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Polemoniaceae*. Produces blue to purple flowers with blue pollen.
Gilia tricolor	Bird's eyes	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Polemoniaceae*. Produces pale to deep purple flowers with yellow-speckled throats and blue pollen.
Ginkgo biloba	Maidenhair tree	k. *Plantae*, p. *Ginkgophyta*, c. *Ginkgopsida*, o. *Ginkgoales*, f. *Ginkgoaceae*. "Living fossil" found growing in secluded Chinese monastery gardens two hundred years ago; popular ornamental worldwide.
Gleditsia triacanthos	Honey locust	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tree with trunk and branches bearing scattered, stout, three-branched thorns.
Glomus pansihalos	Mycorrhizal fungus	k. *Fungi*, p. *Zygomycota*, c. *Zygomycetes*, o. *Glomales*, f. *Glomaceae*. Forms associations with plant roots (mycorrhizae), increasing absorption of water and nutrients.
Gloriosa rothschildiana	Gloriosa lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Climbs by tendrils on tips of leaves; lilylike flowers are bright red with yellow bands.
Glycine max	Soybean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Pea relative grown for high-protein seeds, oil, and fodder; used to produce various meat and dairy substitutes; main source of lecithin.
Gomphrena globosa	Globe amaranth	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Amaranthaceae*. Rounded, papery, colorful, cloverlike flowering heads; used in dried arrangments.

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Goniomonas spp.	Cryptomonads	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Goniomonadaceae*. Nonphotosynthetic cells; may resemble ancestors of photosynthetic cryptomonads.
Gonyaulax tamarensis	Red tide alga	k. *Protista*, p. *Dinophyta*, c. *Dinophyceae*, o. *Gonyaulacales*, f. *Gonyaulacaceae*. One of several algae producing toxic red tides.
Gossypium hirsutum	Cotton	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Tall, branched plants produce hibiscus-like flowers followed by fibrous fruits harvested and processed as cotton.
Gracilaria spp.	Red algae	k. *Protista*, p. *Rhodophyta*, c. *Florideophyceae*, o. *Gracilariales* , f. *Gracilariaceae*. Includes red algae which provide agar used in microbiology and commerically as thickeners.
Graphis scripta	Pencil marks lichen	k. *Fungi*, g. lichen, f. *Graphidaceae*. Thin, smooth, white crustose body bears dark fruiting bodies that resemble pencil marks.
Grifola frondosa	Hen-of-the-woods	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Schizophyllales*, f. *Schizopyllaceae*. Clustered gray-brown caps from a single base; available commercially.
Guaiacum sanctum	Lignum vitae	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Zygophyllaceae*. Small tree; divided leaves with leathery leaflets; blue flowers in small clusters; wood hard and dense.
Gutierrezia dracunculoides	Broomweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Many-branched plant used by pioneers as broom; can cause skin rash and eye irritation in humans.
Gymnocladus dioica	Kentucky coffee tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tall tree producing broad, flat pods; Kentucky state tree.
Gymnodinium spp.	Dinoflagellates	k. *Protista*, p. *Dinophyta*, c. *Dinophyceae*, o. *Gymnodiniales*, f. *Gymnodiniaceae*. Unarmored marine or freshwater cells, with or without chloroplasts.
Gymnosporangium clavariiforme	Rust	k. *Fungi*, p. *Basidiomycota*, c. *Uredinomycetes*, o. *Uredinales*, f. *Pucciniaceae*. Infects hawthorn leaves.
Gypsophila paniculata	Baby's breath	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Caryophyllaceae*. Hundreds of small white flowers are arranged in large, delicate sprays; used in arrangements.
Halobacterium halobium	Extreme halophile	d. *Archaea*, k. *Archaeobacteria*, p. *Euryarchacota*, c. *Halobacteria*, o. *Halobacteriales*, f. *Halobacteriaceae*. Bright red cell uses a primitive form of photosynthesis; needs extremely salty conditions for growth.
Hamamelis virginiana	Witch hazel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Hamamelidales*, f. *Hamamelidaceae*. Tree with yellow, stringy flowers and woody fruits; twigs preferred by water diviners for dowsers.

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Hedera helix	English ivy	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Araliaceae*. Woody vine, climbing, with dark green leaves.
Helianthus annuus	Sunflower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Rough textured plant producing flower heads with yellow fringes and maroon-brown centers; Kansas state flower.
Helianthus maximilianii	Maximillian sunflower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Tall, coarse plants growing in dense clusters; bright yellow flower heads displayed on top half of long, unbranched stalks.
Helianthus tuberosus	Jerusalem artichoke, sunchoke	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Sunflower plant with knobby, starchy, underground stems eaten fresh or boiled or baked like potato.
Helicobacter pylori	Helicobacterium	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Epsilonproteobacteria*, o. *Campylobacterales*, f. *Helicobacteraceae*. Gram-negative curved cells that cause stomach ulcers.
Hemerocallis fulva	Common daylily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Clumps of arching, sword-shaped leaves; clusters of orange flowers on mostly leafless stalks.
Hericium ramosum	Comb tooth	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Cantharellales*, f. *Hydnaceae*. Shaggy-looking with dangling fringes (teeth) on edges of cap; short, hairy stalk.
Heuchera sanguinea	Alum root, coral bells	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Saxifragaceae*. Low clumps of rounded leaves; tall flower stalks bear nodding, bell-shaped, reddish flowers.
Hibiscus esculentus	Okra	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Tall plant producing five-sided pods that are cooked alone or in soups and sauces.
Hibiscus rosa-sinensis	Hibiscus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Vigorous shrub producing glossy leaves and large, showy flowers; Hawaii state flower.
Hibiscus syriacus	Rose of Sharon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Malvaceae*. Shrub with hibiscus-like flowers.
Hosta ventricosa	Plantain lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. One of several *Hosta* grown for showy foliage.
Hoya carnosa	Wax flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Asclepiadaceae*. Trailing plant producing clusters of waxlike, fragrant flowers; popular houseplant.
Humulus lupulus	Hops	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Cannabaceae*. Climbing vine; fruit is a cluster of leafy bracts used in beer production.

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Huperzia lucidula	Fir moss	k. *Plantae*, p. *Lycophyta*, c. *Lycopsida*, o. *Lycopodiales*, f. *Lycopodiaceae*. Horizontal stems belowground produce branches with green leaves; no cone is formed.
Hydrangea macrophylla	Hydrangea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Hydrangeaceae*. Rounded shrub with large leaves and big clusters of flowers, white, pink, red, or blue, depending on soil conditions.
Hydrastis canadensis	Goldenseal	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Small plant with knotty, creeping, bright yellow root; two broad-lobed leaves; small white flowers.
Hydrilla verticillata	Hydrilla	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Hydrocharitales*, f. *Hydrocharitaceae*. Submerged aquatic; can become noxious, invasive pest, clogging waterways and eliminating native plants.
Hydrodictyon spp.	Water net	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*, o. *Chlorococcales*, f. *Hydrodictyaceae*. Forms interconnected, netlike colonies; common in freshwater bodies.
Hygrohypnum bestii	Aquatic moss	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Amblystegiaceae*. Aquatic plant with stiff leaves curved to one side.
Hygrophorus flavescens	Golden waxy cap	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Hydrophoraceae*. Mushroom with slimy yellow cap, yellow gills, and yellow stalk.
Hypericum perforatum	St. John's wort	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Theales*, f. *Clusiaceae*. Aromatic plant with yellow flowers; ancient medicinal remedy, recently studied for treatment of depression.
Hypomyces lactifluorum	Lobster mushroom	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Sphaeriales*, f. *Hypomycetaceae*. Bright orange mold growing on white mushrooms.
Ilex opaca	American holly	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Celastrales*, f. *Aquifoliaceae*. Tree; glossy, green leaves with spiny edges; bright red berries; Delaware state tree.
Ilex vomitoria	Yaupon	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Celastrales*, f. *Aquifoliaceae*. Shrub or small tree; often sheared into shapes.
Illicium verum	Star anise	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Illiciales*, f. *Illiciaceae*. Tree; oil extract used as a substitute for anise in food and drinks.
Ipomoea batatas	Sweet potato	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Convolvulaceae*. Trailing or climbing vines; tuberous roots vary in size, color of skin, and color of flesh; boiled, baked or candied; not related to true yams.
Ipomoea tricolor	Morning glory	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Convolvulaceae*. Trailing climbing vine with heart-shaped leaves and showy, funnel-shaped flowers that open in the morning.

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Ipomopsis rubra	Gilia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Polemoniaceae*. Tall narrow plant; striking red tubular flower with yellow markings in throat.
Iresine herbstii	Bloodleaf	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Amaranthaceae*. Small tender plant; stem and leaves deep red.
Iris spp.	Iris	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Iridaceae*. Tennessee state flower.
Iris giganticaerulea	Giant blue iris	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Iridaceae*. Louisiana state flower.
Ischnoderma resinosum	Resinous polypore	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales*, f. *Polyporaceae*. Hairy, dark, bracketlike cap with thick rim.
Isoetes melanopoda	Quillwort	k. *Plantae*, p. *Lycophyta*, c. *Lycopsida*, o. *Isoetales*, f. *Isoetaceae*. Short underground stem with tuft of upright or curved stiff leaves; found in water or wet ground.
Jacaranda mimosifolia	Jacaranda	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Bignoniaceae*. Small tree producing decorative seed pods used in arrangements.
Jasminum sambac	Arabian jasmine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Oleaceae*. Shrub with glossy leaves and powerfully fragrant white flowers; flowers are used in perfumery, jasmine tea, and Hawaiian leis.
Juglans nigra	Black walnut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Juglanales*, f. *Juglandaceae*. Tree; spherical fruit a thick, yellow-green husk around a woody, corrugated nut with a sweet, oily seed; pith of twigs divided into chambers.
Juglans regia	English walnut	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Juglanales*, f. *Juglandaceae*. Tree; fruit a smooth, green husk enclosing a pale, thin-shelled nut with rounded surface ridges.
Juncus effusus	Rush	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Juncales*, f. *Juncaceae*. Stiff cylindrical green stems; short leaves wrapped around stem base; compact flowerd cluster near top of stem; used to make baskets and wicker chairs.
Juniperus communis	Common juniper	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Sprawling shrub with curved needles and blue fleshy cones.
Juniperus monosperma	One seed juniper	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with scalelike leaves; red-brown fleshy cones contain one seed.
Juniperus scopulorum	Rocky Mountain juniper	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with scalelike leaves; cone blue and fleshy.

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Juniperus virginiana	Eastern red cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with scalelike leaves or, at branch tips, stiff, prickly awl-like leaves; cones blue and fleshy.
Kalanchoe daigremontiana	Maternity plant, mother of thousands	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Crassulaceae*. Tender plant producing small plantlets on toothed edges of full-sized leaves.
Kalmia latifolia	Mountain laurel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Shrub or tree with leathery leaves and clusters of pink, starlike flowers; state flower of Connecticut, Pennsylvania.
Kigelia africana	Sausage fruit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Bignoniaceae*. African tree producing fleshy, red flowers followed by thick, sausagelike fruits hanging from ropelike stalks.
Laburnum anagyroides	Golden chain tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Small tree producing long, dangling clusters of bright yellow flowers.
Lactarius indigo	Indigo milky	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Russulales*, f. *Russulaceae*. Indigo-colored mushroom turns green when bruised.
Lactobacillus spp.	Lactic acid bacteria	d. *Bacteria*, k. *Eubacteria*, p. *Firmicutes*, c. *Bacilli*, o. *Lactobacillales*, f. *Lactobacillaceae*. Gram-positive cells ferment sugars to lactic acid; produce foods like yogurt and sour cream but spoil other foods.
Lactuca sativa	Lettuce	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Dense leafy heads are used in salads.
Laetiporus sulphureus	Chicken mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales*, f. *Polyporaceae*. Clustered yellow-orange stalkless caps.
Lagerstroemia indica	Crape myrtle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Lythraceae*. Shrub or small tree with flaky bark and crepelike, crinkled white, pink, or red flowers.
Laguncularia racemosa	White mangrove	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Combretales*, f. *Combretaceae*. Shrub to large tree; fruits red-brown, leathery, urn-shaped; found in marine tidal zones.
Laminaria spp.	Brown algae	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Laminariales*, f. *Laminariaceae*. Common large algae on rocky shorelines; includes edible species.
Lamium amplexicaule	Henbit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamilales*, f. *Lamiaceae*. Small spring weed with clusters of two-lipped purple flowers.
Lantana camara	Lantana	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Verbenaceae*. Thorny shrub with clusters of yellow and orange flowers; grown as ornamental.
Larix laricina	Tamarack	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Needle-leaf tree; drops needles in fall.

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Larix occidentalis	Western larch	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Needle-leaf tree; drops needles in fall.
Larrea tridentata	Creosote bush	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Zygophyllaceae*. Common branchy aromatic shrub of the desert.
Laurus nobilis	Laurel, bay laurel	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Laurales*, f. *Lauraceae*. Evergreen tree or shrub; dark green leaves used as cooking herb.
Lawsonia inermis	Mignonette tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Lythraceae*. Shrub or small tree; source of henna dye.
Leathesia difformis	Sea potato	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Chordariales*, f. *Chordariaceae*. Amber to olive green, irregular, lumpy, potato-shaped body growing on other seaweeds.
Lemna gibba	Duckweed	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arales*, f. *Araceae*. Tiny aquatic plant on the surface of still-water bodies.
Lens culinaris	Lentil	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Pea relative grown for high-protein seeds, dried and eaten in soups, fried, or ground to flour.
Lentinula edodes	Shiitake mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. Agaricales, f. *Tricholomataceae*. Popular commercial edible mushroom.
Lepidium sativum	Cress	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Seedlings and leaves used in soups and salads for sharp flavor.
Letharia vulpina	Wolf moss	k. *Fungi*, g. lichen, f. *Parmeliaceae*. Bright yellow-green tufted body; once used to poison wolves.
Levisticum officinale	Lovage	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Leaves are used as celery substitute in cooking.
Lewisia rediviva	Bitterroot	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Portulacaceae*. Fleshy root supports a cluster of fleshy, strap-shaped leaves followed by large, showy flowers; Montana state flower.
Liatris spicata	Gayfeather	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Narrow stem produces dense, grasslike leaves; top of stem densely covered with small, fluffy flower heads.
Libocedrus decurrens	Incense cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with flat twigs of scalelike leaves; few cone scales open wide at maturity.
Ligustrum vulgare	Privet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Oleaceae*. Common deciduous hedge plant.
Lily lancifolium	Tiger lily	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Tall stem with hanging, black-spotted orange flowers.

Scientific Name	Common Name	Taxonomy and Characteristics
Linum usitatissimum	Flax	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Linales*, f. *Linaceae*. Tender plants with narrow leaves and blue flowers; grown for fibers used in linen and oil from seeds (linseed oil).
Liquidambar styraciflua	Sweetgum	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Hamamelidales*, f. *Hamamelidaceae*. Tree with star-shaped leaves; fruits burlike, prickly spheres.
Liriodendron tulipifera	Tulip tree, yellow poplar	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Magnoliaceae*. Tall tree with four-lobed leaves and tulip-shaped flowers; state tree of Indiana, Tennessee.
Litchi chinenesis	Lychee	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Sapindaceae*. Evergreen tree producing round, red fruits with warty rinds; fleshy, edible sac surrounding single seed is eaten fresh or dried to make lychee nuts.
Lithops spp.	Living stones	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Aizoaceae*. Stem top at soil surface resembles pebbles; slit across top of stem.
Lobaria pulmonaria	Lung lichen	k. *Fungi*, g. lichen, f. *Parmeliaceae*. Resembles a limp, uninflated lung.
Lobelia cardinalis	Cardinal flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Campanulales*, f. *Campanulaceae*. Tall upright plant; tubular, scarlet, two-lipped flowers.
Lodoicea maldivica	Seychelles palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Large tree with fanlike leaves, native to the Seychelles Islands; produces the largest known seed, sometimes called the double coconut.
Lonicera japonica	Honeysuckle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales*, f. *Caprifoliaceae*. Shrubby vine with fragrant, white, two-lipped flowers.
Lophozia spp.	Liverworts, leafy	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Jungermanniales*, f. *Jungermanniaceae*. Plants green to brown; gemma cups common on young leaf tips; some species accumulate a calcium layer.
Luffa cylindrica	Loofa sponge plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Cucurbitaceae*. Tender vine producing cylindrical gourds with fibrous interiors that can be used as sponges.
Lunaria annua	Money plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Tall stems with clear, circular membranes left when seeds are shed; used in dried arrangements.
Lupinus texensis	Bluebonnet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Upright plant with clusters of blue and white flowers; Texas state flower.

Scientific Name	Common Name	Taxonomy and Characteristics
Lycopersicon esculentum	Tomato	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Straggling bush grown for fleshy, juicy, seedy, yellow to red fruits of various sizes and shapes, used raw, cooked, or processed.
Lycopodium clavatum	Running pine	k. *Plantae*, p. *Lycophyta*, c. *Lycopsida*, o. *Lycopodiales*, f. *Lycopodiaceae*. Leafy horizontal stems produce upright leafy branches; spores in cones on longer branches.
Lycopodium complanatum	Ground cedar	k. *Plantae*, p. *Lycophyta*, c. *Lycopsida*, o. *Lycopodiales*, f. *Lycopodiaceae*. Horizontal stems belowground produce upright branches with four relatively short leaves; cones on short branches from long, nearly leafless stalks; perennial plants produce yearly growth marks.
Lygodium japonicum	Climbing fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Schizaeaceae*. Twining, climbing vinelike stem.
Macadamia integrifolia	Macadamia, smooth-shelled	k. *plantae*, p. *anthophyta*, c. *eudicotyledones*, o. *proteales*, f. *proteaceae*. Tropical tree producing a gourmet nut used in baked goods and other foods.
Macadamia tetraphylla	Macadamia, rough-shelled	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Proteales*, f. *Proteaceae*. Tree; fruit a fleshy husk containing a shelled, gourmet nut.
Maclura pomifera	Osage orange	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Small tree with thorny branches; large, inedible green fruit resembles a bumpy orange.
Macrocystis pyrifera	Giant kelp	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Laminariales*, f. *Lessoniaceae*. Forms vast beds in seas hundreds of feet deep; harvested for industrial uses.
Magnolia grandiflora	Southern magnolia	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Magnoliaceae*. Evergreen tree; leaves large, leathery, glossy green; white flowers large, showy, fragrant; reddish, hairy fruit with exposed red seeds; Mississippi state tree; state flower of Mississippi, Louisiana.
Mahonia aquifolium	Oregon grape	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Berberidaceae*. Spiny, hollylike leaves; bitter blue berries; Oregon state flower.
Malus angustifolia	Southern crabapple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree with small applelike fruits; ornamental or fruits pickled or used in jelly.
Malus x domesticus	Apple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree with crisp,fleshy fruit; many cultivated varieties used fresh or processed; blossom is state flower of Arkansas, Michigan.
Mandragora officinarum	Mandrake	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales* , f. *Solanaceae*. Contorted roots once harvested as fertility treatment.

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Mangifera indica	Mango	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Anacardiaceae*. Tree with thin evergreen leaves; large single-seeded fruit with yellow or orange flesh used fresh or cooked.
Manihot esculenta	Cassava, manioc, tapioca	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Tall tropical shrub with swollen roots; important source of starch in tropical diet.
Manilkara zapota	Sapodilla	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ebenales*, f. *Sapotaceae*. Evergreen tropical tree; edible pulpy fruit; sap collected for chicle.
Maranta leuconeura	Prayer plant	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Marantaceae*. Small leafy plant; leaves pale along veins; brown spots near edges; leaves fold upward at night.
Marasmius oreades	Fairy ring mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Tricholomataceae*. Forms rings of mushrooms in grassy areas; easily confused with poisonous look-alikes.
Marchantia polymorpha	Liverwort, thalloid	k. *Plantae*, p. *Hepatophyta*, c. *Marchantiopsida*, o. *Marchantiales*, f. *Marchantiaceae*. Large pores and gemma cups on lobes; used extensively in laboratory studies.
Marrubium vulgare	Horehound	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Common weed around old fences and buildings; used as a flavoring in candies.
Marsilea spp.	Clover-leaf ferns	k. *Plantae*, p. *Pterophyta*, c. *Marsileopsida*, o. *Marsileales*, f. *Marsiliaceae*. Leaf blade floating or above water surface, divided into four segments like four-leaf clover.
Matteuccia struthiopteris	Ostrich fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Dryopteridaceae*. Cluster of dark green, head-high, plumelike leaves arise from ground level.
Medicago sativa	Alfalfa	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tender plant with blue-purple flower clusters; used as high-quality animal fodder.
Melampodium leucanthum	Blackfoot daisy	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Rounded mounds covered with white, daisylike flower heads.
Melampsoridium betulinum	Birch rust	k. *Fungi*, p. *Basidiomycota*, c. *Uredinomycetes*, o. *Uredinales*, f. *Melampsoracae*. Infects birch and larch leaves.
Melanophyllum echinatum	Red-gilled agaric	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Agaricaceae*. Mushroom with dark red gills.
Melia azedarach	China berry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Meliaceae*. Tree with divided leaves; fleshy yellow fruits in clusters.
Melilotus albus	White sweet clover	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Bushy plant with small white flowers and exotic scent.

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Meliococcus bijugatus	Mamoncillo, Spanish lime	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Sapindaceae*. Tropical tree producing grapelike clusters of fruits with sweet-tart, yellow-orange pulp.
Melissa officinalis	Lemon balm	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Lemon-scented herb used to flavor omelettes, wines.
Mentha piperita	Peppermint	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Vigorous plant with creeping underground stems; leaves used to flavor tea and as a source of peppermint oil.
Mentha spicant	Spearmint	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Vigorous plant with creeping underground stems; source of spearmint flavoring used in jelly or sauces.
Mentha suaveolens	Applemint	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Vigorous plant with creeping underground stems; leaves have aromatic, applelike flavor.
Mentzelia decapetala	Blazing star	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Loasaceae*. Rough, coarse-textured plant with showy, cream-colored flowers.
Mertensia virginica	Virginia bluebells	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Boraginaceae*. Tender plant with drooping, blue, bell-shaped flowers.
Mesembryanthemum crystallinum	Ice plant	k. *Plantae*, p. *anthophyta*, c. *eudicotyledones*, o. *caryophyllales*, f. *aizoaceae*. Fleshy speading plant covered with transparent blisters that glitter in the sun.
Metasequoia glyptostroboides	Dawn redwood	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree; "living fossil" discovered in remote Chinese valley in 1948; flat, pointed needles drop in fall; California state tree.
Methanococcus spp.	Methanogens	d. *Archaea*, k. *Archaeobacteria*, p. *Euryarchacota*, c. *Methanococci*, o. *Methanosarcinales*, f. *Methanosarcinaceae*. Makes methane gas and grows only in places without oxygen, such as aquatic or marine mud.
Methanosarcina spp.	Methanogens	d. *Archaea*, k. *Archaeobacteria*, p. *Euryarchacota*, c. *Methanococci*, o. *Methanococcales*, f. *Methanococcaceae*. One of the most common methane gas producers in cow stomachs.
Mimosa pudica	Sensitive plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Shrubby plant with divided leaves that fold when touched; fluffy clusters of pink-purple flowers.
Mimulus spp.	Monkey flowers	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Tender or small shrubby plants; produce colorful two-lipped showy flowers.
Mirabilis jalapa	Four-o'clock	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Nyctaginaceae*. Shrub-sized stems; trumpet-shaped, red, yellow, or white flowers.

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Mnium spp.	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Mniaceae*. Hexagonal cells cause leaves to shrivel and appear dead when dry.
Mollugo verticillata	Carpetweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Molluginaceae*. Wiry stem with rings of several leaves; produces a spreading circular mat.
Moluccella laevis	Bells of Ireland	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Emerald-green plant with white, two-lipped flowers surrounded by green funnels.
Monilinia fructicola	Brown rot pathogen	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Moniliaceae*. Causes decay of stone fruits such as peaches, cherries, and plums.
Monotropa uniflora	Indian pipe	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Monotropaceae*. Tender fleshy plant; white stems lack chlorophyll; plant turns black when dry.
Monstera deliciosa	Split leaf philodendron	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arales*, f. *Araceae*. Vine with large, divided, glossy leaves; climbs on trees or other supports; fruit edible.
Montia parviflora	Miner's lettuce	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Portulacaceae*. Fleshy plant with saucer-shaped leafy ring around upper stem.
Morchella esculenta	Yellow morel	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Pezizales*, f. *Morchellaceae*. Prized edible mushroom with wrinkled brown cap; easily confused with poisonous look-alikes.
Morus rubra	Red mulberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Moraceae*. Tree; leaves unlobed or with two or three lobes; each blackberry-like fruit formed from entire cluster of small flowers.
Musa acuminata	Finger banana	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Musaceae*. Small banana plant; clusters of finger-sized edible fruits.
Musa textilis	Manila hemp	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Musaceae*. Cultivated for fibers used in paper making.
Musa x paradisiaca	Banana, plantain	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Musaceae*. Commercial banana; tree-sized plant with long, fanlike leaves; seedless fruits in large, hanging clusters.
Muscari neglectum	Grape hyacinth	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Clumps of fleshy, grasslike leaves and a bare stalk with a dense cluster of purple, urn-shaped flowers.
Mycobacterium leprae	Leprosy pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Actinobacteria*, c. *Actinobacteria*, o. *Actinomycetales*, f. *Actinomycetaceae*. Cell with unusual chemical features causing Hansen's disease (leprosy).

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Mycoplasma spp.	Mycoplasma	d. *Bacteria*, k. *Eubacteria*, p. *Firmicutes*, c. *Mollicutes*, o. *Mycoplasmatales*, f. *Mycoplasmataceae*. Parasite; lacks a cell wall and lives entirely within the cells of a host plant or animal.
Mylia taylorii	Liverwort, leafy	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Jungermanniales*, f. *Jungermanniaceae*. Unlobed red to purple leaves; found on rotting logs.
Myosotis alpestris	Forget-me-not	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Boraginaceae*. Trailing plant with small, five-petal blue flowers; Alaska state flower.
Myriophyllum aquaticum	Milfoil	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Haloragales*, f. *Haloragaceae*. Common aquarium plant.
Myriophyllum spicatum	Milfoil	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Haloragales*, f. *Haloragaceae*. Noxious weed overgrowing some lakes and streams.
Myristica fragrans	Mace, nutmeg	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Magnoliales*, f. *Myristicaceae*. Fleshy, netted seed; coating is dried and powdered to flavor pickles and ketchup.
Nandina domestica	Sacred bamboo	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Berberidaceae*. Shrub with canelike stems and delicate divided leaves; flowers in loose clusters followed by red berries.
Narcissus jonquilla	Jonquil	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Showy spring plant with onionlike leaves; golden-yellow flowers with short cups rising from the bases of the petals.
Narcissus tazetta	Polyanthus daffodil	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Clustered flowers on bare stalks with combinations of white and yellow cups and petals.
Navicula spp.	Diatoms	k. *Protista*, p. *Bacillariophyta*, c. *Bacillariophyceae*, o. *Pennales*, f. *Naviculaceae*. Mostly bottom-dwelling cells that grow singly or in connected ribbons.
Neisseria meningitidis	Meningococcus	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Betaproteobacteria*, o. *Neisseriales*, f. *Neisseriaceae*. Gram-negative cells that cause bacterial meningitis.
Nelumbo nucifera	Chinese lotus	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Nymphaeales*, f. *Nelumbonaceae*. Aquatic plant with umbrella-like leaves and large, showy flowers; produces seeds inside a woody, toplike chamber.
Nemophila menziesii	Baby blue-eyes	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Hydrophyllaceae*. Small tender plant with cup-shaped, sky-blue flowers.
Nepenthes reinwardtiana	East Indian pitcher plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Nepenthales*, f. *Nepenthaceae*. "Carnivorous" plant; tips of leaves form water-filled pitchers that trap and digest insects, other small animals; stems used for basket weaving.

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Nepeta cataria	Catnip	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Relative of mints used fresh or dried as a cat treat.
Nephelium lapaceum	Rambutan	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Sapindaceae*. Small tree producing yellow or red fruits; husks covered with soft spines; seeds surrounded by edible, fleshy sac; eaten fresh.
Nephrolepis exaltata	Boston fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Oleandraceae*. Among the most common ferns kept as a houseplants.
Nereocystis leutkeana	Bull kelp	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Laminariales*, f. *Lessoniaceae*. Very long stalk with large air-filled float and many leaflike blades.
Nerium oleander	Oleander	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Apocynaceae*. Shrubby plant with showy white or red flowers.
Neurospora crassa	Pink mold	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Sordariales*, f. *Sordariaceae*. An important model used in early studies of biochemical genetics.
Nicotiana tobacum	Tobacco	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Tall, stout plant with large hairy leaves processed into various products; contains addictive alkaloid, nicotine.
Nitella spp.	Stonewort	k. *Protista*, p. *Chlorophyta*, c. *Charophyceae*, o. *Charales*, f. *Characeae*. Filaments with regular branching, resulting in a tufted appearance; wide size range.
Nitzschia spp.	Diatoms	k. *Protista*, p. *Bacillariophyta*, c. *Bacillariophyceae*, o. *Pennales*, f. *Nitzschiaceae*. Long, thin cells.
Nyssa sylvatica	Black tupelo	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Cornales*, f. *Nyssaceae*. Deciduous tree with dark blue fruit.
Ochroma pyrmidale	Balsa	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Bombacaceae*. Tropical American tree; source of balsa wood.
Ocimum basilicum	Sweet basil	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used to flavor fish, poultry, tomato products.
Oedogonium spp.	Oedogonium	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*, o. *Oedogoniales*, f. *Oedogoniaceae*. Filaments with rings at the ends of cells indicating the number of cell divisions.
Oenothera biennis	Evening primrose	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Onagraceae*. Showy yellow flowers, open near sunset.
Olea europea	Olive	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Oleaceae*. Small evergreen tree producing fruit with thin skin, fleshy pulp, and stony center; used for oil or table olives, ripe (black) or green.

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Olpidium brassicae	Chytrid	k. *Fungi*, p. *Chytridiomycota*, c. *Chytridiomycetes*, o. *Spizellomycetales*, f. *Olpidiaceae*. Parasite on cabbage and relatives; can carry viral diseases of plants.
Onoclea sensibilis	Sensitive fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Dryopteridaceae*. Horizontal stems producing green, lobed leaves and leaves with rolled, berrylike spore cases.
Ophiostoma ulmi	Dutch elm disease pathogen	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Ophiostomatales*, f. *Ophiostomataceae*. One of two fungi that nearly wiped out the American elm.
Opuntia polyacantha	Prickly pear	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Cactaceae*. Stems a series of fleshy, flattened joints with large, showy flowers.
Origanum hortensis	Sweet marjoram	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used to flavor soups, stews, stuffings.
Ornithocercus spp.	Dinoflagellates	k. *Protista*, p. *Dinophyta*, c. *Dinophyceae*, o. *Dinophysiales*, f. *Ornithocercaceae*. Armored marine cells; chloroplasts absent in some; some with other photosynthetic cells growing internally.
Orobanche spp.	Broomrape	k. Plantae, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Orobanchaceae*. Nongreen parasitic plant, conspicuous aboveground only when flowering.
Oryza sativa	Rice	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Cereal grass cultivated in warm climates for edible grain.
Osmunda cinnamomea	Cinnamon fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Osmundaceae*. Stems bear old leaf bases and a tangle of wiry roots.
Osmunda regalis	Royal fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Osmundaceae*. Head-high fern with twice-divided leaves; small, spore-bearing leaflets clustered at ends of leaves.
Ostrya virginiana	Hophornbeam, ironwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Betulaceae*. Tree; fruit a cluster of small pods; wood very dense.
Oxydendrum arboreum	Sourwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Small tree with clusters of small, urn-shaped flowers.
Pachyrhizus erosus	Jicama	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Long vine producing large, fleshy roots eaten raw or cooked as a starch source.
Padina spp.	Brown algae	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Dictyotales*, f. *Dictyotaceae*. Tropical or subtropical brown, fan-shaped algae; some develop calcium carbonate crusts.
Padina pavonia	Peacock's tail	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Dictyotales*, f. *Dictyotaceae*. Clusters of leaves with flat, thin, leathery, rounded, fanlike segments.

Scientific Name	**Common Name**	**Taxonomy and Characteristics**
Paeonia spp.	Peony	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Dilleniales*, f. *Paeoniaceae*. Shrubs; dark green foliage and large, showy, pink, red or white flowers grow from a thick rootstock; Indiana state flower.
Palmaria palmata	Dulse	k. *Protista*, p. *Rhodophyta*, c. *Florideophyceae*, o. *Palmariales*, f. *Palmariaceae*. Edible marine red alga.
Panax quinquefolius	American ginseng	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Araliaceae*. Root harvested for reported medicinal value; endangered plant.
Pandanus amaryllifolius	Screw pine	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyclanthales*, f. *Cyclanthaceae*. Trees with long narrow leaves spiraling up stem; often with many prop roots.
Papaver somniferum	Opium poppy	k. Plantae, p. *Anthophyta*, c. *Eudicotyledones*, o. *Papaverales*, f. *Papaveraceae*. Delicate plant with fernlike leaves, colorful tissuelike flowers, and oval seed pods; sap of seed pods is the source of opium.
Paraphysomonas spp.	Golden brown algae	k. *Protista*, p. *Chrysophyta*, c. *Chrysophyceae*, o. *Chrysosphaerales*, f. *Paraphysomonadaceae*. Cells covered with silica scales; plastids colorless.
Passiflora caerulea	Passion flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Passifloraceae*. Evergreen vine with lobed leaves; green and purple flowers with complex structure; small orange, edible fruit.
Passiflora edulis	Passionfruit	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Passifloraceae*. Vine with lobed leaves; flowers with complex structure; edible, deep purple fruit.
Passiflora incarnata	Maypop	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Passifloraceae*. Evergreen vine with lobed leaves; green, white, blue flowers and yellowish fruit; Tennessee state flower.
Pastinaca sativa	Parsnip	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Long, white, fleshy root with unique flavor; cooked and eaten or fed to livestock.
Paulownia tomentosa	Royal paulownia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Bignoniaceae*. Tree with fragrant purple flowers appearing before large coarse leaves; bat-pollinated.
Pavlova spp.	Haptophytes	k. *Protista*, p. *Haptophyta*, c. *Prymnesiophyceae*, o. *Pavlovales*, f. *Pavlovaceae*. Marine cells with lemon-yellow chloroplasts.
Pedilanthes tithymaloides	Devil's backbone	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Fleshy zigzag stems with pointed leaves; milky sap.
Pelargonium hortorum	Garden geranium	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Geraniales*, f. *Geraniaceae*. Shrubby; tender stem producing kidney-shaped, velvety leaves; colorful, clustered flowers on stalks held above leaves.

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Pellaea spp.	Cliff brake	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Woodsiaceae*. Stiff, brittle, light green leaves.
Pellia neesiana	Liverwort, thalloid	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Metzegeriales*, f. *Pelliaceae*. Delicate, shiny plants on bare soil along streams or lakes.
Peltigera aphthosa	Studded leather lichen	k. *Fungi*, g. lichen, f. *Peltigeraceae*. Leafy body with brown, warty growths on upper surface.
Penicillium notatum	Penicillin mold	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Moniliaceae*. One of the molds that produce the antibiotic penicillin.
Penicillium roqueforti	Cheese mold	k. *Fungi*, g. deuteromycetes, c. *Hyphomycetes*, o. *Moniliales*, f. *Moniliaceae*. Gives appearance, flavor, odor, and texture to cheeses, such as Roquefort, Stilton, and Gorgonzola.
Penicillus dumetosus	Merman's shaving brush	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*., o. *Caulerpales*, f. *Udoteaceae*. Stalk bears thick clusters of branches resembling a shaving brush.
Penstemon spp.	Beard tongues	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Tender and woody species, some ornamental with bright red or blue tubular flowers.
Peperomia spp.	Peperomia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Piperales*, f. *Piperaceae*. Tender plants with fleshy pale green stems and leaves; popular houseplants.
Persea americana	Avocado	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Laurales*, f. *Lauraceae*. Tropical tree; pear-shaped or rounded fruits with yellow-green, oil-dense flesh eaten fresh or prepared as guacamole.
Petroselinum crispum	Parsley	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Frilly or plain leaves used in cooking or as garnish.
Petunia hybrida	Petunia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Tender trailing plant with hairy stems and leaves; colorful, funnel-shaped flowers; popular bedding plant.
Phacus helikoides	Euglenoid	k. *Protista*, p. *Euglenophyta*, c. *Euglenophyceae*, o. *Euglenales*, f. *Euglenaceae*. Twisted body is covered by a rigid sheath.
Phaeocystis spp.	Haptophytes	k. *Protista*, p. *Haptophyta*, c. *Prymnesiaceae*, o. *Coccosphaerales*, f. *Coccolithaceae*. Cells single or in colonies; contribute large amounts of sulfur to acid rain formation.
Phaseolus coccineus	Scarlet runner bean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Climbing vine with scarlet, white, or mixed flowers; grown for beans or flowers.

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Phaseolus lunatus	Lima bean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Climbing vine producing pods harvested for edible seeds, cooked or ground for flour.
Phaseolus vulgaris	Kidney bean, string bean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Most widely grown bean; young pods (string beans) eaten fresh or cooked; dried seeds cooked.
Philadelphus coronarius	Mock orange	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Hydrangeaceae*. Shrub or small tree producing white, fragrant flowers.
Philadelphus lewisii	Syringa	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Hydrangeaceae*. Arching plant producing large, fragrant, satiny flowers; Idaho state flower.
Phleum pratense	Timothy	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Bunchgrass used for pasture or hay, especially for horses.
Phlogiotis helvelloides	Apricot jelly	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Tremellales*, f. *Tremellaceae*. Apricot-colored, rubbery, funnel-shaped cap with stalk attached near edge of cap.
Phoenix dactylifera	Date palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tall tree with featherlike leaves; fruits surround seeds with soft, sugary, fleshy edible pulp.
Phoradendron sertinum	Mistletoe	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Santalales*, f. *Viscaceae*. Parasitic shrub growing from branches of host tree; white berries ripen in winter, used as holiday decoration; Oklahoma state flower.
Photinia serrulata	Chinese photinia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Shrub or small tree with stiff, prickly-edged leaves; white flowers, then red berries, in flat-topped clusters.
Phragmidium violaceum	Violet rust	k. *Fungi*, p. *Basidiomycota*, c. *Uredinomycetes*, o. *Uredinales*, f. *Pucciniaceae*. Causes violet leaf spots on bramble hosts.
Phycopeltis spp.	Green algae	k. *Protista*, p. *Chlorophyta*, c. *Ulvophyceae*, o. *Trentepohliales*, f. *Trentepohliaceae*. Circular body grows on surface of many tropical plants.
Phyllitis scolopendrium	Hart's tongue	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Polypodiaceae*. Undivided leaves in a star-shaped cluster from a hardy base.
Physalis ixocarpa	Tomatillo	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Tender plant producing a large berry surrounded by a lanternlike husk.
Physarum polycephalum	Plasmodial slime mold	k. *Protista*, p. *Myxomycota*, c. *Myxomycetes*, o. *Physarales*, f. *Physaraceae*. Travels as a thin mass of protoplasm; divides into small mounds to reproduce.

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Physoderma alfalfae	Chytrid	k. *Fungi*, p. *Chytridiomycota*, c. *Chytridiomycetes*, o. *Blastocladiales*, f. *Blastocladiaceae*. Causes the minor disease crown wart of alfalfa.
Physostegia virginiana	Obedience plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Blossoms remain in position when twisted on plant.
Phytolacca americana	Pokeweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Phytolaccaceae*. Tall, tender plant with red to purple stems producing shiny purple-black berries.
Phytophthora infestans	Potato blight pathogen	k. *Protista*, p. *Oomycota*, c. *Oomycetes*, o. *Peronosporales*, f. *Pythiaceae*. Cause of the historic Irish Potato Famine (1840's).
Picea abies	Norway spruce	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Picea engelmannii	Engelmann spruce	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Picea glauca	Black Hills spruce	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; South Dakota state tree.
Picea mariana	Black spruce	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Picea pungens	Blue spruce	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; state tree of Colorado, Utah.
Picea sitchensis	Sitka spruce	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; Alaska state tree.
Pilea cadierei	Aluminum plant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Urticaceae*. Small plant with fleshy stems and leaves; leaves bluish green with silver spots.
Pimenta dioica	Allspice	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Myrtaceae*. Small tropical tree; unripe dried berries used as a multipurpose spice in both sweet and savory dishes.
Pimpinella anisum	Anise	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Apiaceae*. Seeds and extracts used in cooking.
Pinus aristata	Bristlecone pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; includes oldest known plant, more than four thousand years old.
Pinus contorta	Lodgepole pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; cones open when heated by fire.
Pinus coulteri	Coulter pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; produces largest pine cone.

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Pinus edulis	Pinyon pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; edible seeds sold as "pine nuts"; New Mexico state tree.
Pinus elliottii	Slash pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Pinus flexilis	Limber pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; twigs extremely flexible.
Pinus lambertiana	Sugar pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree with massive cone.
Pinus monophylla	Single-leaf pinyon	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; edible seeds sold as "pine nuts"; Nevada state tree.
Pinus monticola	Western white pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; Idaho state tree.
Pinus nigra	Austrian pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Pinus palustris	Southern pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; state tree of Alabama, Arkansas, North Carolina.
Pinus ponderosa	Ponderosa pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; Montana state tree.
Pinus resinosa	Red pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; Minnesota state tree.
Pinus strobus	Eastern white pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; state tree of Michigan, Maine; cone and tassel are Maine state flower.
Pinus sylvestris	Scots pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Pinus taeda	Loblolly pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree.
Piper betel	Betel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Piperales*, f. *Piperaceae*. Vine producing leaves chewed with betel nut for stimulant and narcotic effects.
Piper methysticum	Kava	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Piperales*, f. *Piperaceae*. Plant with large stump or root-stock; root extract fermented to produce alcoholic drink.
Piper nigrum	Pepper	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Piperales*, f. *Piperaceae*. Climbing vine producing fruits (peppercorns) in long, hanging clusters; dried, unripe fruits make black pepper; ripe fruits with covers removed make white pepper.

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Pistacia vera	Pistachio	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Anacardiaceae*. Tree; shells of fruits split before harvest; nuts with green seeds eaten alone or added to foods.
Pisum sativum	Garden pea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tender vine producing seeds in pod; seeds used fresh, dried, or ground to flour; vines used as livestock fodder.
Plagiomnium	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Mniaceae*. Rounded hexagonal cells cause leaves to shrivel and appear dead when dry.
Plantago lanceolata	Plantain	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Plantaginales*, f. *Plantaginaceae*. Lawn weed; long, lance-shaped leaves with parallel veins.
Plantago major	Plantain	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Plantaginales*, f. *Plantaginaceae*. Lawn weed; broad, leaves with parallel veins.
Plasmopara viticola	Powdery mildew pathogen	k. *Protista*, p. *Oomycota*, c. *Oomycetes*, o. *Peronosporales*, f. *Peronosporaceae*. Destroys grapes and damages leaves on many plants.
Platanus acerifolia	London plane tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Hamamelidales*, f. *Platanaceae*. Hybrid between American and Asian sycamores; fruit spherical and spiny; commonly planted along city streets.
Platanus occidentalis	American sycamore	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Hamamelidales*, f. *Platanaceae*. Tree with patchy gray-white bark and large, shallowly lobed leaves; fruit spherical and bumpy.
Platanus orientalis	Oriental sycamore	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Hamamelidales*, f. *Platanaceae*. Tree with deeply lobed leaves and spherical fruits.
Platycerium bifurcatum	Staghorn fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Polypodiaceae*. Protruding, branched, "hornlike" leaves with small round leaves forming a collar around their bases.
Platycodon grandiflorus	Balloon flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Campanulales*, f. *Campanulaceae*. Upright plant with swollen, balloonlike flower buds.
Pleurochrysis spp.	Haptophytes	k. *Protista*, p. *Haptophyta*, c. *Prymnesiophyceae*, o. *Coccolithophorales*, f. *Coccolithaceae*. Cells with paired brown chloroplasts and paired flagella.
Pleurotus ostreatus	Oyster mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Tricholomataceae*. Thick cap and gills on short stalks; available commercially.
Plicaturopsis crispa	Crimped gill	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales*, f. *Corticiaceae*. Stalkless, shelflike, hairy-white cap with gilllike folds on top.
Poa pratensis	Kentucky blue grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Grass; widely grown in cool areas in pastures and lawns.

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Podocarpus macrophyllus	Buddhist pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Podocarpaceae*. Evergreen tree; leaves long, narrow, dark green.
Podophyllum peltatum	May apple	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Berberidaceae*. Umbrella-like plant growing in the shade of deciduous forests.
Polemonium caeruleum	Jacob's ladder	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Polemoniaceae*. Upright stem with fernlike leaves; lavender blue, drooping flowers.
Polypodium glycyrrhiza	Licorice fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Polypodiaceae*. Leaves divided nearly to midrib; stem licorice-flavored or acrid.
Polypodium polypodioides	Resurrection fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Polypodiaceae*. Wiry stem with black scales; leaf blades divided nearly to midrib.
Polystichum acrostichoides	Christmas fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Dryopteridaceae*. Stiff evergreen leaves.
Polytrichum spp.	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Polytrichales*, f. *Polytrichaceae*. Stiff, erect individual plants form cushionlike mats.
Pontederia cordata	Pickerel weed	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Pontederiaceae*. Aquatic plant; leaves arrow-shaped; bright blue flowers on tall stalks.
Populus alba	White poplar	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree; leaves three- to five-lobed, woolly white beneath.
Populus deltoides	Eastern cottonwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree; leaves triangular; state tree of Wyoming, Kansas, Nebraska.
Populus nigra	Lombardy poplar	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree; leaves triangular to diamond-shaped; branches rise abruptly from trunk to produce a narrow, cylindrical shape.
Populus sargentii	Plains cottonwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree; leaves roughly egg-shaped.
Populus tremuloides	Quaking aspen	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree; leaves nearly circular; flattened leafstalk causes leaves to shimmer in light breeze.
Populus trichocarpa	Black cottonwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Large tree; leaf blades narrow from rounded base to pointed tip; buds are fragrant in spring.
Porella cordaeana	Liverwort, leafy	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Jungermanniales*, f. *Porellaceae*. Grows on tree trunks or rock outcroppings.
Porolithon craspedium	Coralline red alga	k. *Protista*, p. *Rhodophyta*, c. *Florideophyceae*, o. *Corallinales*, f. *Corallinaceae*. Marine alga that accumulates calcium carbonate in cell walls to form a hard covering.

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Porphyra spp.	Red algae	k. *Protista*, p. *Rhodophyta*, c. *Rhodophyceae*, o. *Porphyridales*, f. *Porphyridaceae*. Large, leaflike blades; an important food crop processed to produce nori, used in sushi and other dishes.
Portulaca grandiflora	Rose moss	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Portulacaceae*. Fleshy bedding plant with bright, colorful flowers.
Portulaca oleracea	Purslane	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Portulacaceae*. Widespread weed with fleshy stems, tiny yellow flowers.
Postelsia palmaeformis	Sea palm	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Laminariales*, f. *Lessoniaceae*. Stout, erect stalk with fringe of long, strap-shaped, leaflike blades sprouting from top; resembles a palm.
Potamogeton spp.	Pondweed	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Najadales*, f. *Potamogetonaceae*. Freshwater plants; floating leaves are broad, submerged leaves narrow.
Pouteria sapota	Mamey sapote	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ebenales*, f. *Sapotaceae*. Evergreen broadleaf tropical tree; edible pulpy fruit.
Primula vulgaris	Primrose	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Primulales*, f. *Primulaceae*. Tender plant with colorful flowers on leafless stalks; popular bedding plants in cool-season gardens.
Propionibacterium acnes	Acne pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Actinobacteria*, c. *Actinobacteria*, o. *Actinomycetales*, f. *Propionibacteriaceae*. Gram-positive rod causes the skin inflammation acne.
Prosopis glandulosa	Mesquite	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Shrub or small tree producing clusters of long pods; aggressively invasive in dry climates.
Protea cynaroides	Giant protea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Proteales*, f. *Proteaceae*. Shrubby plant with many-seeded flower clusters common as dried flowers.
Prunus americana	American plum	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree; white, bad-smelling flowers appear before leaves; fruit round, red with tart yellow flesh; forms thickets.
Prunus angustifolia	Chickasaw plum	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree producing white flowers before leaves; fruit a small red or yellow plum.
Prunus armeniaca	Apricot	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree producing fruit with hairy skin, stony center, and juicy flesh; used fresh, canned, or processed.
Prunus avium	Sweet cherry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree; fruit with thin skin, stony center, and juicy flesh used fresh or processed.

Scientific Name	Common Name	Taxonomy and Characteristics
Prunus dulcis	Almond	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree producing peachlike fruits that dry and split to reveal shell surrounding the almond.
Prunus persica	Peach	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small tree producing fruit with hairy skin, stony center, and juicy flesh; used fresh, canned, processed; blossom is Delaware state flower.
Prunus serotina	Black cherry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree producing white flowers followed by black-fleshed cherries.
Prunus spinosa	Sloe	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Shrub with thorny branches; blue-black, plumlike fruit with sour green flesh used to make sloe wine or gin.
Prunus virginiana	Common choke cherry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Bushy tree producing long clusters of white flowers followed by dark red, puckery cherries.
Psathyrella longistriata	Ringed psathyrella	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Agaricales*, f. *Coprinaceae*. Mushroom with dark brown cap and delicate fringe on stalk.
Pseudotsuga menziesii	Douglas fir	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; cone scales with three-pointed bracts; Oregon state tree.
Psidium guajava	Guava	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Myrtaceae*. Tree with large, berrylike fruit used fresh or processed.
Psilotum nudum	Whiskfern	k. *Plantae*, p. *Psilotophyta*. Wiry green stems without true leaves or roots.
Ptelea trifoliata	Common hop tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Tree with leaves divided into three leaflets; fruits round with paper-thin wing around the edge.
Pteridium aquilinum	Bracken fern	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Dennstaedtiaceae*. Large, upright, pale green leaves; grows in extensive stands.
Ptilidium pulcherimum	Liverwort, leafy	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Jungermanniales*, f. *Ptilidiaceae*. Leaves four-lobed; dense, fuzzy, spreading patches firmly attached to wood surface.
Puccinia graminis	Black stem rust	k. *Fungi*, p. *Basidiomycota*, c. *Uredinomycetes*, o. *Uredinales*, f. *Pucciniaceae*. Economically important parasite of wheat and other grain crops.
Pueraria lobata	Kudzu	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Aggressive trailing or climbing vine; leaves divided into three leaflets; fruit a hairy pod.

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Punica granatum	Pomegranate	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Punicaceae*. Shrub or small tree producing fleshy flower and spherical fruit with leathery skin and many fleshy, juicy seeds; juice used in drinks, syrups, and wine production.
Pusatilla hirsutissima	American pasque flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ranunculales*, f. *Ranunculaceae*. Clumps of feathery gray-green leaves follow bell-shaped flowers; fruits form feathery, gray pompons; South Dakota state flower.
Pyrobaculum aerophilum	Hyperthermophile	d. *Archaea*, k. *Archaeobacteria*, p. *Crenarchacota*, c. *Thermoprotei*, o. *Thermoproteales*, f. *Thermoproteaceae*. Grows best at the temperature of boiling water (100 degrees Celsius).
Pyrus communis	Pear	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree; fruits with thin skin, juicy, soft flesh surrounding seed compartments; used fresh, stewed, canned, or dried.
Pythium spp.	Damping-off pathogen	k. *Protista*, p. *Oomycota*, c. *Oomycetes*, o. *Peronosporales*, f. *Pythiaceae*. Causes damping off: Stems of young seedlings rot at the base soon after sprouting.
Quercus spp.	Oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; fruit an acorn; Iowa state tree.
Quercus alba	White oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with rounded lobes; fruit an acorn; state tree of Maryland, Connecticut, Illinois.
Quercus coccinea	Scarlet oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with toothed, pointed lobes; fruit an acorn; Washington, D.C., tree.
Quercus imbricaria	Shingle oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; oblong to lance-shaped leaves; fruit an acorn.
Quercus marcocarpa	Bur oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with rounded lobes; fruit an acorn with fringe of stiff scale tips.
Quercus marilandica	Blackjack oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves widest near tip; fruit an acorn.
Quercus muehlenbergii	Chinkapin oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with large, blunt teeth; fruit an acorn.
Quercus palustris	Pin oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with toothed, pointed lobes; fruit an acorn.
Quercus rubra	Red oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with toothed, pointed lobes; fruit an acorn; New Jersey state tree.

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Quercus shumardii	Shumard oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with toothed, pointed lobes; fruit an acorn.
Quercus stellata	Post oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with rounded or blocky lobes; fruit an acorn.
Quercus velutina	Black oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; leaves with toothed, pointed lobes; fruit an acorn.
Quercus virginiana	Live oak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fagales*, f. *Fagaceae*. Tree; evergreen, elliptical leaves; fruit an acorn; Georgia state tree.
Rafflesia arnoldii	Rafflesia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rafflesiales*, f. *Rafflesiaceae*. Parasite living within host plant except when flowering; produces the largest flower in the world.
Ramalina menziesii	Lace lichen	k. *Fungi*, g. lichen, f. *Ramilinaceae*. Yellow-green, netlike growth, often in thick curtains dangling from trees.
Raphanus sativus	Radish	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Red or white swollen root with sharp, tangy flavor, eaten raw or cooked.
Ratibida columnifera	Mexican hat	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Flower heads with yellow drooping segments surround brown, upright, cylindrical center.
Ravenala madagascariensis	Travelers palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Strelitziaceae*. Tall, palmlike plant with leaves in two rows, fanlike outline.
Rhamnus caroliniana	Carolina buckthorn	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rhamnales*, f. *Rhamnaceae*. Small tree; birchlike leaves and clusters of black berries.
Rhamnus purshiana	Cascara buckthorn	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rhamnales*, f. *Rhamnaceae*. Small tree; bark harvested for laxative production.
Rheum rhaponticum	Rhubarb	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Polygonales*, f. *Polygonaceae*. Clusters of large leaves with toxic blades on sturdy red stalks; stalks used in pies, preserves.
Rhizobium spp.	Rhizobium	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Alphaproteobacteria*, o. *Rhizobiales*, f. *Rhizobiaceae*. Gram-negative cell converts (fixes) nitrogen in the air to a form used by plants; forms nodules on the roots of plants in the pea family.
Rhizocarpon geographicum	Map lichen	k. *Fungi*, g. lichen, f. *Rhizocarpaceae*. Most common of several lichens with the common name; black lower layer bears yellow fruiting bodies.
Rhizophora mangle	Red mangrove	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rhizophorales*, f. *Rhizophoraceae*. Tree; leathery evergreen leaves; prominent in marine tidal zones.

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Rhizopus stolonifer	Black bread mold	k. *Fungi*, p. *Zygomycota*, c. *Zygomycetes*, o. *Mucorales*, f. *Mucoraceae*. Common mold forms cottony mats on surface of moist bread.
Rhododendron spp.	Azalea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Small to large, deciduous or evergreen shrubs with showy flowers; Georgia state wildflower.
Rhododendron spp.	Rhododendron	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Small to large, deciduous or evergreen shrubs with showy flowers; *R. macrophyllum* is Washington state flower.
Rhododendron maximum	Big laurel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Shrub with leathery evergreen leaves and clusters of showy, funnel-shaped flowers; West Virginia state flower.
Rhodomonas spp.	Cryptomonads	k. *Protista*, p. *Cryptophyta*, c. *Cryptophyceae*, o. *Cryptomonadales*, f. *Cryptomonadaceae*. Cells with single red chloroplasts; form spring blooms in freshwater lakes.
Rhodospirillum rubrum	Purple nonsulfur bacterium	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Alphaproteobacteria*, o. *Rhodospirillales*, f. *Rhodospirillaceae*. Uses a type of photosynthesis that does not produce oxygen.
Rhoeo spathacea	Moses-in-the-cradle	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Commelinales*, f. *Commelinaceae*. Short plant; leaves dark green on top, deep purple beneath; white flowers emerge from boat-shaped pair of bracts.
Rhus typina	Staghorn sumac	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Anacardiaceae*. Shrub with divided leaves producing dense clusters of dry hairy fruits at ends of branches.
Ribes aureum	Golden currant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Grossulariaceae*. Shrub producing clusters of tubular yellow flowers.
Ribes grossularia	Gooseberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Grossulariaceae*. Thorny shrub with yellow, green, or red fruits used in baking, desserts, juices, wine, and other foods.
Ribes nigrum	Black currant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Grossulariaceae*. Shrub with black fruits used in baking, desserts, juices, wine, and other foods.
Ricinus communis	Castor bean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Euphorbiaceae*. Tall plant with large, palmlike leaves; produces attractive mottled seeds; toxic.
Robinia pseudoacacia	Black locust	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tree producing paired spines on twigs.
Roccella tinctoria	Litmus lichen	k. *Fungi*, g. lichen, f. *Roccellaceae*. Source of litmus used to test acidity of liquids.

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Rosa spp.	Roses	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Small to large shrub with prickles on stem and leaves; varieties differ in color of large, showy flowers; New York state flower.
Rosa arkansana	Wild prairie rose	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. North Dakota state flower.
Rosa pranticola	Prairie rose	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Iowa state flower.
Rosa sinica	Cherokee rose	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Georgia state flower.
Rosmarinus officinalis	Rosemary	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used to flavor lamb, poultry, salads.
Roystonea regia	Royal palm	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tree with smooth gray trunk, featherlike leaves, one-seeded purple fruits.
Rozella allomycis	Chytrid	k. *Fungi*, p. *Chytridiomycota*, c. *Chytridiomycetes*, o. *Spizellomycetales*, f. *Olpidiaceae*. Parasite that lives inside host algae and fungi.
Rubus spp.	Blackberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Prickly climbing plant producing stems that radiate from the rootstock; fruit a cluster of small, juicy globes containing seeds; eaten fresh or used in pies or jam.
Rubus idaeus	Raspberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Coarse, thorny bush producing conical, red, seedy fruit on swollen flower base; used fresh, canned, frozen.
Rubus occidentalis	Black raspberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Coarse, thorny bush producing rounded, black, seedy, raspberry-like fruits.
Rubus parviflorus	Thimbleberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Coarse shrub with soft, hairy leaves; produces cap-shaped, red, dry, edible berries.
Rubus spectabilis	Salmonberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Vigorous, invasive shrub with few weak prickles producing bland, yellow to red, raspberry-like fruits.
Rudbeckia hirta	Black-eyed Susan	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Bristly-hairy plant; flower heads with daisylike yellow segments and brown-black centers; Maryland state flower.
Ruellia peninsularis	Ruellia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Acanthaceae*. Shrub with pale purple, bell-shaped flowers.
Rumex acetosa	Sorrel	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Polygonales*, f. *Polygonaceae*. Tender plant with acidic, arrowlike leaves.

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Ruta graveolens	Rue	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Aromatic bush producing decorative brown seed capsules.
Sabal palmetto	Cabbage palmetto	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Tree; fan-shaped leaves with narrow drooping segments; one-seeded black fruits; state tree of South Carolina, Florida.
Saccharomyces cerevisiae	Bakers' yeast, Brewers' yeast	k. *Fungi*, p. *Ascomycota*, c. *Hemiascomycetes*, o. *Saccharomycetales*, f. *Saccharomycetaceae*. Yeast used as leaven in baking and fermenting agent in brewing.
Saccharum officinarum	Sugarcane	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poacea*. Tall tropical grass; solid stem processed for table sugar.
Saintpaulia ionantha	African violet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Gesneriaceae*. Small, delicate plant with rosette of fuzzy leaves and clusters of pale purple flowers; popular houseplant.
Salix alba	White willow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree with olive-green branches; bark the original source of active ingredient in aspirin.
Salix babylonica	Weeping willow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Tree with long drooping branches, narrow lance-shaped leaves.
Salix discolor	Pussy willow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Shrub or small tree; male and female on different trees; male flowers in soft, silky clusters.
Salix interior	Sandbar willow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Shrub or small tree; typically found along waterways.
Salix lasiandra	Pacific willow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Shrub or small tree; young twigs yellow.
Salix nigra	Black willow	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Salicales*, f. *Salicaceae*. Shrub or small tree; young twigs reddish.
Salsola kali	Russian thistle, tumbleweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Chenopodiaceae*. Shrubby, branched, spiny plant; dead stem breaks off to form tumbleweed.
Salvia officinalis	Sage	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used to flavor stuffings, cheeses, meats.
Sambucus canadensis	American elder	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales*, f. *Caprifoliaceae*. Shrub with large, divided leaves; purple-black berries in flat-topped clusters; used in pies, wine making.
Sanguinaria canadensis	Bloodroot	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Papaverales*, f. *Papaveraceae*. Tender plant with grayish lobed leaves and white, spring flowers; cut stems and root bleed orange or red juice.

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Sansevieria trifasciata	Mother-in-law's tongue, snake plant	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Long, strap-shaped, upright leaves patterned with dark and pale green, yellow, gray, and white.
Santalum album	Sandalwood tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Santalales*, f. *Santalaceae*. Tree producing aromatic, sweet-scented wood used in cabinetmaking.
Sapindus saponaria	Soapberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Sapindaceae*. Small tree with divided leaves producing yellow or orange berries; fruit flesh has been used as a soap substitute.
Sarcoscypha coccinea	Scarlet cup	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Pezizales*, f. *Sarcoscyphaceae*. Bright red cup, with white outer surface.
Sargassum spp.	Kelp	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Fucales*, f. *Sargassaceae*. Large kelps that gave the Sargasso Sea its name; includes edible species.
Sassafras albidum	Sassafras	k. *Plantae*, p. *Anthophyta*, g. magnoliids, o. *Laurales*, f. *Lauraceae*. Small tree; leaves unlobed, or with two or three lobes; small, egg-shaped blue fruits; oils used in soaps.
Satureia hortensis	Summer savory	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used to flavor a variety of meat and bean dishes.
Satureia montana	Winter savory	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used as a substitute for summer savory.
Scabiosa atropurpurea	Pincushion flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales*, f. *Dipsacaceae*. Stamens stick out of pinlike flowers, resembling a pincushion; used in fresh and dried flower arrangements.
Scaevola spp.	Scaevola	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Campanulales*, f. *Goodeniaceae*. Low-growing shrub producing deep lilac, fan-shaped flowers.
Scapania cuspiduligera	Liverwort, leafy	k. *Plantae*, p. *Hepatophyta*, c. *Jungermanniopsida*, o. *Jungermanniales*, f. *Scapaniaceae*. Among the most common liverworts on trees in temperate rain forests.
Scenedesmus spp.	Scenedesmus	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*, o. *Chlorococcales*, f. *Scenedesmaceae*. Cylindrical cells arranged in flat colonies of four to sixteen members; found mostly in fresh water.
Schefflera actinophylla	Schefflera, umbrella tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Apiales*, f. *Araliaceae*. Small tree or shrub with an umbrella-like appearance.
Scirpus cernuus	Low bulrush	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Cyperaceae*. Grasslike plant with threadlike drooping stems bearing brown heads at the tips.

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Scleroderma aurantium	Earthball	k. *Fungi*, p. *Basidiomycota*, c. *Basidiocycetes*, o. *Sclerodermatales*, f. *Sclerodermataceae*. Large, roughly spherical body filled with spores.
Scutellaria lateriflora	Skullcap	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Small plant with distinctive flower buds in the shape of helmet.
Secale cereale	Rye	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Grass grown as cereal crop; susceptible to ergot infection.
Selaginella densa	Compact spike moss	k. *Plantae*, p. *Lycophyta*, c. *Lycopsida*, o. *Selaginellales*, f. *Selaginellaceae*. Plant with horizontal stems producing short, upright branches with leaves closely spaced and four-sided stalkless cones.
Selaginella lepidophylla	Resurrection plant	k. *Plantae*, p. *Lycophyta*, c. *Lycopsida*, o. *Selaginellales*, f. *Selaginellaceae*. Branches in a dense rosette; green when wet, rolled brown ball when dry; wetting dried branches reproduces green form; spore-bearing cones form on tips of branches.
Sempervivum tectorum	Hen and chickens	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Crassulaceae*. Compact clusters of scaly leaves produce small clones connected by runners.
Senecio cineraria	Dusty miller	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Woolly gray-silver bedding plant.
Senecio rowleyanus	String of beads	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Wiry hanging stems with spherical green leaves.
Sequoia sempervirens	Coast redwood	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tall tree with flat, sharp needles; cone scales shield-shaped.
Sequoiadendron giganteum	Giant sequoia	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Massive tree with short, awl-shaped leaves and egg-shaped cones.
Serenoa repens	Saw palmetto	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Arecales*, f. *Arecaceae*. Shrub with creeping stems, fan-shaped leaves, stalks with sharp, stiff, curved spines.
Sesamum indicum	Sesame seed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Pedaliaceae*. Leafy plant with tubular flowers followed by capsule full of small seeds pressed for oil or used whole.
Setaria italica	Foxtail millet	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Leafy, few-branched stem bears a long, dense, bristly, flower cluster.
Setcreasea pallida	Purple heart	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Commelinales*, f. *Commelinaceae*. Upright or trailing stems with lance-shaped purple leaves.
Simarouba glauca	Paradise tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Simaroubaceae*. Tree with divided leaves; purple fruit borne in clusters.

Scientific Name	Common Name	Taxonomy and Characteristics
Simmondsia californica	Jojoba	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Euphorbiales*, f. *Buxaceae*. Tree producing seed containing a liquid wax used in place of sperm whale oil.
Sinapis alba	White mustard	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Capparales*, f. *Brassicaceae*. Flour from ground seeds included in table mustard.
Sinningia speciosa	Gloxinia	k. Plantae, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Gesneriaceae*. Popular houseplant with velvety leaves and showy, brightly colored flowers.
Sisyrinchium bellum	Blue-eyed grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Iridaceae*. Grasslike leaves; blue to purple six-petal flowers in spring.
Smilacina racemosa	False Solomon's seal	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Tall, arching stalks with two rows of pale green leaves; cluster of white flowers on top stalk.
Smilax aristolochiaefolia	Mexican sarsaparilla	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Smilacaceae*. Woody vine with clawlike thorns; extracts used as flavoring sarsaparilla.
Smilax bona-nox	Catbrier	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Smilacaceae*. Woody vine with clawlike thorns; leaves shallow-lobed with grayish patches.
Solanum melanogena	Eggplant	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Small, tough, short woolly plant producing a thick, fleshy, white, yellow or purple fruit; eaten cooked.
Solanum tuberosum	Potato	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Solanales*, f. *Solanaceae*. Tender, weakly upright plant cultivated for large fleshy underground stems (tubers).
Sorbus aucuparia	European mountain ash, rowan	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree with clusters of red or orange fruits; ornamental; fruits processed for use in jam.
Sorbus domestica	Service tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Tree producing apple or pear-shaped fruit used for jam; must be allowed to half-rot before it is palatable.
Sorghum bicolor	Sorghum	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Cereal grass widely cultivated for grain, for forage, or as source of syrup.
Sorghum halapense	Johnson grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Coarse grass growing in dense stands from rootstock; aggressively invasive.
Sorghum sudanese	Sudan grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Grass; grown extensively as pasture or silage crop.

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Sphagnum spp.	Peat mosses	k. *Plantae*, p. *Bryophyta*, c. *Sphagnidae*, o. *Sphagnales*, f. *Sphagnaceae*. Green, red, or brown masses; leaves with alternate rows of small living cells and large dead cells; leaves hold twenty times their weight in water.
Spinacea oleracea	Spinach	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Chenopodiaceae*. Green, crinkly leaves eaten raw or cooked.
Spiraea spp.	Spiraea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rosales*, f. *Rosaceae*. Shrubs produce dense clusters of white, pink, or red flowers.
Spirogyra spp.	Spirogyra	k. *Protista*, p. *Chlorophyta*, c. *Charophyceae*, o. *Zygnematales*, f. *Zygnemataceae*. Produces filments with one to sixteen spiral, ribbon-shaped chloroplasts per cell.
Splachnum spp.	Dung mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Splachnaceae*. Broad, skirtlike base on spore-bearing capsules; found only on dung; sticky spores carried to fresh dung by flies.
Sporobolomyces roseus	Rose-colored yeast	k. *Fungi*, g. deuteromycetes, c. *Blastomycetes*, o. *Sporobolomycetales*, f. *Sporobolomycetaceae*. Common on dead or dying leaves; can cause allergic reactions.
Sporodinia grandis	Mushroom mold	k. *Fungi*, p. *Zygomycota*, c. *Zygomycetes*, o. *Mucorales*, f. *Mucoraceae*. Commonly found on decaying mushrooms.
Stachys byzantina	Lamb's ears	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. White-woolly, tongue-shaped leaves on stalks with clusters of small purple flowers.
Stapelia variegata	Carrion flower	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Asclepiadaceae*. Four-sided cactuslike stems with fleshy, mottled flowers that smell like rotting flesh.
Stellaria media	Chickweed	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Caryophyllaceae*. Succulent, creeping plant with glossy, deep green leaves.
Streblonema spp.	Brown algae	k. *Protista*, p. *Phaeophyta*, c. *Phaeophyceae*, o. *Ectocarpales*, f. *Streblonemataceae*. Grows inside brown or red algae, causing disease in some.
Strelitzia reginae	Bird of paradise	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Strelitziaceae*. Clusters of tall, fanlike leaves; orange, blue, and white flowers reminiscent of bright tropical birds; used in flower arrangements.
Streptocarpus spp.	Cape primrose	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Gesneriaceae*. Tender houseplant related to African violet, with longer leaves and long flower stalks.
Streptococcus mutans	Strep mutans	d. *Bacteria*, k. *Eubacteria*, p. *Firmicutes*, c. *Bacilli*, o. *Lactobacillales*, f. *Streptococcaceae*. Gram-positive spherical cell causing tooth decay.

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Suillus luteus	Slippery jack mushroom	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Boletales*, f. *Boletaceae*. Slimy red-brown cap, yellow pores, and pale purple ring on stalk.
Sulfolobus sulfataricus	Thermoacidophile	d. *Archaea*, k. *Archaeobacteria*, p. *Crenarchacota*, c. *Thermoprotei*, o. *Sulfolobales*, f. *Sulfolobaceae*. Irregularly lobed cell grows in very hot and acidic water.
Swietenia mahogani	West Indies mahogany	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Meliaceae*. Tree with divided leaves; fruit splits open to release squarish seeds.
Symbiodinium spp.	Dinoflagellates	k. *Protista*, p. *Dinophyta*, c. *Dinophyceae*, o. *Suessiales*, f. *Symbiodiniaceae*. Cells live inside corals, sponges, and giant clams, providing food through photosynthesis.
Symphoricarpus albus	Snowberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales* , f. *Caprifoliaceae*. Fine shrub producing clusters of white spherical berries.
Symphytum officinale	Comfrey	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Boraginaceae*. Bristly leaves cooked and eaten for reputed medicinal value.
Syringa vulgaris	Lilac	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Oleaceae*. Shrub producing long, dense stalks of pink to purple, fragrant flowers; New Hampshire state flower.
Syzygium aromaticum	Clove	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Myrtales*, f. *Myrtaceae*. Evergreen tropical tree; unopened dried flower buds used as a spice.
Tagetes patula	Marigold	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Flowers from yellow to orange or maroon; popular aromatic bedding plants.
Tamarix parviflora	Tamarisk	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Tamaricaceae*. Shrub or small tree; twigs of scalelike leaves drop in fall; large, loose clusters of pink flowers.
Tanacetum parthenium	Feverfew	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Leaves with strong odor; flower heads with white segments.
Tanacetum vulgare	Tansy	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Clusters of buttonlike yellow flower heads on tall stems.
Taraxacum officinale	Dandelion	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Common lawn weed with yellow flower head; seeds with hairy parachutes.
Tarzetta cupularis	Elf cup	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Pezizales*, f. *Pyronemataceae*. Small, deep tan cup with short stalk.

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Taxodium distichum	Bald cypress	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree often found in standing water surrounded by woody “knees” above water surface; needles drop in fall; nearly spherical cones disintegrate at maturity; Louisiana state tree.
Taxus brevifolia	Pacific yew	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Taxales*, f. *Taxaceae*. Evergreen needle-leaf shrub or small tree; original source of substance used to make anticancer drug, paclitaxel (for Taxol).
Tectona grandis	Teak	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Verbenaceae*. Tropical tree; hard, heavy, durable wood is prized for furniture making and ship building.
Tetragonia expansa	New Zealand spinach	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Caryophyllales*, f. *Aizoaceae*. Leaves fleshy, shallow-lobed, triangular; leaves eaten as a substitute for spinach.
Thalassiosira pseudonana	Diatom	k. *Protista*, p. *Bacillariophyta*, c. *Bacillariophyceae*, o. *Centrales*, f. *Thalassiosiraceae*. Marine cells used as a food source for commercial production of oysters and other shellfish.
Theobroma cacao	Cocoa	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Sterculiaceae*. Tropical tree producing football-shaped fruits on trunk and branches; source of cocoa.
Thermoplasma acidophilum	Thermoplasma	d. *Archaea*, k. *Archaeobacteria*, p. *Euryarchacota*, c. *Thermoplasmata*, o. *Thermoplasmatales*, f. *Thermoplasmataceae*. Very small cell that does not produce a cell wall.
Thermus aquaticus	Taq	d. *Bacteria*, k. *Eubacteria*, p. *Deinococcus-Thermus*, c. *Deinococci*, o. *Thermales*, f. *Thermaceae*. Grows in very hot water and produces the enzyme first used in automated polymerase chain reaction (PCR).
Thiobacillus ferrooxidans	Iron bacterium	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Betaproteobacteria*, o. *Hydrogenophilales*, f. *Hydrogenophilaceae*. Gains energy by converting iron from one form to another.
Thuidium spp.	Feather mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Thuidiaceae*. Highly branched plants with a feathery appearance.
Thuja occidentalis	Northern white cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with flat twigs of scalelike leaves; small cones upright on twigs.
Thuja orientalis	Chinese arbor-vitae	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with flat, vertical twigs of scalelike leaves; small cones upright on twigs.
Thuja plicata	Western red cedar	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Cupressaceae*. Tree with flat, vertical twigs of scalelike leaves; small cones upright on twigs.

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Thunbergia alata	Black-eyed Susan vine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Acanthaceae*. Ornamental vine; bold orange or yellow flared flower tube with purple-black throat.
Thymus serpyllum	Creeping thyme	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Lamiaceae*. Aromatic herb used to flavor fish, meat, and poultry.
Tilia americana	American basswood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Malvales*, f. *Tiliaceae*. Tall shade tree with clusters of nutlike fruits attached to winglike bracts.
Tilletia caries	Bunt fungus, stinking smut fungus	k. *Fungi*, p. *Basidiomycota*, c. *Ustomycetes*, o. *Ustilaginales*, f. *Tilletiales*. Infects wheat, degrades grain quality.
Timmia spp.	Mosses	k. *Plantae*, p. *Bryophyta*, c. *Bryidae*, o. *Bryales*, f. *Tummiaceae*. Large, upright plants with leaf bases wrapping around stems; leaves translucent.
Torreya californica	California nutmeg	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Taxales*, f. *Taxaceae* or *Pinaceae*. Evergreen needle-leaf tree with nutlike seed.
Toxicodendron vernix	Poison sumac	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Anacardiaceae*. Shrub with divided leaves producing one-seeded, white-fleshed fruits; leaves contain oil that causes skin irritation.
Trachelomonas grandis	Euglenoid	k. *Protista*, p. *Euglenophyta*, c. *Euglenophyceae*, o. *Eutreptiales* , f. *Eutreptiaceae*. Single cells encased in a rigid mineralized shell.
Tradescantia virginiana	Spiderwort	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Commelinales*, f. *Commelinaceae*. Clumps of grasslike leaves; three-petal flowers red to purple, rarely white.
Tragopogon dubius	Goat's beard	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Large dandelion-like head on a tall stalk; seeds with hairy parachutes.
Tragopogon porrifolius	Salsify	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Long, narrow, tapering white roots boiled and eaten.
Trametes versicolor	Turkey tail	k. *Fungi*, p. *Basidiomycota*, c. *Basidiomycetes*, o. *Porales* , f. *Polyporaceae*. Cluster of colorful, thin, tough, stalkless caps.
Tribulus terrestris	Goathead, puncture vine	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Zygophyllaceae*; noxious weed of bare ground or lawns; produces a stony, five-headed fruit able to puncture tires or bare feet.
Triceratium spp.	Diatoms	k. *Protista*, p. *Bacillariophyta*, c. *Bacillariophyceae*, o. *Centrales*, f. *Biddulphiaceae*. Single cells, triangular or rectangular in outline.
Trichoglossom hirsutum	Velvety earth tongue	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Helotiales*, f. *Geoglossaceae*. Black mushroom with long, tonguelike clubs on a hairy stalk.

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Trifolium incarnatum	Crimson clover	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Upright plant with tall, flamelike crimson flower heads.
Trifolium pratense	Red clover	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Compact plant with red flower heads; Vermont state flower.
Trifolium repens	White clover	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Trailing plant with white or pale pink flower heads; common lawn weed.
Trigonella foenum-graecum	Fenugreek	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Polygalales*, f. *Trigoniaceae*. Cloverlike plant with pugent flavor used in curries and in imitation maple syrup.
Trillium grandiflorum	Wake robin	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Sturdy upright stems with three heart-shaped leaves and one three-petal white flower; Ohio state wildflower.
Triticum aestivum	Wheat	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Cereal grass widely cultivated for edible grain.
Tropaeolum majus	Nasturtium	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Geraniales*, f. *Tropaeolaceae*. Tender trailing plant with umbrella-like leaves and bright yellow, orange, or red flowers.
Tsuga canadensis	Eastern hemlock	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; Pennsylvania state tree.
Tsuga heterophylla	Western hemlock	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Pinaceae*. Evergreen needle-leaf tree; Washington state tree.
Tuber melanosporum	Truffle, black	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Tuberales*, f. *Tuberaceae*. Grows underground on oak and hazel nut trees; considered a delicacy.
Tulipa spp.	Tulip	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Leaves from bulb surround bare stalk with showy flower.
Typha latifolia	Cattail	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Typhales*, f. *Typhaceae*. Tall plant; flowering stalk with dense-hairy flowers turning from green to brown.
Ulmus americana	American elm	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Ulmaceae*. Tree; leaf bases uneven; disk-shaped fruits with paper-thin wings around the edges; state tree of Massachusetts, North Dakota.
Ulmus crassifolia	Cedar elm	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Ulmaceae*. Tree; small leaf bases uneven; disk-shaped fruits with paper-thin wings around the edges.
Ulmus rubra	Slippery elm	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Ulmaceae*. Tree; leaf bases uneven; disk-shaped fruits with paper-thin wings around the edges.

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Ulothrix spp.	Green algae	k. *Protista*, p. *Chlorophyta*, c. *Ulvophyceae*, o. *Ulotricales*, f. *Ulotricaceae*. Body a filament with one ribbonlike chloroplast per cell.
Ulva spp.	Green algae	k. *Protista*, p. *Chlorophyta*, c. *Ulvophyceae*, o. *Ulvales*, f. *Ulvaceae*. Coastal algae with long, thin, leaflike blades; includes edible species.
Ulvaria spp.	Green algae	k. *Protista*, p. *Chlorophyta*, c. *Ulvophyceae*, o. *Ulvales*, f. *Ulvaceae*. Bodies are small sacs or leaflike blades one cell thick.
Urocystis anemones	Anemone smut	k. *Fungi*, p. *Basidiomycota*, c. *Ustomycetes*, o. *Ustilaginales*, f. *Tilletiales*. Infects members of the *Ranunculaceae*. Family includes *Anemone*.
Uroglenopsis spp.	Golden brown algae	k. *Protista*, p. *Chrysophyta*, c. *Chrysophyceae*, o. *Ochromonadales*, f. *Ochromonadaceae*. Spherical colonies of hundreds of cells.
Urtica dioica	Stinging nettle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Urticales*, f. *Urticaceae*. Tall plant; stems and leaves covered with tiny hairs that produce a sharp, persistent sting when touched; leaves can be boiled and eaten like spinach.
Usnea alpina	Old man's beard lichen	k. *Fungi*, g. lichen, f. *Usneaceae*. Bushy body hanging from tree branches; one of many lichens bearing the common name.
Ustilago maydis	Corn smut	k. *Fungi*, p. *Basidiomycota*, c. *Ustomycetes*, o. *Ustilaginales*, f. *Ustilaginaceae*. Produces a black sooty-looking mass of spores on ears of corn (maize).
Vaccinium angustifolium	Lowbush blueberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Small shrubs; grown commercially on a small scale.
Vaccinium corymbosum	Highbush blueberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Large shrubs; most common commercial blueberry.
Vaccinium macrocarpon	Cranberry	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Ericales*, f. *Ericaceae*. Trailing plant with oval red fruits used to make cranberry products.
Valerianella amarella	Hairy corn salad	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales*, f. *Valerianaceae*. Fleshy, pale green leaves; smells like wet dog hair.
Vanilla planifolia	Vanilla orchid	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Orchidales*, f. *Orchiaceae*. Climbing plant producing fruit pods cured and processed for flavoring.
Verbascum thapsus	Mullein	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Attractive roadside or pasture plant; furry leaves clustered at base; tall, flowering stalks.
Verbena hybrida	Garden verbena	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Verbenaceae*. Spreading plant; produces dense clusters of brightly colored flowers.

Scientific Name	Common Name	Taxonomy and Characteristics
Veronica spp.	Speedwell	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Scrophulariales*, f. *Scrophulariaceae*. Bedding plants and lawn weeds with small, colorful flowers.
Vibrio fisheri	Vibrio	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Gammaproteobacteria*, o. *Vibrionales*, f. *Vibrionaceae*. Gram-negative curved rod glows in the dark (luminesces) when living in special organs of marine life.
Vicia faba	Fava bean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Tender plant; seeds in pods; immature seeds or whole pods cooked; dried seeds eaten or used as livestock fodder.
Vicia villosa	Hairy vetch	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Rangy plant with dense clusters of purple flowers.
Victoria amazonica	Royal water lily	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Nymphaeales*, f. *Nymphaeaceae*. Aquatic plant of the Amazon River and its tributaries; enormous round floating leaves and large, showy flowers.
Vigna radiata	Mung bean	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Hairy vine pruduces pods of olive green seeds; used for bean sprouts.
Vigna unguiculata	Black-eyed pea, cowpea	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Climbing vine; very long pods harvested for edible seeds; white seeds with single black spot are black-eyed peas.
Vinca major	Periwinkle	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Gentianales*, f. *Apocynaceae*. Evergreen trailing vine with showy purple flowers; used as a ground cover in shaded areas.
Viola spp.	Native violet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Violaceae*. Illinois state flower.
Viola palmata	Violet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Violaceae*. Rhode Island state flower.
Viola papilionacea	Wood violet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Violaceae*. Wisconsin state flower.
Viola pedata	Bird's foot violet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Violaceae*. Heart-shaped leaves and purple flowers rise from a study root stock.
Viola sororia	Meadow violet	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Violaceae*. New Jersey state flower.
Viola tricolor	Johnny-jump-up	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Violales*, f. *Violaceae*. Oval, deeply lobed leaves; yellow and purple flowers on long stalks.

Scientific Name	Common Name	Taxonomy and Characteristics
Vitex agnus-castus	Chaste tree	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Lamiales*, f. *Verbenaceae*. Shrub with fanlike leaves and long clusters of fragrant flowers.
Vitis vinifera	Grape	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Rhamnales*, f. *Vitaceae*. Woody vine producing a juicy berry; many cultivated varieties are used fresh or are processed for juice.
Volvox spp.	Volvox	k. *Protista*, p. *Chlorophyta*, c. *Chlorophyceae*, o. *Volvocales*, f. *Volvacaceae*. Green algae that form hollow, spherical colonies of hundreds of cells.
Weigelia florida	Weigelia	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Dipsacales* , f. *Caprifoliaceae*. Rangy shrub with red, funnel-shaped flowers.
Wisteria sinensis	Wisteria	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Fabales*, f. *Fabaceae*. Woody vine producing large, grapelike clusters of pale purple flowers.
Wollemia nobilis	Wollemi pine	k. *Plantae*, p. *Pinophyta*, c. *Pinopsida*, o. *Pinales*, f. *Araucariaceae*. Tree; "living fossil" discovered in Australia in 1994; needles arranged in four rows along twigs in mature trees.
Woodsia spp.	Woodsia	k. *Plantae*, p. *Pterophyta*, c. *Filicopsida*, o. *Filicales*, f. *Woodsiaceae*. Leaves clumped; blades green, with rust-colored scales, hairs, or glands.
Xanthidium armatum	Desmid	k. *Protista*, p. *Chlorophyta*, c. *Charophyceae*, o. *Desmidiales*, f. *Desmidiaceae*. One of thousands of single-celled desmid species; easy to recognize by pinched center.
Xanthium strumarium	Cocklebur	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Asterales*, f. *Asteraceae*. Obnoxious weed producing seed heads that cling to clothing and hair.
Xanthomonas campestris	Xanthomonas	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Gammaproteobacteria*, o. *Xanthomonadales*, f. *Xanthomonadaceae*. Gram-negative cell producing xanthan gum, used as a thickener in foods and paints.
Ximenia americana	Hog plum, tallowwood	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Santalales*, f. *Olacaceae*. Small tree with thorny twigs producing small clusters of plumlike fruits with thin puckery flesh.
Xylaria hypoxylon	Carbon antlers	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Xylariales*, f. *Xylariaceae*. Forked white, woody club with dark, thin stalk.
Xylaria polymorpha	Dead man's fingers	k. *Fungi*, p. *Ascomycota*, c. *Euascomycetes*, o. *Xylariales*, f. *Xylariaceae*. Stumpy, gnarled clubs darkening from pale to black with age.
Xyris spp.	Yellow-eyed grass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Commelinales*, f. *Xyridaceae*. Clusters of grasslike leaves and flower clusters on top of bare stalks.

Scientific Name	Common Name	Taxonomy and Characteristics
Yersinia pestis	Plague pathogen	d. *Bacteria*, k. *Eubacteria*, p. *Proteobacteria*, c. *Gammaproteobacteria*, o. *Enterobacteriales*, f. *Enterobacteriaceae*. Gram-negative rod that causes bubonic plague.
Yucca spp.	Yucca	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Blossom is New Mexico state flower.
Yucca brevifolia	Joshua tree	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Agavaceae*. Small tree; leaves clustered near the ends of thick, upraised branches.
Zamia floridana	Cycad	k. *Plantae*, p. *Cycadophyta*, c. *Cycadopsida*, o. *Cycadales*, f. *Zamiaceae*. Palmlike shrub with seeds borne in cones; native of Florida.
Zanthoxylum americana	Common prickly ash	k. *Plantae*, p. *Anthophyta*, c. *Eudicotyledones*, o. *Sapindales*, f. *Rutaceae*. Shrub with spiny branches; aromatic leaves are divided.
Zea mays	Corn, maize	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Cereal grass widely cultivated for edible kernels.
Zebrina pendula	Wandering jew	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Commelinales*, f. *Commelinaceae*. Trailing stems with teardrop-shaped, green or striped leaves.
Zigadenus venenosus	Death camas	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Liliales*, f. *Liliaceae*. Grasslike leaves; sturdy stalks bear clusters of white flowers; poisonous; can be confused with edible camas.
Zingiber officinale	Ginger	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Zingiberales*, f. *Zingiberaceae*. Tall, leafy, grasslike plant with knobby underground stems used medicinally or as spice.
Zizania aquatica	American wild rice	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Cyperales*, f. *Poaceae*. Grows in shallow freshwater bodies; long, shiny, brown-black grain harvested in some areas.
Zostera maritima	Eelgrass	k. *Plantae*, p. *Anthophyta*, c. *Monocotyledones*, o. *Najadales*, f. *Zosteraceae*. Grasslike plant growing in marine intertidal zones.

TIME LINE

c. 1800 B.C.E. Hand pollination of date palms is mentioned in the Code of Hammurabi, king of Babylon.

c. 323-286 B.C.E. In Athens the philosopher Theophrastus of Eresos, a student of Aristotle and Plato, publishes numerous works about plants, including the nine-volume *Peri phyton historias* (also known as *Historia plantarum*; translated into English as "Enquiry into Plants," in *Enquiry into Plants and Minor Works on Odours and Weather Signs*, 1916), which describes the external and internal structures and habitats of plants, and the six-volume *Peri phyton aition* (also known as *De causis plantarum*; translated into English 1976-1990), discussing the physiology of edible and medicinal plants. He is regarded as the father of botany.

c. 235-150 B.C.E. *De agri cultura* (*On Agriculture*, 1913), the earliest surviving treatise on farming, is written by the Roman statesman Marcus Porcius Cato (Cato the Elder).

c. 60-65 C.E. Lucius Junius Moderatus Columella, a Roman citizen born in Spain, completes the twelve-volume *De re rustica* (on rural matters; translated in *Of Husbandry*, 1745) that lists plants and collects practical information about agriculture and *De arboribus* ("on trees," also in *Of Husbandry*).

c. 77 The Roman philosopher Pliny the Elder publishes the encyclopedic *Historia naturalis* (*Natural History*, 1938-1963), of which books 12 through 27 collect information about agriculture, horticulture, and medicinal plants, information that is widely influential throughout antiquity and the Middle Ages.

c. 78 The Greek physician Pedanius Dioscorides publishes *De materia medica* (*The Greek Herbal of Dioscorides*, 1934), in which he instructs readers on the morphology and useful properties of six hundred plant species in the Mediterranean region. The book remains a basic text for physicians and botanists well into the modern era.

c. 1248 The German philosopher Albertus Magnus writes *De vegetabilibus et plantis* (on vegetables and plants), the most significant theoretical work on plants since Theophrastus.

1267 Roger Bacon of England argues that philosophers should use experimentation to investigate natural phenomena.

c. 1450 Nicholas of Cusa suggests that plants grow by absorbing water.

1530 Otto Brunfels's *Herbarum vivae eicones* (living pictures of herbs) offers accurate drawings of plants that encourage the scientific study of them.

1539 Hieronymus Bock (Jerome Boch) groups plants by physical similarity, the first attempt at a strictly natural classification.

1542 The German Leonhard Fuchs makes the first modern attempt to establish a botanical terminology in *Historia stirpium* (the study of vegetation).

1551-1571 Konrad Gesner publishes the widely influential *Opera botanica* (botanical works) and *Historia plantarum* (the study of Plants).

1583 Italian botanist Andrea Cesalpino, in *De plantis libri* (the book of plants), introduces the first comprehensive classification of plants since that of Theophrastus, although it is not

	widely accepted and is centered on the classical master's two major classes, woody plants and herbs.
1620	In *Prodromus theatri botanici* (an introduction to the botanical realm), the German botanist Gaspard Bauhin carefully distinguishes between species and genera of plants and proposes a binomial nomenclature on that basis.
1621	The Oxford Physic Garden opens, the first botanical garden in England.
1626	Jardin des Plantes, a botanical garden, is established in Paris. It becomes a major biological research center.
1648	In *Ortus medicinae* (*Oriatrike: Or, Physick Refined*, 1662), Jan Baptista van Helmont describes experiments which suggest to him that plants derive their substance from water.
1665	Using a microscope, Robert Hooke distinguishes "little boxes," or *cells*, in pieces of cork, a discovery that he describes in *Micrographia*, along with other anatomical and histological features never before seen.
1670	Kaibara Ekiken writes *Yamato honzō* (the flora of Japan).
1676	English scientist Nehemiah Grew proposes an accurate explanation for the nature of ovules and pollen.
1683	Antoni van Leeuwenhoek of Holland discovers bacteria.
1686-1704	John Ray of England releases his three-volume *Historia plantarum* (*A Catalogue of Mr. Ray's English Herbal*, 1713), which contains descriptions of all plants then known and is prefaced by a theoretical introduction that recognizes plants' different sexes and adumbrates the distinction between monocotyledons and dicotyledons.
1694	Rudolph Jakob Camerarius, or Camerer, in *De sexu plantarum epistola* (the sex of plants), explains plant sexuality.
1701	Jethro Tull invents the first agricultural machine, a seed drill.
1716	The American clergyman Cotton Mather records the first unambiguous account of plant hybridization, concerning the red and blue kernels of *Zea mays*.
1727	Vilmorin-Andrieux et Cie, a seed-breeding company, is established, which later in the century develops the sugar beet.
1727	Stephen Hales concludes that part of a plant's nourishment comes from the atmosphere.
1730	England's Kew Royal Botanic Gardens opens. The facility soon becomes a leading center for collection and research.
1752	James Lind argues that fresh fruit prevents scurvy.
1753	In *Species plantarum* (the species of plants) Carolus Linnaeus of Sweden proposes the first truly natural classification of plants. Its binomial nomenclature, indicating genus and species, is based upon species' sexual characteristics and soon becomes the leading system throughout the scientific world.
1754	Charles Bonnet is the first to note plant respiration when he finds that a leaf under water, if exposed to light, emits air bubbles.
1772	Joseph Priestley of England demonstrates that plants discharge oxygen.

1789	Bernard and Antoine-Laurent de Jussieu propose the taxonomic concept of families to supplement the Linnaean system. The latter argues that all species within a family derive from a common prototype.
1794-1796	Erasmus Darwin (grandfather of Charles) publishes *Zoönomia: Or, The Laws of Organic Life*, in which he contends that environmental influences foster changes in species.
1796	Jan Ingenhousz finds that photosynthesis and plant respiration occur simultaneously and that respiration involves carbon dioxide.
1801	French scientist Jean-Baptiste Lamarck proposes that organisms evolve as disused characteristics are lost while characteristics in continuous use are preserved.
1801	Johnny Appleseed (John Chapman) starts on his quest to plant apple trees throughout the Ohio Valley.
1802	Charles François Brisseau de Mirbel deduces that plants are composed of continuous cellular membranous tissue.
1806	Louis-Nicolas Vauquelin and Pierre-Jean Robiquet derive asparagine from asparagus. It is the first amino acid to be isolated.
1810	Scottish botanist Robert Brown draws a distinction between angiosperms and gymnosperms.
1813	Augustin Pyramus de Candolle lays out the principles of comparative morphology in *Théorie élémentaire de la botanique* (elementary botanical theory).
1818	Thomas Nuttall publishes *The Genera of North American Plants*, an important study of New World flora.
1821	Giovanni Battista Amici of Italy explains the exact nature of sexual union in plants. His microscopic studies of pollen in the stigma of portulaca show that the pollen grains grow tubes that penetrate the tissue of the stigma.
1831	Robert Brown identifies a rounded core in most cells that is denser than the surrounding medium. He dubs this core the nucleus.
1837	Henri Dutrochet finds that chlorophyll must be present for photosynthesis to occur.
1838	In Germany botanist Matthias Jakob Schleiden and zoologist Theodor Schwann advance the cell theory, which holds that for all living organisms, plant or animal, the cell is the basic structural unit and that growth is the proliferation of cells.
1839	Hugo von Mohl describes details of mitosis in plants and recognizes that the phenomenon is common in root tips and terminal buds.
1840	Justus von Liebig recognizes that plants produce organic compounds with atmospheric carbon dioxide and nitrogenous compounds with chemicals taken from the soil.
1843	John Lawes and Henry Gilbert open the Rothamsted Experimental Station in England, the first such purely agricultural research center.
1845	Karl Wilhelm von Nägeli demonstrates that cells in a plant organ grow from a progenitor "apical" cell.
1849	Wilhelm Hofmeister of Germany discovers that plant embryos develop in the embryo sac of the ovule.

1855 Alphonse de Candolle introduces the idea of competition between species to explain their geographic distribution in his monograph *Géographie botanique raisonnée*.

1859 In *On the Origin of Species by Means of Natural Selection*, Charles Darwin sets forth a theory of evolution based upon natural selection, citing examples of both plant and animal species. The book's influence on botany is profound and lasting because it accounts for the great diversity of life.

1860 Alfred Russel Wallace, cofounder of the theory of natural selection, describes the biogeography of the Malay Archipelago, adding extensive evidence to Darwin's in support of the theory of evolution.

1861 Anton de Bary founds mycology and modern plant pathology with his explanation of the means by which fungi parasitize plants and animals and his description of the sexual organs of fungi.

1862-1883 English taxonomists George Bentham and Joseph Dalton Hooker publish the seven-volume *Genera plantarum* (genera of plants), which proposes relationships among species that become widely accepted.

1863 French scientist Louis Pasteur invents a process to inactivate wine-souring microbes with heat. The process becomes known as pasteurization.

1866 Gregor Mendel publishes an article detailing his experiments with peas, laying out the laws governing how physical traits pass from one generation to the next. Mendel argues that traits behave as units, which he calls inheritance "factors." His article goes largely unread until biologists rediscover it in 1900.

1866 Ernst Haeckel introduces the word "ecology" to denote the interactions of living organisms among one another and with their physical environment.

1879 During investigation of apple and pear blight, Thomas Jonathan Burrill and Joseph Charles Arthur demonstrate that some plant diseases are caused by bacteria.

1887-1899 German botanist Adolf Engler issues the multi-volume *Die natürlichen Pflanzenfamilien* (the natural plant families), an encyclopedic work of great influence for its survey of the plant kingdom based upon evolutionary principles.

1893 Liberty Hyde Bailey releases the first detailed study of plants grown under artificial lighting and later edits *Cyclopedia of American Horticulture* (1900-1902) and *Cyclopedia of American Agriculture* (1907-1909).

1898 Charles Reid Barnes coins the term "photosynthesis."

1898 Sergey Gavrilovich Navashin notes double fertilization in plants.

1904 In a discovery with revolutionary importance to agriculture, Fritz Haber devises an efficient method for producing artificial nitrogen-bearing fertilizers by combining atmospheric with nitrogen in ammonia. In 1918 he is awarded the Nobel Prize in Chemistry for the achievement.

1905 Frederick Frost Blackman reveals that photosynthesis involves several processes. The rate of each is controlled by several possible parameters.

1905 The "factors" that Gregor Mendel believed responsible for the inheritance of physical traits from one generation to the next are found to be genes.

1905 Rowland Harry Biffen, an English researcher, demonstrates that resistance to rust fungus in one type of wheat can be heritable, beginning the scientific development of disease-resistant crop varieties.

1906 Mikhail Semenovich Tsvet introduces the technique of chromatography, which gets its name from its usefulness in separating plant pigments.

1906 Richard M. Willstätter publishes the first of a series of papers establishing that two types of chlorophyll are involved in photosynthesis and describing methods for extracting plant pigments, such as carotenoids and anthocyanins. In 1915 he receives the Nobel Prize in Chemistry for the work.

1909 Rollins Adams Emerson detects multiple allelomorphism, variations in the forms of genes, in corn and beans.

1910 P. Boysen-Jensen demonstrates that plants are phototropic (move toward light) because of the presence of auxins, hormones that transmit the growth response.

1911 Andrew Ellicott Douglass establishes a method of dating trees and analyzing ancient environmental conditions by examining tree rings. He calls the technique dendrochronology.

1914 George Harrison Shull elucidates heterosis, or hybrid vigor. Inbred strains of plants that have inferior characteristics, when crossed, can produce a new strain with far more yield and general hardiness than either parental line.

1914 George Washington Carver makes public the first fruits of his extensive research into the practical uses of peanuts and other plants.

1915 *The Mechanisms of Mendelian Heredity*, by Thomas Hunt Morgan, Calvin Bridges, and Alfred Sturtevant, confirms the chromosomal theory of Mendelian heredity. For his work in experimental evolutionary biology, Morgan receives the 1933 Nobel Prize in Physiology or Medicine.

1920 Wightman Wells Garner and Harry Ardell Allard discover the phenomenon of photoperiodism in the growth and reproduction of plants.

1922 Otto Warburg devises what becomes the standard tool for measuring metabolism in plants as he monitors the efficiency with which photosynthesis uses light energy. He wins the 1931 Nobel Prize in Physiology or Medicine but the German government does not allow him to accept it.

1923 Thorsten Ludvig Thunberg correctly analyzes photosynthesis as an oxidation-reduction reaction: Carbon dioxide is reduced as water is oxidized.

1924 Ralph Erskine Cleland solves a puzzle involving a peculiar genetic inheritance in *Oenothera lamarckiana*, which produced only heterozygous offspring, by showing that some of its chromosomes form into rings, which are lethal if paired in homozygous offspring.

1925 Roy E. Clausen and Thomas H. Goodspeed provide experimental evidence that species differentiation involves polyploidy, an excess of chromosomes.

1925 Artturi Ilmari Virtanen of Finland develops a method for preserving green fodder by controlling the pH level, for which he is awarded the 1945 Nobel Prize in Chemistry.

1926 Working with jack beans, James Batcheller Sumner becomes the first scientist to isolate enzymes in a pure state and to demonstrate that they are proteins. He receives the 1946 Nobel Prize in Chemistry for his efforts.

1926 Nikolai I. Vavilov publishes *Tsentry proiskhozhdeniia kul'turnykh rastenii* (*Studies on the Origin of Cultivated Plants*, 1926), in which he expounds an influential theory accounting for the genetic variation and geographical distribution of crops since ancient times.

1930 Cornelis Bernardus van Niel points out that the photosynthetic processes of bacteria and green plants are similar.

1930 While investigating mutation rates in maize, Lewis J. Stadler learns that genes mutate at greatly different rates.

1931 Paul Karrer becomes the first person to determine the chemical structure of a vitamin during his studies of carotene and vitamin A.

1931 During studies of *Zea mays*, Barbara McClintock realizes that chromosomes exchange "transposable elements" of deoxyribonucleic acid (DNA) larger than genes. Discovery of this crossover effect wins her the 1983 Nobel Prize in Physiology or Medicine.

1933 Walter Norman Haworth of England defines the chemical structure of vitamin C (extracted from oranges and cabbage), shows it to be a cure for scurvy, and later artificially synthesizes it. For this work he shares the 1937 Nobel Prize in Chemistry with Paul Karrer of Switzerland.

1934 Wendell Meredith Stanley isolates the tobacco mosaic virus, which in contradiction to earlier theories, proves to be a large, complex protein. In 1946 he shares the Nobel Prize in Chemistry for the discovery.

1935 Arthur Tansley propounds his ideas about the natural interplay among the community of organisms and their environment—that is, the ecosystem.

1937 Albert Francis Blakeslee and George S. Avery demonstrate that environmental chemicals can cause alterations in chromosome structure when they use the alkaloid poison colchicine to produce polyploidy in plant cells.

1939 Samuel Ruben, William Hassid, and Marten Kamen are the first plant science experimenters to employ radioactive isotope tracers, which they use to study photosynthesis.

1940 Paul Hermann Müller of Switzerland synthesizes dichloro-diphenyl-trichlorethane (DDT), which first proves a boon to agriculture as a pesticide and then becomes the *cause célèbre* of the popular movement to ban pesticides because of their destructive effect on animals and people. In 1948 Müller wins the Nobel Prize in Physiology or Medicine for his work.

1940 Willard Libby realizes that the radioactive decay of carbon 14 absorbed by living matter provides a means for establishing the age of long-dead organisms. His carbon 14 dating method, developed five years later, earns him the Nobel Prize in Chemistry in 1960.

1941 Samuel Ruben, Martin Kamen, Merle Randall, and James L. Hyde announce that oxygen molecules produced during photosynthesis are the byproduct of the decomposition of water.

1941 While investigating variant strains of pink bread mold (*Neurospora crassa*), George Wells Beadle and Edward L. Tatum show that specific genes are responsible for different enzymes involved in growth processes—called the "one gene, one enzyme" phenomenon.

1951 Examining the adenosine triphosphate (ATP) of plant cells, Alexander Robertus Todd deciphers the chemical structure of the nucleic acids composing deoxyribonucleic acid (DNA). He wins the 1957 Nobel Prize in Chemistry for the achievement.

1953 Englishman Francis Crick and American James Watson define the three-dimensional structure of deoxyribonucleic acid (DNA), which enables botanists to study the coding of genetic information and to analyze inheritance from a biochemical perspective.

1954 Daniel Arnon discovers that cholorplasts can photosynthesize even when removed from cells.

1957 Melvin Calvin publishes "The Path of Carbon in Photosynthesis," in which he describes the second of the two major cycles of photosynthesis, during which atmospheric carbon dioxide is fixed and reduced into carbohydrates in plant tissue. Named the Calvin cycle in his honor, the discovery brings him the 1961 Nobel Prize in Chemistry.

1957 Tree-ring analysis shows the bristlecone pine (*Pinus aristata*), which grow in California's White Mountains, to be the longest-lived tree species. Some specimens are more than four thousand years old.

1959 Sterling Hendricks isolates phytochrome, a key enzyme in flowering.

1960 Robert Burns Woodward synthesizes the green plant pigment chlorophyll. For this and synthesis of other valuable compounds, including quinine, Woodward is awarded the Nobel Prize in Chemistry in 1965.

1961 Peter D. Mitchell outlines his chemiosmotic hypothesis, which describes how cells derive energy by oxidizing organic molecules in order to synthesize adenosine triphosphate (ATP). For his work, Mitchell receives the 1978 Nobel Prize in Chemistry.

1962 Rachel Carson publishes *Silent Spring*, a scientific indictment of the environmental hazards posed by commercial pesticides. The book inspires the modern environmental movement.

1967 A. E. Porsild succeeds in germinating ten-thousand-year-old Arctic lupine seeds found in Yukon territory. The mature plants turn out to be identical with the modern species.

1970 Norman Borlaug wins the Nobel Peace Prize for his work in developing high-yield strains of rice and wheat.

1983 Scientists develop the first transgenic plant. It is a species of tobacco resistant to antibiotics.

1984 Johann Deisenhofer of Germany publishes a paper describing the complete structure of the photosynthetic reaction center of a bacterium, which he analyzed by X-ray crystallography. This work earns him the 1988 Nobel Prize in Chemistry.

1994 Flavr Savr tomato, produced by the American biotechnology firm Calgene Corporation, is the first genetically engineered food to reach the marketplace.

1996 In its first report on biodiversity, the United Nations claims that 26,100 plants face extinction and that the overall extinction rate is fifty to one hundred times higher because of human impact on the environment.

1998 Soil fungi that are symbiotic with plant roots are shown to be important to diversity and productivity in plant communities.

1999 Laboratory tests suggest that the pollen of corn bioengineered to release the pesticide *Bacillus thuringiensis* (*B.t.*) endangers monarch butterfly caterpillars. Although later evidence calls the finding into question, it prompts controversy over the safety of transgenic plants.

2000	More than two-thirds of the processed foods in U.S. markets contain genetically modified ingredients, primarily soybeans or corn.
2000	The environment organization Friends of the Earth reveals that StarLink, a genetically engineered corn variety meant only for animal fodder, has contaminated the human food supply, setting off a public backlash to genetic engineering of food plants.
Jan. 28, 2000	At a meeting in Montreal, Canada, the United Nations Convention on Biological Diversity approves the Cartegena Protocol on Biosafety, which sets the criterion internationally for patenting genetically modified organisms, including agricultural products.
Dec. 13, 2000	At a press conference, a team of more than three hundred scientists from throughout the world announce that they have sequenced the genome of a plant for the first time. The plant is the model organism *Arabidopsis thaliana*.
Nov. 2001	Scientists report that genetic material from transgenic corn mysteriously has turned up in the genome of native corn species near Oaxaca, Mexico. Mexico banned transgenic crops three years earlier, and the closest known crop was located beyond the range of wind-borne pollen.

Roger Smith

GLOSSARY

abscisic acid (ABA): A hormone associated with regulation of growth and rapid closure of stomata, produced in root caps and mature leaves.

abscission: Separation of leaves and fruits from stems that occurs when a layer of cells cuts off water supply to the leaf or fruit. Abscission occurs in the autumn in moist, temperate climates and during drought in deserts, causing leaves and fruits to drop.

abscission zone: Region in a leaf petiole or the stalk of a fruit where the abscission layer forms.

absorption spectrum: That portion of the sun's wavelengths that a plant is able to use in photosynthesis.

acaulescent: Lacking an aerial stem.

accessory fruit: Fruits develop from the matured ovary of a flower. An accessory fruit includes the matured ovary and other parts of the flower as well, such as the receptacle in apples.

accessory pigment: These pigments, including carotenes and xanthophylls, absorb light energy and pass it to chlorophyll during photosynthesis.

acetyl coenzyme A: Two-carbon compound formed during the breakdown of glucose in cell respiration. It combines with an existing four-carbon compound to begin the Krebs cycle.

achene: Type of single-seeded fruit which is dry at maturity. The outer layer is formed by the fusion of the seed coat and the fruit wall, as in wheat grain or sunflower seeds.

acropetal: Pattern in which development occurs from the base upward. The development of veins into leaves as they form is acropetal.

actin filaments: Component of a cell's cytoskeleton that gives a cell shape and allows communication between the cell membrane and the nucleus.

actinomorphic flower: Flower that is radially symmetrical when viewed from above. Examples include roses, tulips, and daffodils.

action spectrum: Measure of the ability of a type of pigment to use a particular wavelength of light in photosynthesis.

active site: That specialized region of an enzyme into which the substrate fits as tightly as a key in a lock. Alteration of the active site prevents the enzyme from being functional.

active transport: Movement of substances into or out of a cell across the cell membrane from a region of low concentration of the substance to a region of high concentration. Expenditure of cellular energy is required for this to happen.

acuminate: Leaf that ends in a long, tapered point.

adaptation: Alteration in a plant's anatomy or physiology that improves its ability to survive in a particular environment. Adaptations are the result of permanent genetic change.

adaptive radiation: Evolution of multiple related species from one ancestral species. The different species which evolve can live in proximity to one another because they occupy different niches.

adenosine triphosphate (ATP): Chemical which is the "energy currency" of cells. This molecule can provide energy for all sorts of cellular processes and is regenerated during cellular respiration and photosynthesis. Energy is stored in an easily broken covalent bond that attaches a phosphate ion to the molecule adenosine diphosphate (ADP).

adventitious root: Root that develops from some plant organ other than another root, such as a stem or leaf. For example, adventitious roots form on stem cuttings of philodendron placed in water and from the stems of corn plants, where they are known as prop roots.

adventitious shoot: Shoot that develops from some plant organ other than another shoot, such as a root or leaf. African violet leaf stalks, when placed in water, develop both adventitious shoots and adventitious roots.

aeciospores: In the complex life cycle of rust fungi, these spores infect another host plant. In the disease black stem rust of wheat, aeciospores are produced on the alternate host, American barberry, and when released infect young wheat plants.

aecium: The usually flat and colored lesion on a host plant in which aeciospores are produced.

aerial root: Root which grows exposed to the air rather than growing in soil or water. Plants with aerial roots are normally limited to moist environments, such as tropical rain forests, where many kinds of orchids, bromeliads, and ferns grow, with their roots exposed, on tree trunks and limbs.

aerobes: Organisms that require oxygen in order to produce adequate amounts of energy during cellular respiration.

aerobic: Describes organisms which need oxygen for the maximum release of energy from their food. *See also* anaerobes.

aethalium: Structure formed from the fusion of several sporangia, found in some slime molds.

after-ripening: Period of time following the ripening of seeds, during which physiological changes must occur before the seed is able to germinate.

aggregate fruit: Fruit formed from a flower that has more than one pistil; each pistil develops into a tiny fruit. Raspberries are examples of aggregate fruits.

agricultural revolution: Marked the transition by humans from hunting and gathering all their food to domesticating plants for food.

akinetes: Specialized, thick-walled resting spores that form in the filaments of cyanobacteria. These permit survival during periods of cold or drought.

albuminous cell: Specialized companion cells found in the phloem of gymnosperms.

alcohol fermentation: Cellular process in plants, yeasts, and bacteria whereby sugars are converted to alcohol and carbon dioxide in an environment low in oxygen.

aleurone: The outermost layer of tissue under the seed coat of a monocot seed, such as that of corn or barley.

algin: Carbohydrate produced by certain types of brown algae, used to prevent crystal formation in foods, such as ice cream and jelly beans.

alkaloids: Nitrogen-containing chemicals produced by some plants which are used as hallucinogens or medicines. Examples include nicotine, caffeine, morphine, and cocaine. Plants produce these as protection against being eaten by herbivores.

allele: Different forms of a particular gene. Any individual possesses two alleles for every gene pair in its cells. These alleles may be the same or may be different.

allelopathy: Observed phenomenon in which plants produce and release chemicals into the air or soil that inhibit the growth of other plants, either of the same or different species.

allopatric speciation: Evolution of two new species when the two evolving groups are separated from each other.

allopolyploidy: Formation of a new species resulting from the mating of two different species. Normally such a mating produces a sterile interspecific hybrid. If the total number of chromosomes is accidentally doubled, then the resulting plant is fertile but reproductively isolated from the two parent species.

allosteric enzymes: Enzymes that change shape to expose the active site. Many inactive enzymes exist in one shape; the binding of ATP alters the shape of these enzymes into their active forms.

alternate: Arrangement of leaves on a stem in which only one leaf is found at each node.

alternation of generations: Plant sexual reproductive cycle in which a diploid generation that produces spores by meiotic division (sporophyte phase) follows a haploid generation (gametophyte phase) that produces gametes.

amino acids: Simple nitrogen-containing molecules which are the building blocks of proteins. Plants are able to produce all the essential amino acids from carbohydrates formed as a result of photosynthesis.

ammonification: The breakdown of protein during decomposition, producing ammonium ions which are then available for reuse.

anabolism: That part of all the metabolic reactions in a cell which results in the building of larger molecules from smaller ones. Construction of proteins from amino acids is one example of an anabolic process.

anaerobes: Organisms, including many bacteria, which live where oxygen is in short supply and do not use the oxygen-requiring pathways of cell respiration.

anaerobic pathways: Series of metabolic reactions that break down complex food molecules for energy release without the involvement of oxygen gas. Typically, these pathways are not efficient ways to release energy, and organisms that depend solely on anaerobic pathways do not become very large.

analogy: Similarity in function among parts of plants.

anaphase: Stage in cell division during which time the sister chromatids separate and become two identical groups of chromosomes. In the specialized anaphase I of meiosis, homologous chromosomes separate to reduce the chromosome number for sexual reproduction.

androecium: Whorl of stamens of a flower. Literally means "house of males."

aneuploidy: Literally, "not true sets." Condition in which a cell or individual is missing one or more chromosomes or has one or more extra chromosomes. Does not include the condition in which all chromosomes are present in extra numbers.

angiosperm: A flowering plant. Angiosperms have flowers as their reproductive organs and produce their seeds inside fruits that develop from the ovary of the flower.

annual: Flowering plant which comes up from seeds every year after the parent plant dies in the autumn.

annual ring: In woody plants, the xylem that is added during a growing season by activity of the cambium. Annual rings are visible because the xylem added in the spring has larger diameter vessels than the xylem which grows in the summer. Addition of annual rings causes a tree to increase in circumference.

annulus: Ring of weak cells that rupture during the life cycle of a plant. The annulus in a fern sporangium breaks to allow the release of fern spores.

antenna complex: Photosynthetic light-gathering apparatus of chloroplasts. A number of pigment molecules are arranged in a complex which allows them to collect light energy and direct it to one central chlorophyll molecule.

anther: Part of the stamen of a flower. In many flowers the anther appears as a swollen area at the free end of a stalk (filament). Pollen is produced inside the anther.

antheridium (*pl.* antheridia): Male reproductive structure that produces sperm in algae, mosses, and lower vascular plants.

anthocyanin: Red or purple pigment produced in some flowers, fruit, and leaves. It collects in the central vacuole of plant cells and can be easily seen under a microscope in the epidermis of red onions.

anticodon: Series of three nucleotides in the structure of a transfer RNA that enable the RNA to position an amino acid in the correct location within a protein. The anticodon is complementary to a codon contained in messenger RNA.

antipodals: Three of the eight cells of an angiosperm embryo sac. These cells are furthest from the end of the sac at which the egg can be found. They usually degenerate following fertilization of the egg.

apical bud: Structure at the tip of a stem in which an apical meristem is enclosed in a protective layer of scales.

apical dominance: Production of hormones by the terminal (apical) bud on a branch that keep the lower lateral buds from growing into side shoots. Apical dominance leads to slender, unbranched stems.

apical meristem: Growing point within an apical bud where the cell division occurs that leads to the elongation of stems and formation of leaves.

appressed: Closely pressed against another object; a lateral bud that grows close to a stem is appressed.

apomixis: Reproduction that occurs without fertilization.

apoplast: In a stem or root cortex, that region which is outside the cell membranes. It includes the space occupied by the cell wall and any open spaces between cells.

apoplastic loading: Movement of substances into phloem tissue from the apoplast.

apoplastic pathway: Route taken by substances as they move through the apoplast.

apoptosis: Programmed cell death, sometimes called cell suicide, often caused by stresses within the cell. Cells dying in this manner undergo a predictable series of events that leave neighboring cells in a healthy condition. Apoptosis often occurs during development to sculpt the shape of leaves and flowers.

arbuscule: A branched organ which is tree-shaped in appearance.

archegonium (*pl.* archegonia): Female reproductive structure in which the egg is produced. Found in algae, mosses, lower vascular plants, and gymnosperms. Archegonia have a jacket of sterile cells surrounding the egg.

Arctic tundra: Treeless biome of very cold climates near to and north of the Arctic Circle, in which the predominant plants are low-growing, perennial woody plants and grasses. Lichens and mosses may also be common.

aril: Fleshy outer layer of the seed coat. These "yew berries" look superficially like fruits but do not develop from a floral ovary.

artificial selection: Choices made by plant breeders to produce varieties of plants that have some desirable quality, such as improved yield, greater height, or an unusual flower color.

artificial taxon: A grouping of plants based on something other than evolutionary relationships. Grouping sunflowers, daffodils, and yellow roses because they are all yellow would be an example of an artificial taxon.

ascogonium: Female reproductive structure in an ascomycete fungus.

ascospores: Eight spores produced by meiosis during the reproduction of ascomycete fungi. The spores are enclosed in a tiny sac and are often arranged side by side in a linear fashion.

ascus (*pl.* asci): Small sac common to the reproduction of ascomycete fungi. The ascospores develop within the ascus.

assimilate stream: Movement of a substance along a pathway from where it is manufactured to a location where is it is being used. For example, sucrose is manufactured in leaves and moves via an assimilate stream to a developing fruit.

ATP. *See* adenosine triphosphate.

ATP synthase: Enzyme, found in membranes, necessary for the formation of ATP.

ATPases: Enzymes that remove the terminal phosphate from a molecule of ATP and usually transfer that phosphate to some other molecule in the process of phosphorylation.

autoecious: Fungi that spend their entire life cycle as parasites on a single host.

autopolyploidy: Formation of a new species by the doubling of chromosomes of a single existing species. Many related species of plants within a genus have been found to result from repeated occurrences of autopolyploidy.

autotroph: Organism that can make its own food from simple substances. Green plants and algae that make carbohydrates from carbon dioxide and water are the best-known autotrophs, although autotrophic bacteria exist which build food molecules from other simple molecules.

auxin: Plant hormone that regulates growth by causing cell elongation.

awn: A slender, usually terminal, bristle. The flowers of many kinds of grasses have awns.

axial system: Combination of the cells, other than the cells of rays, in secondary xylem and phloem and the initials in the vascular cambium that produce those cells.

axil: Acute angle formed between a stem and a leaf on that stem. In woody plants, a lateral axillary bud will be located at the axil.

axillary bud: Bud located at the base of a leaf, where the leaf petiole joins the stem. This bud contains a meristem that may in time grow into a new branch.

axillary bud primordium: Very young developing axillary bud found in an apical meristem.

bacillli (*sing.* bacillus): Rod-shaped bacteria.

bacterial chromosome: Single circular piece of DNA that contains the hereditary information for a bacterium. This chromosome must replicate prior to bacterial cell division.

bacteriophage: Virus that infects bacteria. The virus uses the bacterial cell machinery to produce and assemble more viral particles. The bacterial cell then ruptures, spilling the new particles, which can then infect neighboring bacteria.

bark: Layers of cork cells and phloem covering the outside of a woody plant. The cork cells are dead at maturity. They reduce evaporation from stems and roots and help protect the living tissue underneath from physical damage.

basidiospores: Either four or eight spores produced by meiosis in *Basidiomycete* fungi. The spores are borne on the outside of a basidium.

basidium (*pl.* basidia): A club-shaped reproductive structure common to *Basidiomycete* fungi on which the spores are produced. Basidia form layers on the surface of the gills of mushrooms.

basipetal: Pattern of development in which maturation occurs from the tip downward.

bearded: Having long or stiff hairs. An example are the bearded petals of many irises.

berries: Fleshy fruit in which the seeds do not have a hard or stony seed coat. Tomatoes, cucumbers, and blueberries are examples.

betacyanins: Red pigments of beets and certain kinds of flowers; similar to anthocyanins, except betacyanins contain nitrogen and do not change color with changes in acidity or alkalinity.

biennial: Flowering plant that requires two years to flower and set seed. A typical biennial plant forms a rosette of leaves during its first growing season. It lies dormant over the winter, then makes a flower stalk during its second growing season. Carrots are biennial plants.

binary fission: Reproduction of one-celled organisms in which the original cell divides into two cells of approximately the same size and shape.

binomial system of nomenclature: Accepted method for naming new plants in which every plant receives two Latin names, a genus name (listed first) and a species name. Sugar maple trees are named *Acer saccharum* under this system. Species of the same genus are considered to be more closely related than species in different genera.

biogeochemical cycles: Movement of elements or water through both living and nonliving parts of an ecosystem. Carbon as carbon dioxide is made into carbohydrate during photosynthesis and released through decay to the nonliving atmosphere, from which it can later be reused in photosynthesis.

biological clock: Internal mechanism by which plants are given a cue to perform activities at a particular time.

biomass: Total amount of living plants and animals found in a particular location at a particular time.

biome: Large-scale type of ecosystem that is characterized by the appearance of its vegetation, which is similar throughout, and in which live similar animals. The grassland biome and the deciduous forest biome are two examples found in North America.

biosphere: That part of the world where living organisms are found.

biotechnology: Combination of techniques whereby humans are able to alter permanently the genetic makeup of organisms. Includes the industrial application of these techniques.

bivalent: Homologous chromosomes that have paired up during the early part of meiosis; also called a tetrad.

blade: Expanded, usually flat portion of a leaf.

bolting: Process in which a stalk bearing flowers rapidly grows from a plant that had consisted of a rosette of leaves attached to its stem.

bottleneck effect: In evolution, the reduction in size of a population causing a major loss of genetic variation. If the population size later expands, the new larger population will be genetically uniform and may lack the ability to survive in a changing climate.

bract: Modified leaf associated with a flower or an inflorescence. The red-colored structures of poinsettias and the white-colored structures of dogwood are examples of bracts.

branch roots: Roots which develop from the inner part of a root and which grow outward to lateral roots.

branch trace: Strand of xylem and phloem which diverges from the conducting tissue of the main stem and enters a branch.

bud primordium: *See* axillary bud primordium.

bud scales: Highly modified leaves that cover the apical meristem of terminal and axillary buds. These are especially important as protection in the winter.

bulb: Modified stem that grows underground. The leaves of the stem are fleshy because they contain stored food that will be used by the plant when it begins its next period of growth. Onions are an example.

bulk flow: Movement of a liquid, for example sap in phloem, in which all molecules move in the same direction under the influence of a driving force, such as gravity or difference in water potential.

bulliform cells: Special cells found near the base of leaves of grasses. These cells are large, and when water flows out of them the leaf curls, thereby reducing surface area for evaporation.

bundle scar: Located within a leaf scar, these scars mark the locations of veins.

bundle sheath cell: One of the cells that make up a bundle sheath.

bundle sheath extension: In some leaves a riblike portion of a bundle sheath that extends outward toward the surface of a leaf, giving added support and strength.

bundle sheaths: Cylinders of cells that surround the veins of leaves and vascular bundles of stems. The cells may be fiberlike and provide support or may be filled with chloroplasts and help in the process of photosynthesis as in the case of C_4 plants.

buttress root: Winglike thickening which develops on the trunk of a tree at the base of a root. Most common among trees that grow in wet, and thus soft, soils.

C_3 plants: Plants whose system of photosynthesis produces a three-carbon compound as the first identified compound after the uptake of carbon dioxide during the light-independent reactions.

C_4 plants: Plants whose system of photosynthesis produces a four-carbon compound as the first identified compound after the uptake of carbon dioxide during the light-independent reactions. C_4 photosynthesis is distinguished from CAM photosynthesis (see below) because C_4 occurs during the day and CAM occurs during the night. C_4 plants are especially adapted to hot, dry climates. Corn is an example.

callose: Type of carbohydrate that lines the pores of the sieve plates of sieve tube elements in phloem.

callus: Group of undifferentiated plant cells. In tissue culture, a callus is first grown from pith or other parenchyma, and then it is treated to induce the formation of roots and stems.

Calvin cycle (three-carbon pathway): Complex set of biochemical reactions of photosynthesis whereby the sugar glucose is synthesized from carbon dioxide and existing precursor sugars. Also known as the Calvin-Benson cycle.

calyptra: Fibrous or leaflike cap cover over the top of a sporangium of a moss plant. The calyptra grows up from the gametophyte and thus is haploid, unlike the sporangium, whose walls are diploid.

calyx: Outermost and lowest whorl of a flower, composed of the sepals.

CAM plants: Crassulacean acid metabolism plants of the desert, which are able to take in carbon dioxide during the night and store it as an acid, and then use the carbon dioxide in the light independent reactions during the day, when sunlight is available. Cacti are CAM plants.

cambial zone: That region of a stem or root in which is found the cambium.

cambium: One-cell-thick cylinder of cells that separates xylem and phloem in stems and roots and which divides to form new xylem and phloem, thereby leading to growth in diameter.

canopy: Uppermost portion of a forest in which are found the leafy branches of the trees.

capillary water: Water which is held in surface films and in small spaces of the soil against the pull of gravity.

capsid: Protein coat that encloses the DNA or RNA of a virus and enables it to attach to a host cell.

capsule: Sporangium of bryophytes; also a type of dry fruit that splits open upon maturity.

carbohydrates: Large class of organic molecules containing carbon, hydrogen, and oxygen and in which the ratio of hydrogen to oxygen is two to one, the same as in a molecule of water. Sugars, starch, and cellulose are examples.

carbon cycle: Biogeochemical cycle of the element carbon.

carbon fixation (CO_2): Process by which carbon dioxide is made into glucose during photosynthesis. This occurs during the part of photosynthesis called the Calvin cycle.

carnivorous plant: Plant that traps insects and digests them. These plants usually live in nitrogen-poor habitats and use the insect proteins to supplement their nitrogen intake.

carotene: Orange or orange-red pigments of plants. One of the groups of the carotenoids.

carotenoid: Group of pigments in green plants which can absorb light and pass the energy to chlorophyll. These yellow and orange pigments enable a plant to tap into wavelengths of light.

carpel: This structure is the basic component of the pistil in a flower. A pistil may be formed from one or more carpels, which are highly modified leaves.

carposporophyte: One of the three stages in the complex life cycle of a red alga.

carrier proteins: Proteins, often membrane-bound, that are responsible for the transport of materials across a cell membrane. Cellular energy is necessary for these proteins to function.

caryopsis: Dry, indehiscent fruit that contains only one seed and in which the seed coat is fused to the dry fruit wall. Typical of the grasses.

Casparian strip: Waterproof strip encircling cells of endodermis. Necessary for control of substances entering a plant root.

catabolism: Set of metabolic reactions that result in complex molecules being degraded to simpler ones. *See also* anabolism.

catalyst: Molecule or ion that lowers the energy required for a reaction to occur. In plant cells, most catalysts are enzymes.

cation exchange: Displacement of one type of positive ion (cation) from the surface of a soil particle because it has been replaced by a different cation, often a hydrogen ion.

catkin: Soft, furry, and flexible inflorescence in which many small flowers are attached on one stalk. Birch trees and willow trees are two examples of plants that produce flowers in catkins.

caulescent: Possessing an aboveground stem.

cell cycle: The series of events through which a cell progresses, from the time it is formed by cell division until it has completed mitosis and formed two new cells.

cell plate: First cellular structure which forms following mitosis. The cell plate partitions the cytoplasm for the new cells. It becomes incorporated in the cell walls of the new cells.

cell sap: Cytoplasm that fills in the spaces between adjacent cell organelles.

cell wall: Rigid, nonliving structure, often made of cellulose and a matrix, that surrounds the membrane and contents of plant cells.

cells: Basic building blocks of living organisms. In multicellular plants, many different kinds of cells exist, which have different appearances and different functions.

cellular respiration: Breakdown of glucose and other small molecules within cells to release energy. Some of the energy released in this way is trapped in ATP.

cellulose: Polymer of glucose that is not easily dissolved in water. Cotton, linen, and paper have very high cellulose content.

cellulose synthase: Enzyme responsible for the construction of cellulose from smaller molecules.

central cell: In an archegonium, the precursor of the egg.

centric: Refers to the location of the centromere on a chromosome with respect to the rest of the chromosome. Usually combined with a prefix, as metacentric. Also one of the two categories of diatoms; these are circular when viewed from above.

centromere: Gene-poor region on a chromosome where the kinetochore forms to attach chromosomes to the spindle during cell division.

chalazal: The end of an embryo sac away from the micropyle.

channel proteins: Membrane-bound proteins that form pores or channels through which ions or small molecules can pass into or out of cells.

chaparral: Biome found along the coast of Southern California, characterized by short trees with leathery leaves, shrubs, and open grassy areas.

chelation: Process by which metal ions are taken out of solution by a molecule known as a chelating agent.

chemiosmotic coupling: The process in which energy released from serial oxidation-reduction reactions during photosynthesis or cell respiration is captured in the bonds of an ATP molecule.

chemosynthetic autotroph: Organisms (usually bacteria) that make complex food molecules from simpler molecules using energy of chemical reactions rather than light energy used by photosynthetic autotrophs.

chiasmata: X-shaped figures observed in chromosomes during the first meiotic division. Chromatids of homologous chromosomes lie across each other and may swap pieces. Formation of chiasmata is necessary for the proper separation of homologous chromosomes.

chlorophyll: Green pigment found in plants and algae that captures light energy during the process of photosynthesis. Chlorophyll is similar in structure to animal hemoglobin, with magnesium replacing iron.

chloroplasts: Complex cell organelles found in the green parts of green plants and algae, where chlorophyll is located and where the photosynthetic reactions occur.

chlorosis: Bleaching of green plants when they have been deprived of light or adequate mineral nutrition.

chromatin: Combination of DNA and protein that composes a chromosome.

chromoplasts: Organelles of plant cells that contain pigments other than chlorophyll. Chromoplasts that develop in the skin and flesh of tomatoes make them red.

chromosome: Molecule of DNA wrapped around supporting proteins. Segments of the DNA are the genes on the chromosome.

chromosome mutations: Changes in chromosome number or structure from what is normal for the species. Plants can tolerate the addition of extra chromosomes or sets of chromosomes better than can animals.

chrysolaminarin: Polysaccharide found in the chloroplasts of yellow-green algae.

circadian rhythms: Observable cycles in a plant's physiology that take about twenty-four hours to complete.

clade: Group of organisms considered to be related because they all have one or more characteristics in common.

cladistics: System of describing evolutionary relationships in which only two groups, or clades, branch from each ancestral group. The more recently two clades diverged, the more characteristics they have in common and the closer they will appear in a cladistic diagram.

cladogram: Pictorial representation of the evolutionary relationship of different groups of organisms.

cladophyll: Leaflike segment of a stem in a cactus.

clay: Type of soil particle that is less than 0.002 millimeters in diameter and stays in suspension when mixed in water. Clay particles have negatively charged surfaces, which attract positively charged ions to them. Clay soils are fertile but do not drain well.

cleistogamy: The production of flowers that never open completely and are therefore required to be self-pollinated.

climacteric: During fruit ripening, the point at which the fruit is carrying on maximum respiration.

climax community: Group of plants that appear late in succession and are not replaced by plants of different species unless the climate changes or the area is disturbed, as by fire or cultivation.

cline: A graduated series of plants of the same species. Each plant or group of plants in the series has a slightly different physiology from the ones on each side. Clines typically develop where environmental factors change in a gradual way, such as from the bottom of a mountain to the top.

clonal propagation: Asexual reproduction, as by stem or leaf cuttings. Because no gametes are involved, the products of this reproduction are genetically identical to one another and to the plant that produced them.

clone: A group of genetically identical plants derived from a single cell or individual, or one of the members of the group.

coated pits: Depressions in a cell membrane in which receptor molecules gather.

cocci (*sing.* coccus): Sphere-shaped bacteria.

codon: Three-nucleotide sequence in nucleic acid that specifies a particular amino acid in a protein.

coenocytic: Having multiple nuclei in a single cell.

coenzyme: Small molecule or ion that completes the structure of an enzyme. Many vitamins act as coenzymes.

coenzyme A: A sulfur-protein important in the breakdown of glucose and the release of energy.

coevolution: Simultaneous change through time of two species, such as a flower and its pollinating insect. Over a period of time, the two species become dependent on each other, so that one will not survive the disappearance of the other.

cofactor: A small inorganic molecule or ion necessary to complete the structure of an enzyme.

cohesion-tension (or cohesion-adhesion) theory: Explanation for the movement of water to the tops of tall trees. Interactions among water molecules cause them to stick together (cohesiveness). In the small tubes that form the xylem tissue of plants, the evaporation of water from the leaf ends of the tubes creates a pull (tension) that moves water up the xylem.

cold hardening: Physiological changes that prepare a plant to survive in winter temperatures. Loss of some water is one of the changes that occurs.

cold hardiness: Ability of a plant to withstand cold temperatures. Like other adaptations, cold hardiness is based on genetic variation.

collenchyma: Plant tissue with primary cell walls in which the corners of the cell walls are thicker than the rest of the wall. The "strings" found in celery are an example of collenchyma.

columella: Strand of sterile tissue located in the center of the sporangium of mosses and some fungi.

communities: Groups of plants and animals that live together in a particular set of environmental conditions.

companion cell: Nucleated nonconducting cell that is part of phloem tissue. The conducting cells (sieve tube elements) lack a nucleus when they are mature, and the companion cell directs their activities as well as function in loading of sugars into sieve tube elements for transport out of leaves.

competition: Condition created when two different organisms in a community vie for the same resource.

complementary DNA (cDNA): DNA produced from an RNA template by the action of RNA-dependent DNA polymerase, also known as reverse transcriptase.

complete flower: A flower that has sepals, petals, stamens, and pistil.

composite head: Inflorescence composed of many small flowers arranged to give the appearance of a single large flower. A daisy, member of the *Compositae* family, is an example.

compound leaf: Leaf in which the blade is composed of several small leaflets. Hickory, ash, and horse chestnut trees all have compound leaves.

concentration gradient: Gradual change through space of the concentration of a dissolved substance. The amount of the substance will be greatest at one end of the gradient and lowest at the other end.

conidia: Asexual reproductive spores produced by ascomycete fungi, such as powdery mildew.

conidiophore: Slender stalk of a hypha that produces conidia.

conifer: Woody plants with needlelike leaves. They form seeds in cones rather than in fruits, and their sperm do not have flagella.

coniferous forest: Large group of trees that are predominantly conifers. A pine forest and a spruce-fir forest are examples.

conjugation: Type of sexual reproduction that occurs in green algae such as *Spirogyra* and in certain kinds of fungi. Also, the transfer of genetic material from one bacterium to another through a cytoplasmic bridge.

contractile root: Root which contracts during development; that contraction causes the shoot to be shifted in position. Many bulb-forming plants have these.

contractile vacuole: Osmoregulatory structure in one-celled plants that collects excess water from the cell and squeezes it to the outside.

convergent evolution: Typified by two or more groups of organisms that appear superficially to be closely related. Closer inspection shows that they have both adapted to a particular set of environmental conditions but are only distantly related. Cacti and other succulents are an example.

coralline algae: Species of marine red algae that secrete calcium carbonate on their cell walls.

cordate: Heart-shaped leaves, such as the leaves of philodendron.

cork: Cells that are dead at maturity. They have suberin (a waterproofing substance) in their cell walls and cover the outside of a woody plant in many layers. Layers of cork form the outer bark.

cork cambium: Living cells directly below the layers of cork that undergo cell division to form new cork cells as the plant increases in diameter.

corm: Fleshy, underground stem of a perennial plant that stores food for the winter and can divide via asexual reproduction. A gladiolus corm is an example.

cormel: One of the subdivisions of a corm.

corolla: All the petals of a flower.

corona: Cup-shaped structure that sits on the petals of a daffodil flower.

cortex: Thin-walled parenchyma cells found under the epidermis of stems and roots. The cortex surrounds the vascular tissue.

corymb: Flat-topped inflorescence in which the outer flowers open first.

cotransport systems: Movement of negatively charged ions across a cell membrane, with simultaneous movement of protons in the opposite direction.

cotyledon: Component of a seed. In eudicot seeds, the cotyledons are the two fleshy halves of a seed, such as a peanut; they store food for the seed's germination. In monocot seeds, the single cotyledon digests the food stored in the seed.

coupled reactions: Two reactions in which the occurrence of one is dependent on the occurrence of the other.

crassulacean acid metabolism: *See* CAM plants.

crista (*pl.* cristae): Fold(s) in the inner membrane of a mitochondrion resulting in increased surface area for cell respiration.

critical photoperiod: Specific day length necessary to produce flowers in long-day and short-day plants.

cross-pollination: Transfer of pollen from one flower of a species to a different flower of the same species.

crossing over: Exchange of genetic information between chromatids of homologous chromosomes. This occurs during early meiosis, when the chiasmata form.

crown: The branched, leafy part of a tree.

cultivar: Plant variety that has been bred for particular characteristics, such as variegated leaves or a particular flower color.

cuspidate: Possessing a stiff, sharp point.

cuticle: Waxy coat covering the outside of epidermal cells of leaves, stems, and fruit. The cuticle prevents excessive evaporation from these surfaces.

cutin: Waxlike substance that is the principal component of the cuticle; waxes are embedded in the cutin.

cyanobacteria: Photosynthetic prokaryotes that were once called blue-green algae.

cyclic photophosphorylation: Photosynthetic pathway in which the electrons from a chlorophyll molecule excited by light energy are raised to a higher energy level and then fall back to the same chlorophyll molecule, releasing the energy. The released energy is used to make a molecule of ATP.

cyme: Flat-topped inflorescence in which the central flowers open first.

cypsela: Type of dry, indehiscent fruit in which the seed coat is separate from the dry fruit wall. A sunflower seed is an example.

cytochromes: Electron acceptor molecules capable of repeated oxidation and reduction. Energy from electrons is released in small, controlled bursts as the electrons are passed from one cytochrome to another.

cytokinesis: Division of the cytoplasm following mitotic division of the nucleus.

cytokinin: Growth-promoting hormone that stimulates cell division.

cytology: The study of cells.

cytoplasm: General term for the contents of a cell inside of the cell membrane and outside of the nucleus.

cytoplasmic membrane: Lipid-protein membrane that surrounds the cytoplasm and selectively controls what substances enter and leave the cell.

cytoplasmic streaming: Continuous flow of cytoplasm and its organelles near the outer edges of a cell, probably under the control of microfilaments. Materials are distributed through the cell faster than would occur by diffusion alone.

cytoskeleton: Collective name for the filaments and microtubules that can be found throughout the cytoplasm. The cytoskeleton helps the cell maintain shape and is involved in signaling from the cell membrane to the nucleus.

cytosol: Liquid part of cytoplasm in which the organelles are located.

damping-off: Fungal disease of seedlings and young plants. The stem appears to pinch in and die at a point just above the soil level.

daughter chromosome: One of the two chromosomes which form in anaphase of mitosis when two chromatids separate.

day-neutral plant: Plant whose flowering does not depend on a particular day length.

deciduous: Describes plants that lose their leaves in response to adverse environmental conditions, such as cold or drought. Maple trees and crown-of-thorns are examples.

deciduous tropical forest: Forests of tropical regions that shed their leaves during annual dry periods.

decomposers: Bacteria and fungi that break down dead organic matter. In the process, they obtain energy and facilitate the recycling of elements.

defoliant: Chemical that kills the leaves of trees.

dehiscent fruit: Fruit that splits open to release the seeds when they are ripe. A milkweed pod is an example.

dehydration synthesis: Common type of reaction resulting in the buildup of larger molecules from smaller ones. A bond is created between the two smaller molecules by the removal of a water molecule. This is also called a condensation reaction.

deletions: Loss of pieces of a chromosome. Deletions may encompass large sections of a chromosome or just a few genes.

denitrification: Process in which bacteria convert nitrogenous compounds in the soil to nitrogen gas.

dentate: Describes margin of a leaf that has coarse, sharp-pointed "teeth."

deoxyribonucleic acid: *See* DNA.

desert: Biome that receives less than 10 inches of precipitation per year.

desmotubule: Tube made of membrane that runs through the center of a plasmodesma. The tube is believed to be an extension of the endoplasmic reticulum and connects the membrane systems of two adjacent cells.

determinate: Plant that exhibits determinate growth. Determinate plants are short and bushy.

determinate growth: Growth pattern in which the terminal bud does not grow indefinitely, allowing extensive growth of lateral buds.

deuteromycetes: Fungi in which sexual reproduction has never been observed.

developmental plasticity: Ability of a cell to adopt different developmental fates and therefore become one of several different types of mature cell.

diageotropic: Describes a plant organ that grows horizontally rather than vertically.

dichogamy: Mechanism by which the stamens and pistils ripen at different times, thereby ensuring cross-fertilization.

dichotomous: Branching into two.

dicot: A flowering plant whose seeds has two cotyledons.

differentiation: Process by which an embryonic cell with no distinguishing features becomes a mature cell with a specific form and function.

diffuse-porous: Type of wood in which all the conducting cells are approximately the same size in cross-section.

diffuse root system: Root system that lacks a central taproot and is made up of numerous, finely branching lateral roots. This type of root system is an adaptation to life in habitats with low amounts of rainfall. Grass roots are an example.

diffuse secondary growth: Secondary growth that occurs throughout a structure, not limited to one region.

diffusion: Movement of atoms, molecules, or ions from an area of high concentration to an area of lower concentration. This movement is driven by the kinetic energy of the diffusing substance.

dihybrid: A plant that has different alleles (heterozygous) at two different genetic loci.

dioecious: Species of plant in which the male and female reproductive structures are borne on different individuals. Gingko trees are an example.

diploid: Having two complete sets of chromosomes. The diploid number is the number of chromosomes in each cell of the sporophyte generation.

disaccharides: Sugars that have been synthesized by a dehydration reaction between two simple sugars. These simple sugars may be the same or may be different. Maltose and sucrose are examples.

disc flower: In many composite heads, the tiny flowers that compose the center. These flowers are radially symmetrical. In a daisy, the disc flowers are yellow.

DNA: Deoxyribonucleic acid. Contains and transmits the genetic information of a plant or animal. DNA is also responsible for directing the production of a set of proteins within the cell.

DNA ligase: Enzyme that seals linear breaks between two fragments of DNA.

DNA polymerase: Enzyme that adds nucleotides to a growing strand of DNA.

DNA sequencing: Determination of the order in which nucleotides containing the bases adenine (A), guanine (G), cytosine (C), and thymine (T) occur along the length of a strand of DNA.

dolipore: Opening in the cell walls between two cells in the hyphae of a *Basidiomycete* fungus.

domains: Regions of a protein that perform different functions.

dominant gene: An allele that is able to mask the presence of a different allele when both are together in the same genotype.

dominant species: In a plant community, those species that are most numerous and occupy the largest amount of space.

dominant trait: The phenotypic expression of a dominant allele. Plants heterozygous at one genetic locus will often appear to have only one type of allele.

dormant, dormancy: Period of inactivity that allows a plant to survive unfavorable cold or dryness.

drip tip: Structural feature of tropical plant leaves that facilitates the removal of condensed water or rain from the leaf surface.

drip zone: The region below the outer edge of the crown of a tree in which rain water tends to accumulate.

drupes: Type of fleshy fruit that has one seed; this seed is enclosed inside of a hard, stony pit. Cherries are an example.

dry matter: Dead leaves and other plant parts forming the litter on the surface of the soil.

duplication: Change in a chromosome causing a repetition of a segment already existing on that chromosome. Duplications contribute to the raw material from which new genes develop.

early summer species: Species that blooms early in the summer season.

early wood: Part of an annual ring in wood that develops in the early summer. It is often less dense than late wood.

ecology: The study of plants and animals living as a community and their interactions with one another and with the nonliving factors of their environment.

economic botany: The study of plants that have agricultural or medicinal or other human value.

ecosystem: The community of living organisms and their controlling environment that function together in complex ways.

ecotype: A plant that has gained genetic variants that allow it to live in a specific environment. The genetic changes are not great enough to prevent interbreeding with other ecotypes of the same species.

egg: A female gamete, usually distinguishable by size and location from a male gamete.

elaters: In *Equisetum* (horsetails) and liverworts, structures that are secreted by spore walls and that expand and contract with changes in moisture to bring about spore dispersal.

electrochemical gradient: Gradient across a cell membrane that results from differences in electrical charge.

electromagnetic spectrum: The range of wavelengths of energy from very long to very short. Visible light is one part of the spectrum.

electron transport chain: Series of molecules capable of being serially oxidized and reduced by electrons from the Krebs cycle. Oxygen is the last molecule in the chain. Energy from food is released in short bursts as electrons travel down the chain.

electrophoresis: Separation of molecules or fragments of molecules of different sizes in an electrical field. The smaller molecules migrate faster than the larger ones.

electroporation: Insertion of naked DNA into cells using an electrical shock. The shock makes the cell membrane more porous.

embryo: A young organism that does not have its adult form.

embryo sac: Eight-celled structure inside an ovule. It is the female gametophyte of flowering plants. One of the eight cells is an egg.

embryophytes: Plants that form embryos during their life cycle. Flowering plants and gymnosperms are examples.

endergonic: Reaction that requires extensive input of energy to occur. Syntheses of complex molecules from smaller ones are typically endergonic.

endocytosis: Uptake of particles or molecules by a cell when its membrane surrounds and engulfs the particle.

endodermis: A cylinder of specialized cells that separate the cortex from the vascular tissue of a root. Endodermis functions in regulating the flow of dissolved substances into the center of the root.

endomycorrhizae: A symbiotic relationship between a fungus and a root in which the fungus grows inside the cells of the root and aids the root in absorption of minerals and water. The fungus receives food from the root.

endophyte: An organism living within a plant, as a fungus living in a root.

endoplasmic reticulum: Membranes in the cytoplasm that form transport pathways and other compartments. Rough endoplasmic reticulum has ribosomes attached to its cytoplasmic face.

endosperm: Triploid cells modified for food storage in a seed. In a monocot seed, the endosperm is the tissue where corn starch or wheat starch is stored. In a dicot seed, the endosperm is usually absorbed into the cotyledons early in seed development.

endospore: Thick-walled, resilient resting cell formed by some bacteria.

endosymbiotic theory: Theory that chloroplasts and mitochondria developed from bacteria that moved into and became essential to the survival of an early eukaryotic cell.

energy: The ability to do work. Energy takes several forms, such as chemical energy in the bonds of a compound, light energy, and kinetic energy, the energy of movement.

energy of activation: A small amount of energy necessary to start an exergonic reaction.

entire: Describes a smooth leaf margin that has no teeth or lobes.

entrainment: Capture of a circadian rhythm by a particular time period, commonly twenty-four hours. Without external cues, circadian rhythms may complete one cycle in more than twenty-four hours.

entropy: The tendency of complex molecules and structures to lose energy and become degraded into simpler forms.

enzyme: A molecule, usually a protein, that lowers the energy of activation necessary for a reaction to occur.

ephemeral: Name given to a plant or plant part that lasts for only a short period of time.

epidermal hair: Multicellular hair growing from the epidermis of a leaf, stem, or fruit.

epidermis: Layer of thin-walled cells covering the surface of a plant organ.

epigeous germination: Seed germination in which the cotyledons emerge above the soil.

epigynous: Type of flower in which the petals are attached above the ovary.

epiphyte: A plant that lives nonparasitically on another plant. Usually, epiphytes are not rooted in the ground and are typically found in habitats with high humidity. Spanish moss is an epiphyte.

epistasis: Genetic phenomenon in which the expression of one pair of genes is prevented by the presence of a second pair.

essential elements: Chemical elements that must be available from the environment for healthy plant growth. Carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur are the major essential elements.

ethylene: Plant growth hormone that is a gas produced by the plant.

etiolation: Process that occurs when a plant is deprived of light. The stem becomes over-elongated and weak.

eudicot: Member of one of two major classes of angiosperms, *Eudicotyledones*. Eudicots' embryos have two cotyledons.

eukaryotic cell: Cell that contains a nucleus. The hereditary material is separated from the cytoplasm by an envelope of membrane.

eusporangium: Type of spore-producing organ of vascular plants, such as club mosses. The sporangium develops from a group of more than one cell and has no stalk.

eustele: The arrangement of the vascular bundles in a ring as found in the stems of dicots.

evergreen: Plant that keeps its leaves during adverse climatic conditions, such as cold temperatures. Examples are pine trees and rhododendrons.

exergonic: Chemical reaction in which large amounts of energy are released. Burning wood and the breakdown of food for cellular energy are examples.

exine: The outer layer of the coat of a pollen grain.

exocytosis: Movement of particles or molecules out of a cell.

exodermis: In monocot roots, a layer of thick-walled cells that forms under the epidermis.

exon: A length of DNA within a gene that codes for part of a protein.

eyespot: Photosensitive structure in many one-celled plants and microorganisms that orients them to light.

facilitated diffusion: Movement of molecules from an area of higher concentration to an area of lower concentration across a cell membrane. A carrier protein is involved.

facultative anaerobe: Organism that can survive in an oxygen-poor environment when necessary, using the small amount of energy available from fermentation.

$FADH_2$: Electron acceptor that has received electrons directly from the Krebs cycle and is thereby reduced. $FADH_2$ passes electrons to the lower part of the electron transport chain.

fascicle: A cluster or bundle. Pine needles occur in fascicles.

fascicular cambium: Portion of vascular cambium located within the vascular bundles of a dicot stem.

feedback inhibition: Process by which a buildup of the product of a reaction slows the rate at the reaction occurs.

fermentation: Set of reactions that change glucose into alcohol and carbon dioxide. A small amount of energy is produced, some of which is captured as ATP.

fertilization (agriculture): Addition of minerals or decayed organic matter to soil that has been depleted of nutrients by farming or other means.

fertilization (sexual reproduction): The fusion of sperm and egg to form a fertilized egg (zygote).

fiber: Thick-walled, long, slender plant cell that provides mechanical support. These cells die at maturity.

fibrous root system: Root system in which no one root is more prominent than any other.

field capacity: Water remaining in soil following rain or irrigation after excess water has been drained off by gravity.

filament: The stalk of a stamen that supports the anther.

fimbriae: Fringe of narrow teeth that surrounds the mouth of a moss capsule.

fixation: Process by which a gas has been converted to another type of molecule, usually organic.

flavonoids: Plant pigments that give flowers colors including scarlet, pink, purple, blue, and yellow.

flavonols: One of the three major groups of flavonoids.

floret: The tiny flower of a grass.

floridean starch: A special kind of storage carbohydrate made by red algae.

flower: The reproductive structure of an angiosperm.

fluid mosaic model: Current model that describes the distribution of lipid and protein molecules within a membrane.

follicle: A dry, dehiscent fruit that opens by splitting along one side. The fruits of milkweeds are follicles.

food chain: Organisms in a community, each of which serves as food for the next higher organism in the chain. A grass seed, a mouse, and an owl form a short food chain.

food web: Interwoven complex of food chains in a community. In a food web, a particular organism may be preyed on by more than one other organism. For example, a plant may be eaten by a deer, a vole, or an insect.

foot: The part of the moss sporophyte that connects it with the gametophyte. Nutrition passes through the foot from the photosynthetic gametophyte to the nonphotosynthetic sporophyte.

founder effect: Expansion of the frequency of a recessive phenotype in a community. A small initial population (founders) passed the same recessive allele to many members of subsequent generations.

four-carbon pathway: The series of reactions that occur in C_4 photosynthesis.

free-energy change: Alteration in the energy level of one of the components of a substance, such as water in a salt solution.

free-running period: Time necessary for completion of one cycle by an organism whose circadian rhythm is not restricted (entrained) to a twenty-four-hour period.

frond: The leaf of a fern or a palm.

fruit: Structure that develops from a mature ovary of an angiosperm. Fruits may be fleshy or dry and are often involved in seed dispersal.

fruitlets: In an aggregate fruit, one of the subsections that developed from a single pistil. An example is the tiny spheres in a raspberry.

frustules: The overlapping cell walls of a diatom.

fucoxanthin: A brownish-colored pigment found in the cells of brown algae.

functional phloem: That portion of the phloem that is able to conduct sugars in solution.

funiculus: Stalk of an ovule. It becomes the stalk that attaches a seed to a fruit.

fusiform initials: The long, slender cells of vascular cambium that divide to form secondary xylem and phloem.

G_0 phase: Cells that have exited from the cell cycle and are no longer actively dividing.

G_1 phase: Part of the cell cycle following mitosis. Cells grow and satisfy the requirements of the checkpoints that guard entry into the part of the cell cycle when DNA is replicated.

G_2 phase: Part of the cell cycle following replication of DNA (S-phase). Reactions within cells prepare those cells for entry into mitosis.

gamete: A haploid reproductive cell, usually a sperm or egg.

gametic meiosis: Reduction division that results in the production of cells destined to become gametes.

gametophores: Small branches on which gametes are formed in gametangia; found in some liverworts.

gametophyte: Part of a life cycle in plants with alternation of generations. The gametophyte is haploid. Some gametophytes are green and capable of independent existence; others are not.

gaps: Type of junction between adjacent cells through which cytoplasmic connections extend. Cells joined by gap junctions are electrically and chemically linked.

gas exchange: A swap of one gas for another. Often the first gas is the reactant in a chemical reaction, and the other gas is a product of the same reactions. Thus in photosynthesis, carbon dioxide (a reactant) enters the stomata of leaves by diffusion, and oxygen (a product) builds up inside the leaf tissue until it begins to diffuse out of the leaf.

gemma cups: Structures associated with asexual reproduction in liverworts. The gemmae form inside the cup-shaped structures on the liverwort surface and can be splashed out by a raindrop.

gemmae: Small, flat, green circles of cells produced asexually by liverworts inside gemma cups.

gene flow: Change in frequency of specific alleles within a population. This normally occurs where two populations with differing allele frequencies meet. Exchange of genetic material between the two adjacent populations results in gene flow.

gene (point) mutation: A change within the hereditary material of a single gene. These tiny mutations cannot be observed by inspecting pictures of chromosomes.

gene pool: All the alleles of all the genes present in a population. There is no limit to the number of alleles in a gene pool; however, an individual may not possess more than two different alleles.

generative cell: Cell in a pollen grain responsible for the production of the pollen tube.

genetic code: Form in which information relative to protein production is contained in DNA and RNA.

genetic drift: Phenomenon observed in small populations. Dramatic changes in allele frequency occur within a few generations, due to random chance.

genetic (linkage) map: Diagram of the location of specific genes on specific chromosomes.

genetic modification: Alteration of an organism's genetic material by manipulation in the laboratory. The addition of new genes or the removal of genes are examples.

genetic recombination: Process that results in new gene combinations on a chromosome.

genetics: The study of genes, chromosomes, the inheritance of hereditary characteristics, and the biochemical mechanisms controlling this inheritance.

genomic DNA library: A collection of the hereditary material from a species. The genes are fragmented into groups, and each group is stored in a bacterium or modified virus.

genotype: Alleles possessed by a plant that control traits being studied; the plant's genetic makeup.

genus: A group of related species having many traits in common and descended from a common ancestor.

geotropism: Tendency of plant parts to respond to gravity. Roots grow downward (positive geotropism); stems grow upward (negative geotropism).

germination: The beginning of growth of a plant embryo inside a seed. For germination to occur, the seed must be moist and given a moderately warm temperature. Once a seed is committed to germination, it cannot dry out and survive.

germination inhibitor: Substance that prevents germination. Many seeds make their own germination inhibitor that prevents them from beginning to grow in adverse conditions. For example, seeds of desert annuals will not germinate until sufficient rain has fallen to wash out the inhibitor. At this point, sufficient soil moisture will support the growth of the plant.

gibberellins: Class of plant growth hormones that cause stem elongation, flowering, and digestion of starch in germinating seeds.

glabrous: Without hairs.

gland: Structure that secretes substances such as nectar or salt.

glaucous: Taxonomic characteristic of lacking hairs and with a whitish coloration.

glycolysis: Series of chemical reactions beginning with glucose and ending with pyruvic acid. A small amount of ATP is produced during glycolysis.

glycoproteins: Proteins with sugar chains attached.

Golgi complex: Stacks of membranes located near the nucleus where cell products are modified and prepared for secretion from the cell.

Gondwanaland: Mega-continent that broke up during continental drift into Pangaea and Laurasia.

gradualism model of evolution: Accumulation of small genetic changes over an extended period of time.

grafting: Process by which a piece of one plant, usually a small branch, is attached to the stem of another plant.

gram-negative: Bacteria that do not stain darkly when exposed to a stain made of crystal violet and iodine. The lighter colors of these bacteria are the result of picking up color from the counterstain.

gram-positive: Bacteria that become dark-colored when exposed to a stain made of crystal violet and iodine. The thickness or other aspect of the bacterial cell wall determines whether a bacterium is gram-positive.

granum (*pl.* grana): A stack of membrane-bound compartments in a chloroplast. Grana are covered in chlorophyll and are the locations of the light-dependent, energy-capturing reactions of photosynthesis.

grassland: Biome in which the dominant plants are grasses.

gravitropism: Plant growth response to gravity. *See also* geotropism.

Green Revolution: Several decades of dramatic advances in yield and quality of crop species. This was the outcome of attempts to increase food production begun in the 1940's.

greenhouse effect: Increase in carbon dioxide and other gases in the earth's atmosphere. These gases serve to trap heat radiating from the earth into space. The result of the greenhouse effect is global warming.

ground meristem: A meristematic region behind the apical meristem of a stem or root in which cells divide and differentiate to become cortex and pith.

ground tissue system: The cortex and pith of stems and roots.

growth: Increase in size and complexity. This process turns a fertilized egg into a mature adult.

growth retardant: A chemical that slows the growth of a plant.

growth ring: Xylem tissue added to a tree during the growing season in a temperate climate. The age of a tree may be approximated by counting growth rings.

guard cell: One of a pair of cells surrounding a stoma on the surface of a leaf. Guard cells shrink and swell to open or close the stoma, thereby regulating the rate of evaporation from the inside of the leaf.

gum: Resinous carbohydrates produced by a variety of angiosperm trees and other plants. Gums are soft when moist and hard when dry. Chicle, which forms the base of chewing gum, is an example.

guttation: Production of water at the tips of grass blades as a result of the presence of special secretory structures called hydathodes. This process is most visible when the soil is well-watered and humidity is high.

gymnosperm: Large group of plants whose seeds are not covered by a fruit but are borne naked on modified leaves.

gynoecium: The group of carpels that make of the female part of a flower.

hadrom: The conducting cells of xylem.

halophile: Plant that is adapted to an above-average amount of salt in its environment.

haploid: Having one set of chromosomes and one of each kind of gene. This condition is common in eggs, sperm, and the somatic cells of gametophytes.

hardwood: Species of trees in which there are fibers in the xylem. All angiosperms are hardwoods.

Hardy-Weinberg theorem: Statement of genetic change within populations. Given a stable population, the frequency (commonality) of alleles and genotypes will not change from one generation to the next.

haustorium: Branch of a hypha of a parasitic fungus that enters host cells and extracts nutrients.

heartwood: The dark-colored wood in the center of a tree trunk. The color results from tannins that accumulate in the cells of this part of the wood.

heliotropism: Growth response in which a flower turns toward the sun. Sunflowers display heliotropism as their flower heads move in the course of a day.

hemicelluloses: A group of polysaccharides that, along with pectins, make up the matrix of a primary cell wall. Cellulose fibers are embedded in the matrix.

hemiparasite: Plant with some chlorophyll which lives as a parasite. Mistletoe is an example.

herb: Type of plant that does not make woody tissue. Also, a fragrant plant whose leaves or stems are used as flavorings in cooking.

herbaceous: Adjective describing a plant that does not make wood.

herbicide: Chemical that is lethal to plants.

herbivores: Animals that eat living plants.

heterocyst: A specialized cell found in cyanobacteria filaments that facilitates vegetative reproduction.

heteroecious: Describes fungi that spend parts of their life cycle on entirely different species of plants. Black stem rust of wheat spends part of its life cycle on wheat and part on American barberry.

heterokont: Type of yellow-green algae that have flagella of two different lengths.

heterosporous: Plants that produce two distinct types of spores. The different spores grow into separate male and female gametophytes.

heterothallic: Describes certain fungi and algae that have separate haploid mating strains.

heterotroph: An organism that cannot make its own food from simpler materials but must ingest and digest complex molecules made by other organisms. Animals are heterotrophs, but so are nongreen plants such as Indian pipes.

heterotrophic nutrition: Acquisition of energy-rich molecules made by other heterotrophs or by autotrophs.

heterozygous: Organism having two different alleles at a particular gene locus.

hilum: Scar on a seed where the seed stalk was attached.

homeotic mutation: Developmental gene with task of specifying the developmental fate of a group of undifferentiated cells.

homologous chromosomes: Paired chromosomes that carry the same genes in the same positions along their length.

homology: Similarity in DNA sequence shown by genes from unrelated organisms. Homology of genes implies a common ancestor.

homosporous: Producing only one type of spore. The gametophytes that grow from these spores are bisexual. Most ferns are homosporous.

homothallic: Types of algae and fungi that produce both male and female reproductive structures on the same plant.

homozygous: Organism that has both alleles in a gene pair alike.

horizons (soil): Layers of soil with different appearance and different chemical composition. In a forest, the horizon closest to the top will contain more organic matter than will the deeper layers.

hormogonia: Elongated portions of filaments of cyanobacteria.

hormone: Chemical compound produced in small amounts in one part of an organism that has an effect in a different part of the same organism. Auxins, gibberellins, cytokinins, and ethylene are examples in plants.

host: In a parasitic relationship, the host is the organism that is giving up energy-containing molecules to the parasite.

humus: Decayed organic matter of plant or animal origin that has broken down sufficiently to lose most recognizable structure.

hybrid: An organism that is heterozygous at one or more genetic loci. Many crop plants, such as wheat or corn, are hybrids.

hybrid maize: Variety of corn developed as a hybrid.

hybrid vigor: Improved growth and hardiness of hybrid organisms. This vigor is one of the benefits of producing and growing hybrids.

hydathode: Specialized structures at the tips of blades of grass that exude water when water is in plentiful supply in the soil.

hydroids: Water-conducting cells of some mosses.

hydrolysis: Breaking a covalent bond by adding the two fragments of a water molecule to either end of the bond.

hydrophilic: Compound or part of a compound that is attracted to and mixes well with water. The hydrophilic end of a molecule shows slight charge differences, as do the different parts of a water molecule.

hydrophobic: Compound or part of a compound that does not mix with water.

hydrophyte: Plant that is adapted to living in a very wet environment. Water lilies are hydrophytes.

hydrotropism: Plant growth response in which the root grows toward moisture.

hymenium: Layer of basidia that forms on the surface of the gills of a mushroom.

hypertonic: Solution that has a lower concentration of water and greater concentration of solutes than a second solution. The first solution is said to be hypertonic to the second solution.

hypocotyl: The part of an embryo between the embryonic root and the point where the cotyledons attach to the embryonic stem. In eudicot germination, it is usually the first structure to appear above the ground.

hypogeous germination: Seed germination in which the cotyledons remain in the soil.

hypogynous: Flower in which the petals attach below the ovary.

hypotonic: Solution that contains a greater concentration of water and less dissolved solute than another solution. The first solution is said to be hypotonic to the second solution.

imbibition: Uptake of water by dry seeds.

imbricate: Overlapping, like the shingles on a roof; usually refers to bud scales.

incomplete dominance: Intermediate phenotype produced by a heterozygous genotype. The single allele which is capable of producing a product cannot produce enough to equal the appearance of an individual with two such active alleles.

incomplete flower: Flower that lacks one of the whorls of parts found in a complete flower.

indehiscent fruit: Dry fruit that does not split open when mature.

indeterminate growth: Growth in which the terminal meristem remains active for the life of the plant.

indusium: In many ferns, a flap of tissue that covers or surrounds a group of sporangia.

inferior: Describes the ovary of an epigynous flower.

inflorescence: The group of flowers that forms at the top of a flower stalk. Inflorescences may be compact, like that of a daisy, or loose, like that of a mustard.

initials: The generalized name for any cell in a meristem.

insectivorous plant: Plant that traps insects and digests them for the nitrogen-containing compounds they possess. Plants of this type grow in boggy soil that is typically low in nitrogen.

integral proteins: Proteins that are part of a cellular membrane. These are also known as intrinsic proteins.

integuments: Layers of tissue that form the outer wall of an ovule. They become the seed coat in a mature seed.

intercalary meristem: Group of dividing cells that forms in the center of a group of mature cells. Grass blades have these meristems within the leaf blade near the base. As a consequence, they can keep growing upward even after having been cut.

interfascicular cambium: That portion of the vascular cambium that forms out of the cortex between the vascular bundles of a dicot stem. *See also* fascicular cambium.

interfascicular parenchyma: Parenchyma that fills the spaces between vascular bundles in stems.

internode: A length of stem from the base of one leaf to the base of the next leaf.

interphase: The major part of the cell cycle that includes all phases except mitosis. Replication of the chromosomes occurs during S of interphase.

intine: Inner layer of the wall of a pollen grain.

intron: Segment within a gene that is transcribed into RNA but eliminated prior to translation of the RNA.

inversion: Chromosome mutation in which a piece of the chromosome breaks, turns 180 degrees, and reattaches. Inversions place genes into new regions of the chromosome, where they may be more or less active than normal.

involucre: Ring of bracts surrounding the base of an inflorescence. The thick, edible bracts on an artichoke are its involucre.

iron-sulfur proteins: Proteins found associated with reaction centers in photosystems of photosynthesis.

irregular or bilaterally symmetrical: Refers to a flower that can only be divided one way to give two mirror halves. Snapdragons and orchids have irregular flowers.

isotonic: Two solutions containing the same concentration of water and dissolved solutes.

isozymes: Slightly different forms of the same enzyme that can be separated by biochemical means.

jojoba: Desert shrub whose seeds produce a liquid wax that is used in cosmetics, as a lubricant, and as a cooking oil.

kinetochores: Structures that form at the centromere of chromosomes in prophase. The microtubules of the spindle attach to the kinetochores prior to separation of the chromosomes.

Kranz anatomy: Pattern of cellular arrangement found in C_4 plants, in which the veins of the leaves are surrounded by a ring of large cells filled with many chloroplasts.

Krebs cycle: Part of the process of cell respiration in which two-carbon molecules derived from glucose are broken down into carbon dioxide. Electrons are removed from the fragment; these are picked up by the electron acceptor at the top of the electron transport chain.

lanceolate: Long, slender, and tapering to a point.

late summer species: Plants that flower late in the growing season.

late wood: Secondary xylem for forms at the end of the summer.

lateral bud (also called axillary bud): Bud found in the axil between a leaf and a stem. Lateral buds become branches from the main stem.

lateral meristem: Group of actively dividing cells located around the circumference of a woody stem or root. Vascular cambium and cork cambium are the two lateral meristems.

lateral roots: Roots that branch from the original or from a large main root.

latex: Often milky fluid containing rubber or similar compounds; produced in stems and leaves of plants, such as rubber and milkweeds.

laticifer: Parenchyma-lined canal that produces latex in stems and leaves.

layering: Formation of adventitious roots from a stem that comes in contact with the soil. In horticulture, adventitious root production is stimulated by scarring the stem, wrapping it in wet peat moss, and covering the area with plastic.

leaf: The usually broad, flattened photosynthetic organs attached to stems.

leaf gap: Space in the vascular tissue of a stem formed as the result of a strand of vascular tissue leaving the stem and entering a leaf.

leaf primordium: An undifferentiated group of cells in the apical region of a stem that will grow into a leaf.

leaf rosette: A ring of leaves that grows near the ground; often the first year's growth of a biennial plant. The flower stalk grows out of the center in the second year.

leaf scar: Corky area on a woody stem that marks the location where a leaf fell off. Leaf scars indicate the arrangement of leaves on a woody twig and are useful in plant identification.

leaf tendril: Long, flexible strand of leaf tissue that is a highly modified leaf. Used by climbing plants, such as peas, to attach to a support.

leaf trace: The strand of vascular tissue that leaves a stem and enters a leaf.

leaflet: One section of the blade of a compound leaf.

leghemoglobin: Proteins in legumes that are capable of binding oxygen.

legumes: Plants capable of extracting gaseous nitrogen from the air and turning it into nitrogen-containing organic compounds. Legumes can do this because of bacteria that live in swellings in the legume roots. Legume seeds are particularly rich in protein as a result. Peas, beans, and soybeans are examples of legumes.

lenticel: Pore in the bark of some trees that facilitates gas exchange with the living cells under the bark.

leptoids: Conducting cells found in gametophytes of some mosses, which resemble phloem.

leptom: The conducting cells of phloem.

leptosporangium: Type of sporangium produced by most ferns. It is characterized by a long slender stalk and an annulus.

leucoplasts: Plastids that do not contain chlorophyll but are the repository for starch manufactured by the plant. Thin sections of potato tuber show large numbers of leucoplasts.

liana: Tropical vine.

lichen: A symbiotic relationship between a fungus and an alga. The alga is protected from drying by the fungus, while the fungus receives food molecules from the alga.

light absorption: Acquisition of light energy by a pigment molecule, such a chlorophyll, during photosynthesis. Light must be absorbed before it can be fixed in the bonds of glucose.

light reactions: Series of reactions that occur in a chloroplast during photosynthesis. Light energy is captured as ATP and NADPH.

lignin: Phenolic compound that is the matrix of secondary cell walls and makes them strong and hard.

linked genes: Genes that are located near each other on the same chromosome and tend to segregate into the same gamete during meiosis. The result is that they are frequently inherited together.

lipids: Organic molecules composed of carbon, hydrogen, and oxygen; the amount of oxygen is very small compared with the amount in carbohydrates. Lipids form a large part of cell membranes.

living stone: A succulent plant native to dry regions that has the general shape and appearance of a small stone.

loam soils: Soils having a mineral particle size larger than clay particles but smaller than sand grains.

locule: Space inside a carpel where seeds develop.

locus: A point on a chromosome where a particular gene is found. Homologous chromosomes will normally have the same genes at the same loci.

long-day plant: Plant that flowers under the influence of a long light period and a short dark period in successive twenty-four-hour days. Poinsettias and chrysanthemums are long-day plants.

M phase: That part of the cell cycle where the chromosomes separate into two groups. M phase includes prophase, metaphase, anaphase, and telophase.

macroevolution: Evolution that results in new taxa above the species level.

macromolecule: Large organic molecule important in living organisms. Starch, cellulose, protein, and nucleic acids are examples.

macronutrients: Chemical elements required for plant growth in relatively large amounts.

magnoliids: Members of the class of flowering plants called the *Magnoliopsida*.

maize: Individuals of the species *Zea mays*, commonly called corn in the United States In other countries, "corn" can refer to other grains.

major vein: Largest bundle of conducting tissue found in a leaf.

mannitol: Sugar alcohol that is the form in which carbohydrates are transported in many members of the rose family.

mediterranean scrub: Type of vegetation found in places, such as Southern California, which experience wet winters and long, dry summers.

megaphyll: Leaf type which has branching veins and is associated with a leaf gap.

megasporangium: Reproductive structure in which megaspores are produced.

megaspore: Cells produced by meiosis that grow into female gametophytes.

megasporocyte (megaspore mother cell): The single cell that divides by meiosis to produce four megaspores.

meiosis: Process of cell division that results in the formation of cells with only half as many chromosomes as the original cell. In plants with alternation of generations, meiosis occurs prior to the formation of the gametophyte.

membrane: Lipid bilayer with embedded proteins. Membranes form the basis of many subcellular structures as well as surrounding the cytoplasm and the nucleus.

membrane potential: Gradient in voltage across a cell membrane that results in the movement of ions.

meristem: Region of active cell division. Meristems occur primarily at the tips of stems, at the tips of roots, and around the circumference of woody plants under the bark.

mesophyll: Tissue composed of mesophyll cells.

mesophyll cells: Chloroplast-filled parenchyma cells of a leaf.

mesophyte: Plant species whose requirements for moisture place it midway on the scale between wet and dry.

messenger RNA (mRNA): RNA that carries information for the construction of a protein from the DNA in the nucleus to a ribosome.

metabolic pathway: A series of reactions leading to the production of a particular product.

metabolism: The sum of all the synthetic (anabolic) and degrading (catabolic) reactions an organism can carry out.

metabolites: Compounds formed as the result of biochemical pathways in an organism.

metaphase: Phase of mitosis in which chromosomes line up on the equator of the spindle.

metaxylem: That part of the primary xylem of a stem or root that matures last.

methanogen: Type of bacterium that produces methane during its autotrophic activities. Methanogens live in oxygen-poor environments.

microevolution: Change within a group of plants that results in large-scale differences. Macroevolution produces new genera, families, and orders.

microfibril: Strands of cellulose molecules connected to one another by hydrogen bonds.

micronutrients: Chemical elements necessary for plant growth, required in very small quantities.

microphyll: Leaf that possesses a single unbranched vein and is not associated with a leaf gap.

micropyle: Opening in an ovule through which the pollen tube grows.

microsporangium: Reproductive organ in which meiosis produces spores that upon germination form male gametophytes.

microspores: The products of a microsporangium.

microsporocyte (microspore mother cell): A cell that undergoes meiosis to produce four microspores.

microtubules: Hollow cylinders of tubulin protein molecules that form networks in the cytoplasm and the mitotic spindle.

middle lamella: Material that cements two adjacent plant cells to each other. May be pectin or lignin.

mimicry: The phenomenon in which one plant species has evolved to look superficially like a second species. Often the mimic benefits because the second species is bad-tasting or poisonous, and thus herbivores avoid both species.

minerals: Chemical elements in ionic form absorbed from the soil and used by plants in a variety of metabolic pathways.

minor vein: One of the small, branching veins that form a network in a leaf.

mitochondria: Cellular organelles responsible for the breakdown of food and the release of energy from that food.

mitochondrial matrix: The portion of a mitochondrion that is enclosed by the inner membrane.

mitosis: Separation of replicated chromosomes into two equal groups. The result of mitosis is two nuclei that are identical to each other and to the original nucleus.

mitotic spindle: Football-shaped structure of microtubules that forms in the early stages of mitosis. Chromosomes attach to tubules of the mitotic spindle by kinetochores that form at the centromeres.

molecular biology: Study of the molecules of living organisms, their pathways, and their interactions.

molecular clock: Accumulation of genetic changes that develops when two species diverge. The longer two species have been separate, the more changes will be evident. The clock does not tick at the same rate in every species or every molecule.

molecular systematics: Study of the classification of organisms based upon differences at the molecular level, particularly in DNA.

molecule: Chemical unit composed of two or more atoms. The atoms may be of the same element or different elements.

monocot: One of the two major groups of flowering plants, *Monocotyledones*. The seeds of monocots have only one cotyledon. Corn and grass are examples.

monoecious: Describes plants in which both the male and female sex organs are produced in the same flower.

monohybrid: Organism that is heterozygous for one pair of genes.

monomer: Small molecules that are the building blocks for more complex molecules. Glucose is the monomer that is built up into starch and cellulose.

monophyletic: Evolutionary concept in which a group of related organisms can be shown to be descended from a single ancestor.

monosaccharide: Simple sugar, such a glucose or fructose. These can combine to make larger carbohydrates.

monospore: In the algae, a diploid spore that germinates to form another diploid plant.

monounsaturated fats: Lipid that has only one carbon-carbon double bond in each of its three fatty acid chains. Olive oil is composed mostly of a monounsaturated lipid.

monsoon forest: Forest type found in tropical regions of the world where there are annual periods of high rainfall.

morphogenesis: Development of patterns of form or structure.

motor proteins: Specialized proteins capable of moving chromosomes, organelles, or molecules from one part of a cell to another.

mucigel: The combination of mucilage secreted by a root, bacteria that are attracted to the mucilage, and fine soil particles that accumulate around the root.

multiple alleles: Situation that occurs when a gene has more than two different allelic forms.

multiple fruit: A fruit that forms from an inflorescence made of many flowers. A pineapple is an example.

mutagen: A chemical or energy source that causes permanent alteration of the genetic material.

mutation: Permanent change in an organism's genetic material.

mutualism: Symbiotic relationship in which both organisms benefit.

mycobiont: The fungal part of a lichen.

mycology: The study of fungi.

mycoplasmas: The smallest known free-living microorganisms. Unlike bacteria, they have no cell walls. Some have been shown to cause diseases.

mycorrhiza (*pl.* mycorrhizae): A symbiotic relationship between a root and a fungus in which the fungus lives either in or on the root and gains food from it. The fungus increases absorption of water and minerals for the root.

mycotoxins: Poisonous substances produced by fungi. Aflatoxin that sometimes contaminates stored food is an example.

myxamoebas: Uninucleate stage in the life cycle of slime molds.

NADH: Reduced form of the electron-accepting molecule nicotinamide adenine dinucleotide. NAD+, the oxidized form, receives electrons from the breakdown of carbohydrates in the Krebs cycle and passes those electrons down the electron transport chain.

nastic movements: Movements that occur in a plant during the daytime. The plant stem or tendril rotates around the vertical axis.

natural selection: The evolutionary process in which organisms of a species are produced in quantity larger than the environment can support. These organisms differ slightly from one another in their genetic makeup. Those with genetic changes that best suit them to live in a particular environment will survive better and produce more offspring than organisms that are not as fit.

neck canal cells: Found in archegonia in plants, such as ferns and mosses, these cells fill the canal protecting the egg until it is ready for fertilization. Then the neck canal cells break down and permit the passage of sperm to the egg.

necrosis: Death of tissue from disease, damage, or nutrient deficiency.

nectar: Sugary solution produced by flowers that attracts pollinators.

nectar guide: Ultraviolet light reflecting lines found on some flower petals that direct pollinating insects to the nectar.

nectary: Gland in a flower that produces and secretes nectar.

netted venation: Type of vein pattern found in dicot leaves, in which veins branch to form a network of large and small veins throughout the leaf.

niche: The combination of the habitat and ecological role of a species within an ecosystem. It includes the resources the species needs, the way it finds them, and the way it harvests them.

nitrification: Process by which bacteria convert ammonium ions or ammonia to nitrate.

nitrogen cycle: The biogeochemical cycle of the element nitrogen.

nitrogen fixation: Process by which bacteria convert atmospheric nitrogen to nitrogen-containing compounds, such as amino acids.

nitrogenase: Enzymes that convert atmospheric nitrogen into ammonia.

node: The location on a stem at which leaves and lateral buds are attached.

nodules: Swellings on roots of legumes and other plants in which symbiotic nitrogen-fixing bacteria live.

noncyclic photophosphorylation: Production of ATP following the absorption of light energy by electrons of a chlorophyll molecule. The electrons release their energy in a stepwise fashion but are then picked up by a different molecule of chlorophyll. The original chlorophyll molecule receives replacement electrons from the breakdown of water molecules.

nonvascular plants: Plants that lack the special conducting tissues xylem and phloem. The nonvascular plants are the bryophytes—liverworts, hornworts, and mosses—and were the earliest colonizers of land.

NPK ratio: In commercial fertilizer, the relative amounts of nitrogen (N), phosphorus (P), and potassium (K). For example, a fertilizer labeled 12-12-12 has equal amounts of these three mineral nutrients.

nucellus: Thin-walled cells found in sporangia that provide nutrition to developing spores.

nucleic acid hybridization: Hydrogen bonding of two nucleic acid strands that are somewhat complementary in their base sequence. The two strands were not originally part of the same molecule but, as single-stranded molecules in solution, are attracted to each other. Hybrids may form from the same type of nucleic acid (such as DNA-DNA hybrids) or two different types (such as DNA-RNA hybrids).

nucleic acids: Large molecules made up of nucleotides. These molecules are involved with the transmission of inherited characteristics from one generation to the next and with the production of products encoded in the genes.

nucleoid: The part of a bacterium that includes its chromosome.

nucleolus (*pl.* nucleoli): Collection of protein and RNA molecules that form at specific sites on chromosomes (nucleolar organizing centers). The function of the nucleolus is the production of ribosomes.

nucleosome: A length of DNA wrapped twice around a collection of histone proteins. Six nucleosomes form one turn of a coil that is the interphase chromosomes.

nucleotides: Building blocks of nucleic acid. Each nucleotide consists of a five-carbon sugar, an organic base, and three phosphate groups.

nucleus: Cell structure of eukaryotic cells in which the hereditary material is separated from the cytoplasm by a double lipid-protein membrane (the nuclear envelope).

nut: Type of fruit in which the outer wall of the fruit is fleshy or leathery and the inner wall of the fruit is woody or stony. The seed coat is fused with the woody inner wall.

nutrient cycles, nutrient cycling: Large-scale movements of elements and water through the living and nonliving portions of an ecosystem.

nutrient uptake: Process of absorption of minerals as ions from soil.

nyctinastic movements: The opening and closing of flowers corresponding with day and night.

obovate: Oval-shaped but broader toward the tip than toward the base.

Okazaki fragments: During the replication of DNA, one of the two strands is replicated continuously from beginning to end; the other strand is replicated in successive short pieces (Okazaki fragments). The difference comes about because of different orientation of the two DNA strands.

oogonium: The female reproductive structure of algae, in which a single egg is formed from one precursor cell. These have no sterile jacket.

oospore: In the life cycle of water molds (*Oomycota*), name applied to fertilized eggs.

operculum: Flaplike structure that closes the opening to the moss capsule, composed of sporophyte tissue. *See also* calyptra.

operon: In bacteria, a group of genes regulated by the same promoter. The genes usually make products involved in the same biochemical pathway.

opposite: Leaf pattern in which two leaves come off the stem at the same node.

organ: A complex anatomical structure composed of different types of tissues, all functioning together for a particular purpose. A leaf, a stem, and a root are all plant organs.

organelle: Structures within a cell, surrounded by membranes. Mitochondria, chloroplasts, and Golgi bodies are examples.

organic: Chemical compounds containing both carbon and hydrogen and having some of the hydrogen attached directly to the carbon atoms.

organism: Any individual living creature.

osmosis: Movement of water through a selectively permeable (also called differentially permeable) membrane from an area of higher concentration to an area of lower concentration.

osmotic potential: Difference in concentration of water in two adjoining solutions separated by a selectively permeable membrane.

osmotic pressure: The amount of free energy of water in a solution.

outgroup: A group of organisms only distantly related to the groups being examined in a cladistic study.

ovary: Female reproductive structure that houses the ovules and matures into a fruit. Among plants, ovaries are found only in angiosperms.

ovate: Oval-shaped but broader toward the base than toward the tip.

ovulary: The swollen base of a pistil; also called an ovary.

ovule: Female reproductive structure that matures into a seed containing an embryo.

ovuliferous scales: Flat plates of a gymnosperm cone to which ovules are attached.

oxidation-reduction (redox) reaction: Coupled reactions in which the loss of electrons from one molecule (oxidation) results in the gain of electrons by a second molecule (reduction).

oxidative phosphorylation: Production of ATP driven by the movement of electrons from the Krebs cycle of cell respiration to oxygen.

P-protein: In sieve tube elements, a special protein that clumps together to seal the ends of the elements when they are injured or when the plant goes dormant.

paleobotany: Study of fossil plants or plant parts, such as pollen.

palisade cell: In a leaf, the sausage-shaped parenchyma cells found just below the upper epidermis. Palisade cells are well supplied with chloroplasts and packed beside one another with minimal space between them.

palisade parenchyma: All the palisade cells of a leaf. The tissue gets its name from its resemblance to a stockade fence (palisade). Much of the photosynthesis in a typical plant occurs in this tissue.

palmate venation: Pattern of major veins in a leaf. The veins spread out from a central point where the petiole meets the blade of the leaf. There is a superficial resemblance to spread fingers "branching" from the palm of the hand.

palmately compound leaf: Leaf with palmate venation but with the blade divided into leaflets. Each leaflet receives one major vein. These leaves look like groups of long fingers. Horse chestnut leaves are an example.

panicle: Type of inflorescence with branches from a main stalk. Those branches are branched in turn. An example is the inflorescence that results in a cluster of grapes.

pappus: Fine hairs, bristles, or flattened awns attached to a seed of a composite that aid in wind dispersal. Dandelion seeds are examples.

parallel venation: Pattern of veins in a monocot leaf. The large veins do not intersect as they traverse the length of the leaf.

paraphyletic: Taxonomic grouping that includes some, but not all, of a group of related species.

parasexuality: Special type of reproduction found in some deuteromycetes involving nuclear fusion in a hypha without normal processes of meiosis and zygote formation.

parasite: Organism that uses a living plant or animal as a source of nutrition. Parasites often have adaptations for this lifestyle.

parenchyma: Thin-walled plant cells that may contain chloroplasts. Parenchyma cells fill spaces in leaves, stems, roots, and fruit.

parthenocarpic fruits: Fruits that develop without pollination and fertilization. Hothouse tomatoes are produced this way by spraying them with an auxin.

passage cells: Found in the endodermis of some roots, these specialized cells are not suberized and allow unimpeded movement of water and dissolved minerals into the xylem.

passive transport: Movement from one side of a cell membrane to the other without the expenditure of metabolic energy.

pectin: Carbohydrate that is a major part of the matrix of primary cell walls and the middle lamella. Extracted pectin is sold for jelly-making.

pedicel: The stalk of a single flower, whether the flower is borne singly or in an inflorescence.
peduncle: The stalk that supports an inflorescence of flowers.
pellicle: Tough outer layer of the cell membrane of some one-celled organisms.
pennate: Describes a diatom which is long and slender when viewed from above, as opposed to centric, which is circular.
PEP carboxylase: An enzyme necessary for C_4 photosynthesis. It combines CO_2 with PEP (phosphoenolpyruvate) to form malic or aspartic acid.
pepo: Type of berry that has a hard or leathery rind when ripe; squash is an example.
peptide bond: A covalent bond that connects two amino acids in a protein.
peptidoglycans: Compound molecule composed of sugar chains and a polypeptide.
perennial: Plant that comes up in successive years from the same root.
perfect: Describes a flower that contains both male and female sex organs.
perforation plate: Region in the cell wall of a sieve tube element that is characterized by small pores through the wall. These plates are found in end walls and sometimes in lateral walls.
perianth: The combination of sepals and petals in a flower.
pericarp: Outer layer of a fruit. Examples are the fleshy part of a berry, the stony part of a nut, and the pod of a pea.
pericycle: Layer of potentially meristematic cells separating the endodermis from the phloem and xylem of a root.
periderm: In the bark, the combination of cork, cork cambium, and cork parenchyma.
perigynous: Describes a flower in which a rim of the receptacle grows up around the base of the ovary. The petals, sepals, and stamens are attached to this rim of tissue.
peripheral protein: Proteins that are loosely bound to the surface of a membrane, not embedded in the membrane.
perisperm: Nutritive tissue found in a seed outside of the embryo sac and distinct from the endosperm.
peristome: Ring of small, toothlike projections that surround the opening of a moss capsule.
permafrost: Permanently frozen layer of soil underlying tundra vegetation.
permanent wilting percentage: Amount of water remaining in soil when plants rooted in that soil reach the point of permanent wilting. If the soil is not watered, the plants will die.
peroxisomes: Organelles that contain enzymes which produce hydrogen peroxide.
petal: One of the parts of a flower that is flat and often brightly colored, found in a whorl between the whorl of sepals and the whorl of stamens.
petiolate leaf: Leaf that has a stalk attaching it to a stem.
petiole: Stalk that connects the flat blade of a leaf to the stem. The vascular tissue to the leaf runs through the petiole.
pH: Measure of acidity of a solution. The lower the pH, the higher the concentration of hydrogen ions, and the more acidic the solution.
phagocytosis: Process of ingestion by a cell in which the cell engulfs large particles; a form of endocytosis.
phelloderm: Technical name for cork parenchyma that is produced by the cork cambium.
phenolics: Aromatic chemical compounds produced by plants. Included are tannins, lignin, and flavonoid pigments.
phenotype: Any gene-based anatomical or physiological trait that can be observed is part of a plant's phenotype.
phloem: Conducting tissue responsible for moving food manufactured in the leaves to other parts of the plant, including the roots.
phloem loading, phloem unloading: Process by which sugars and other substances are transferred into or out of sieve tube elements in phloem.
phloem ray: A flat, vertically oriented sheet of parenchyma cells that extends from the vascular cambium outward through the phloem. These rays permit lateral movement of substances within the phloem and into the xylem.
phosphoglycolate: Chemical important in photorespiration.
phosphorylation: The attachment of a phosphate group to another molecule, often a protein or molecule of ADP. Phosphorylation increases the potential energy of the molecule to which the phosphate is added.
photoinduce: Stimulating or triggering a plant response by light.
photolysis: Use of light to break molecules.
photomorphogenesis: Growth response to light by plants.

photons: Packets of light energy.
photoperiodism: Regulation of a plant process, such as flowering, by the relative length of light and dark periods in a twenty-four hour day.
photophosphorylation: Use of light to attach a phosphate group to another molecule, usually to ADP.
photorespiration: Physiological process that occurs during photosynthesis when the ratio of carbon dioxide to oxygen becomes too low. It results in the production of less sugar than during regular photosynthesis, and some carbon dioxide is formed.
photosynthesis: Production of food molecules, six-carbon sugars, from simple chemical compounds in the presence of light energy.
photosynthetic autotrophs: Organisms capable of using light energy to manufacture food.
Photosystem I, Photosystem II: Stages in the energy-capturing light reactions of photosynthesis. Photosystem II yields ATP, whereas Photosystem I yields reduced NADPH.
phototropism: Growth response in which the plant stem, leaf, or flower grows either toward or away from light.
phragmoplast: Set of microtubules that organizes the formation of a new cell wall separating two daughter cells as part of cytokinesis.
phragmosome: Area within a dividing cell in which the phragomoplast forms.
phycobilins: Found in red algae and cyanobacteria, a special class of pigments that absorb green light and reflect blue and red light.
phycoplast: Similar to phragmoplast but found only in a few green algae.
phyllotaxy: Study of the arrangement of leaves on a stem.
phylogenetic tree: Branching diagram, also called an evolutionary tree, that illustrates the evolutionary relationship among groups of organisms.
phylogeny: Study of evolutionary origins of related groups.
phytoalexins: Chemicals produced by plants that help to limit the spread of bacterial and fungal infections.
phytochrome: Class of pigments found in leaves that regulate photoperiodic responses in plants.
phytoplankton: Small plants, often single-celled, that float in water. Phytoplankton in the ocean are responsible for much of the earth's oxygen production.
phytotoxin: Chemical produced by a plant that is harmful to another plant. *See also* allelopathy.
pigment: An organic molecule capable of absorbing and reflecting specific wavelengths of light.
pili: Bridges of cytoplasm that form between conjugating bacteria. Genetic material is transferred from one cell to another through a pilus.
pilose: Having long, soft hairs.
pinnate venation: Pattern of leaf veins that resemble a feather, with a main vein up the middle of the leaf and smaller veins branching in parallel from the main vein.
pinnately compound leaf: Leaf with pinnate venation but with the blade divided into sections (leaflets). A large vein branching from the main midrib enters each leaflet.
pinocytosis: Intake of liquids as tiny vesicles formed when the cell membrane invaginates.
pistil: The female part of a flower composed of stigma, style, and ovary.
pit: Often circular or oval gap in the secondary cell wall. Plasmodesmata pass from cell to cell through the pits and associated pit fields in the primary cell wall.
pith: Region of parenchyma tissue found in the center of a dicot stem.
pith meristem: The part of the ground meristem in which the cells of the pith divide and differentiate.
pith ray: In the young stem of a dicot, the parenchyma tissue that separates the vascular bundles from one another.
pits: Plural of pit (see above). Also refers to the stony inner part of a drupe. Prune pits are an example.
placenta: Point at which an ovule attaches to the carpel wall. Nutrients stored in the developing seed pass from the plant through the placenta.
placentation: Pattern of ovule attachment to the carpel wall. In central placentation, all the ovules are attached to the innermost axis of the carpel.
plagiotropic: Pattern of growth that results in branches growing more or less parallel to the ground. Lateral tree limbs are plagiotropic.
plankton: Small plants and animals that float freely in water; their small size prevents them from having to swim to keep from sinking.
plant anatomy: Study of plant structure, especially the arrangement of different types of cells to make tissues and organs.

plant biotechnology: Alteration of plant hereditary material, particularly by the insertion of foreign genes. Biotechnology has applications in agriculture, industry, and medicine.

plant growth regulator: Chemicals produced in one location in a plant that have a growth-modifying effect elsewhere in the plant. Auxins, gibberellins, cytokinins, and ethylene are classes of growth regulators.

plant morphology: Study of the plant kingdom, especially with regard to evolution, reproduction, and structure.

plant physiology: Study of the functioning of plants.

plant taxonomy: Science of the naming and classification of plants.

plasma membrane: Lipid-protein bilayer that surrounds the cytoplasm and regulates movement of compounds in and out of the cell.

plasmid: Circle of DNA found in the cytoplasm of bacteria that contains genes not found in the nucleus.

plasmodesma (*pl.* plasmodesmata): Small strands of cytoplasm that extend through the cell membranes and cell walls connecting two adjacent cells.

plasmodiocarp: Fruiting body of a slime mold.

plasmodium: Amoebalike thallus of a plasmodial slime mold.

plasmolysis: Loss of water from the central vacuole of a plant cell that causes the cytoplasm and cell membrane to pull away from the cell wall. Continued plasmolysis leads to the death of the cell.

pleiotropy: When one gene is able to affect several different structures in a single organism.

plurilocular gametangia: In brown algae, a group of several cells, all of which produce either eggs or sperm.

plurilocular sporangia: In brown algae, a group of several cells, all of which produce spores.

pneumatophores: Projections of roots upward from saturated soils or water, such as the knees of bald cypress.

pod: Type of dry, dehiscent fruit; known also as a legume.

polar nuclei: Two nuclei located in the center of an embryo sac. These nuclei fuse with a sperm to produce the endoderm tissue in a seed.

polar transport: Movement of a substance from the tip of a stem downward.

pollen: Male gametophytes of gymnosperms and angiosperms. Pollen is adapted to transfer from one plant to another by wind or insects.

pollen grain: A single male gametophyte. Most pollen grains have distinctive sculpturing of their outer surfaces.

pollen sac: Chamber inside an anther where pollen is produced.

pollen tube: Tube which grows from an angiosperm pollen grain after it has landed on a compatible stigma. The tube grows down the style and into an ovule in the ovary. The sperm move down the tube to effect fertilization.

pollination: Transfer of pollen to a stigma in angiosperms or an ovule in gymnosperms.

pollinium: Pollen sac produced by orchids. Insects entering orchid flowers must pass the pollinia and inadvertently pick them up. They stick to the insect's body and are transferred to another orchid flower.

polyembryony: The development of more than one embryo in a seed.

polygenic inheritance: Several genes cooperating to produce a single trait. Each gene adds only a small increment to the final end product, making polygenic traits, also known as quantitative traits.

polymerase chain reaction: Laboratory process for copying strands of DNA. A single piece of DNA is separated into two strands by heating. Primers are added to the strands, and DNA polymerase uses each strand to make a complete piece of DNA. The process is repeated over and over.

polymerization: Chemical process by which many similar small molecules (monomers) are joined to make one large complex molecule.

polymers: Complex molecules composed of repeating units. A protein made of amino acids is an example.

polypeptides: Strands composed of several amino acid molecules. A single polypeptide may become a functional protein, or it may join with other polypeptides to form a protein.

polyphyletic: Describes a group of organisms that have similar characteristics but which originated from more than one ancestor.

polyploid: Organism having more than two complete sets of chromosomes.

polyploidy: Genetic condition in which the hereditary material is present in three or more complete sets. Plants may be triploid (three sets of chromosomes), tetraploid, or have even greater numbers.

polysaccharides: Polymers built up from monosaccharide molecules. Starch and cellulose are examples of plant polysaccharides.

polysome (polyribosome): Piece of messenger RNA attached to several ribosomes, each of which is producing a nascent protein at a different stage of completion.

pome: A type of fleshy fruit in which the seeds are found in chambers that are lined with a tough, papery material. Most of the flesh develops from the receptacle of the flower, rather than exclusively from the ovary. Apples and pears are examples.

population genetics: Branch of genetics that examines the movement of genes through populations. A population geneticist might study genetic drift, founder effect, or Hardy-Weinberg theorem.

predaceous fungi: Soil fungi that form loops to lasso nematode worms. The trapped worm is then digested by the fungus.

preprophase band: Ringlike group of microtubules that encircles a cell where a future equatorial plane will form during mitosis.

pressure-flow hypothesis: Model to explain the movement of dissolved substances in the phloem. The solutes are swept along with moving water. The water is moving because of differences in water pressure between the top of the column and the bottom.

prickle: A slender thorn or spine, often found in groups.

primary cell wall: The first wall, and often the only wall, to form around a plant cell. Primary walls are thin. Apple flesh, for example, is composed of cells with primary walls.

primary consumers: Animals that eat plants as their primary source of food. Deer, cows, mice, and seed-eating birds are examples.

primary endosperm nucleus: Nucleus formed by the fusion of the two polar nuclei and a sperm nucleus in an embryo sac. This nucleus divides to form the endosperm of a seed.

primary growth: Stem and root elongation and expansion of leaves resulting from cell division and elongation.

primary metabolites: Sugar phosphates, amino acids, lipids, proteins, and nucleic acids, all of which comprise the basic molecules necessary for a cell to function.

primary phloem: Phloem produced in stems, roots, and leaves during the process of primary growth.

primary pit-fields: Regions of primary cell walls adjacent to pits in the secondary cell wall. Plasmodesmata are concentrated in these pit-fields.

primary plant body: The stems, roots, and leaves produced by primary growth of an embryo.

primary producers: In an ecosystem, those organisms that form foods from energy and simple chemical molecules.

primary root: The first root produced by an embryo.

primary structure: Part of the primary plant body.

primary tissue: Tissue produced during primary growth. Cortex, pith, and epidermis are examples.

primary xylem: That xylem that is formed during primary growth.

principle of competitive exclusion: If two or more species compete for the same niche, one of them will be successful, and the other will be eliminated over time.

principle of parsimony: When two different explanations are offered, the most likely one is the simplest one.

prochlorophyte: Ancestral green plant.

prokaryotic cell: Cell in which the hereditary material is not separated from the cytoplasm by a nuclear envelope. Bacteria are prokaryotes.

prop roots: Adventitious roots that grow from stems and help support the stem. Corn plants produce prop roots just above the soil.

prophase: First phase of mitosis, during which the chromosomes condense and the spindle forms.

proplastids: The precursors of plastids, such as chloroplasts.

proteins: Complex polymers composed of amino acid monomers. Although many proteins function as enzymes, there are proteins that have other functions in a cell.

prothallial cells: Sterile cells produced in pollen grains of gymnosperms.

prothallus: Name given to the haploid, free-living gametophyte of ferns.

protonema (*pl.* protonemata): A filament of cells produced by a germinating spore of a moss.

protoplasm: General term for living matter.

protoplast: The living contents of a cell.

protoplast fusion: The merging of the protoplasts of two different cells.

protostele: Arrangement of xylem and phloem in which the xylem is a solid strand in the center of a root or stem, and the phloem is arranged in a concentric ring around it. Typical of primitive vascular plant stems.

protoxylem: During the differentiation of cells to become primary xylem, the first cells to differentiate into vessel elements or tracheids. In dicot roots these are at the ends of the arms of primary xylem, and in dicot stems they are in the part of the vascular bundle nearest the pith.

protracheophyte: The ancestor of plants that have vascular tissue.

pseudoplasmodium: In cellular slime molds, the name given to the multinucleate, amoeba-like structure that forms from the merger of thousands of uninucleate single cells.

pubescent: Possessing hairs.

pulvinus: Zone of cells at the base of a leaf or leaflet that can rapidly lose water and cause the leaflet or leaf to fold up.

pumps: Cellular mechanisms to move substances against a concentration gradient into or out of cells.

punctuated equilibrium model of evolution: Theory that evolution occurs in bursts of large changes followed by extended periods of time when little change occurs.

pyrenoid: Regions of a chloroplast in some algae where starch accumulates.

pyruvate: End product of glycolysis. During cell respiration, glucose is converted to two molecules of pyruvate with a small number of ATPs formed in the process.

quiescent center: A dome-shaped mass of cells at the very tip of a root. In this region cell division is far less frequent than in the apical meristem immediately above it or the root cap below it.

raceme: Inflorescence type in which there is a single stalk with individual flowers attached directly to the stalk.

rachis: The stiff midvein of a pinnately compound leaf, to which the leaflets are attached. This term is used especially with fern leaves.

radial system: All of the rays together in the secondary xylem and phloem of a plant.

radicle: The embryonic root.

rain forest: Biome found in regions of the world where rainfall is high and there are no dry periods. Rain forests occur in the tropics and along the northwest coast of the United States.

raphide: A needle-shaped type of crystal of calcium oxalate found in leaves, stems, bark, and roots. These are irritating to the skin.

ray flower: In a composite inflorescence, those asymmetrical flowers that have a long, straplike petal.

ray initials: Cells of the vascular cambium that divide to form new parenchyma cells of rays.

ray parenchyma cell: One of the cells of a ray, such as are found in xylem and phloem.

reaction center: Located in the membranes of thylakoids, these are groups of chlorophyll and carotenoid pigments along with associated proteins, where the light-dependent reactions of photosynthesis begin. Reaction centers absorb light energy and transfer it to pathways where it is incorporated in molecules of ATP and NADPH.

reaction wood: When a tree bends horizontally, secondary xylem grows on the lower side, in response to gravity, and causes the tree's trunk to grow back into an upright position.

receptacle: Usually expanded tip of the stalk to which the whorls of a flower are attached.

receptors: Proteins or protein-carbohydrate combinations located on the outer surface of cell membranes, which are the sites to which various chemicals attach, causing reactions to occur within the cell.

recessive allele: Form of a gene whose expression is masked by a dominant allele in the same genotype.

recessive trait: Phenotypic characteristic that normally is observable only when two recessive alleles are present in the genotype.

recombinant DNA: DNA that is formed by the splicing of DNA fragments from two different species.

region of cell division: That part of the meristem where mitosis occurs.

region of elongation: That part or zone of a primary root or primary stem in which cells grow to their maximum length.

region of maturation: That part of a primary root or primary stem in which cells differentiate to forms the primary tissues.

regular or radially symmetrical: Describes a flower that has its parts organized along radii, much like the spokes of a wheel. When cut along any diameter, the flower will produce two mirror images.

repetitive DNA: DNA sequences found repeated many times in a single cell. The repeated sequences may exist in the same region of a chromosome, in which case they are known as tandem repeats.

replication: Copying of a DNA molecule, so that the two molecules formed are identical to each other and to the original molecule. The two molecules formed are each composed of one strand from the original DNA molecule and one newly synthesized strand.

reporter genes: Genes that make a detectable product, such as one that is colored. Reporter genes are used in genetic research to show the tissues or stages of development in which a particular gene is active.

reproductive (genetic) isolation: Describes any of many mechanisms that prevent one organism from sexually reproducing with a second.

resin: Sticky, aromatic substance produced in the wood, bark, and needles of conifers. When injured, the resin oozes out and reduces the risk of insects, fungi, or bacteria getting into the plant.

resin canal: A tube that forms through the wood, bark, or needles of a conifer. The tube is lined with parenchyma cells that produce and secrete resin. Also called a resin duct.

respiration: The stepwise breakdown of glucose or fragments of lipids and proteins with the release of energy to molecules of ATP.

restoration ecology: A subdivision of the field of ecology that works to reclaim damaged ecosystems and return them to their original condition.

restriction enzyme: Bacterial enzyme that cuts DNA at a location marked by a specific base sequence.

reticulate venation: A pattern of veins in leaves in which the branch veins form a complete network with a regular pattern throughout the leaves.

rhizobia: Any bacteria of the genus *Rhizobium*. These bacteria live in nodules on the roots of legumes, where they fix atmospheric nitrogen.

rhizoids: Small filamentlike growths out of the bases of bryophytes, some algae, and some fungi, which help attach the plant to the substrate and channel water into the plant.

rhizome: A stem that grows horizontally either in the soil or right on the top of the soil. Irises and many grasses have rhizomes; those of irises are fleshy.

rhizosphere: Region of soil in the immediate vicinity of the root system of a plant. It is in this rhizosphere that the plant absorbs its needed water and minerals.

ribonucleic acid. *See* RNA.

ribosomal RNA (rRNA): RNA that makes up part of the structure of the ribosome and is necessary to its functioning.

ribosome: Subcellular structure composed of RNA and protein. The ribosome is the cellular machinery for the production of proteins from amino acids.

ribulose 1,5-bisphosphate (RuBP): First and last compound in the Calvin cycle of photosynthesis. RuBP combines with carbon dioxide to start the cycle and is regenerated at the end of the cycle.

ring-porous: Describes wood in which the early wood (produced in spring and early summer) has significantly larger vessel elements than does the late wood (produced in late summer and fall). The wood of oaks is ring-porous.

ripeness-to-flower: Physiological condition that must be met before a plant will be able to respond to external stimuli, such as temperature or photoperiod, that are the cues to flowering.

RNA: Ribonucleic acid, a nucleic acid formed on chromosomal DNA; involved in protein synthesis.

RNA polymerase: Enzyme that connects nucleotides to form RNA. The sequence of nucleotides in the RNA is copied in complementary fashion from the sequence of nucleotides in a DNA template.

root: Portion of a plant axis that typically grows underground, possesses a root cap, branches internally from its pericycle, and does not have the ability to produce leaves or buds.

root cap: Mass of thin-walled cells that covers the tip of a root. These cells lubricate the pathway of the root through the abrasive soil and protect the delicate root tip from damage.

root hairs: Single-celled outgrowth of root epidermal cells. Root hairs vastly increase the absorbing surface of a root.

root nodules: Small, tumorlike growths that form on roots of legumes and other kinds of plants. Roots produce nodules in response to bacteria, such as the genus *Rhizobium*, which grow in them and fix atmospheric nitrogen.

root pressure: Force created by differences in concentration of water between the soil and a root that causes water to ooze out of a stem if it is cut just above the junction with its root.

root primordium: A very young, still-developing branch root.

root system: All the roots, large and small, that are part of an individual plant.

root tuber: Swollen portion of a root in which are stored large amounts of food. Sweet potatoes and yams are root tubers.

rugose: Having a wrinkled surface.

runner: Stem that grows horizontally along the ground, periodically sending up new upright branches. Strawberries produce numerous runners.

RuPB carboxylase/oxygenase (Rubisco): Enzyme that causes the combining of ribulose-bisphosphate with carbon dioxide during the light-independent reactions of photosynthesis. During photorespiration (see above), Rubisco causes the combining of ribulose-bisphosphate with oxygen. Rubisco is the most abundant enzyme on earth.

rusts: Type of parasitic pathogenic *Basidiomycete* fungi that have more than two types of spores in their life cycle. One of the stages in the life cycle causes lesions on the host plant in which are formed reddish-brown spores. Black stem rust of wheat is a notorious plant disease caused by a rust fungus.

S phase: That portion of the cell cycle when DNA is synthesized and the chromosomes replicate.

sagittate: Shaped like an arrowhead.

samara: Type of dry fruit that grows a flat wing. The seed in enclosed in a swollen region at one end. Maples and ashes produce samaras.

sand: Class of mineral particles of soil in which the particles are between 0.05 and 2.0 millimeters in diameter.

saprophyte: Type of fungus or plant that gets its nutrition by digesting dead plants. Many mushrooms grow as saprophytes.

sapwood: Lighter-colored wood toward the outside of a stem. *See also* heartwood.

saturated fats: Lipids in which many or all of the carbons in the fatty acid chains have hydrogen atoms bonded to them.

savanna: Biome type characterized by widely spaced trees separated by open, grassy regions.

scabrous: Having a rough surface.

scarification: Physical abrasion of the seed coat of a seed. Many seeds, especially of desert plants, have hard seed coats that must be scarified before water can get in to start germination. Occurs naturally when seeds are tumbled over rocks in running water, when seeds are blown over rock, or when seeds are chewed by insects.

schizocarp: Type of dry, indehiscent fruit made of several individual chambers that separate from one another when mature. The members of the celery and parsley family form schizocarps.

scion: Branch or twig that is grafted onto another plant, the stock.

sclereid: Type of cell that has extremely thick and hard secondary cell walls and that is more or less spherical in shape. Also called stone cells. The "grit" in a pear is a mass of sclereids.

sclerenchyma: Simple tissue of plants in which the cells have extremely thick and hard secondary cell walls. Elongated sclerenchyma cells are fibers, and more or less spherical ones are sclereids.

sclerotium: Dried, dense mat of hyphae of a fungus.

scrub community: Plant community characterized by stunted trees and shrubs that may be widely spaced. Typical of poor soils.

second messengers: Part of the signaling pathways in a cell. The arrival of one signal at the cell surface begins a chain of events that can result in the production of multiple small molecules (second messengers). These, in turn, trigger other reactions, but due to their larger numbers, the original signal is now amplified.

secondary consumers: Carnivorous animals that eat herbivorous animals (primary consumers).

secondary growth: Growth in diameter of a stem or root resulting from divisions of the vascular cambium and the cork cambium. Secondary growth occurs after the section of stem or root has reached its maximum length (primary growth).

secondary metabolites (secondary products): Chemicals synthesized by a plant that are not part of the basic molecular structure of a cell. Chlorophyll is an example.

secondary phloem: Phloem produced by activity of the vascular cambium.

secondary wall: Plant cell wall formed inside of the primary cell wall after a cell has reached its mature size.

secondary xylem: Xylem produced by activity of the vascular cambium.

seed banks: Storage facilities where numerous strains of cultivated plants are kept as seeds. These seeds are preserved to maintain a large pool of genetic variation that may have been eliminated from modern highly inbred stocks.

seed coat: Outer layer of a seed.

seed dispersal: Process by which the seeds of a plant are distributed over a wide area, away from the parent plant. Many seeds are adapted for dispersal by wind or animals.

seed germination: Initiation of growth by the embryo of a seed. The emergence of the primary root is usually the first indication that germination has occurred.

seed leaf: A cotyledon in a dicot seed. These are the first leaflike structures to appear when the seed germinates.

seed-scale complex: The combination of bract, scale, and seed in a cone of a confer.

seedling: A young plant, usually with at least one set of true leaves.

seeds: Mature ovules that contain an embryo and a source of nutrition for the growth of the embryo enclosed in a seed coat.

selectively permeable membranes: Membranes that permit water to pass easily but solutes in the water to pass very slowly, if at all.

self-pollination: When pollen from the anther of a flower lands on the stigma of the same flower.

senescence: Normal part of the aging process that results in the death of a plant organ or a whole plant.

sensitivity: In bacteria, the lack of ability to tolerate an antibiotic. Bacteria that are killed by ampicillin are said to be ampicillin-sensitive; those that are not killed are called ampicillin-resistant.

sepal: Member of the outermost whorl of flower parts.

septate: Divided into sections by partitions.

septum: A wall between two compartments.

serial endosymbiotic theory: Endocytosis (see above) that occurred by the progressive incorporation of one type of bacteria in an evolving eukaryotic cell, later followed by the incorporation of another type of bacteria.

serrate: Having a leaf margin with many small teeth.

sessile leaf: Leaf without a petiole that is attached directly to the stem.

seta: Stalk of a moss sporophyte.

shade-tolerant: Describes a species that is able to grow in low light intensity, such as on the floor of a forest.

sheath: Thin, leaflike structure that surrounds or encloses a plant part.

shoot: That part of the plant that includes the stem and leaves.

short-day plant: Plant that flowers under the influence of long, unbroken nights and short days. Chrysanthemums are an example of short-day plants.

shrub: Woody plant with multiple stems.

sieve area: Region on the wall of a sieve cell or sieve tube element in which are located numerous small pores.

sieve cell: Type of cell found in phloem of gymnosperms and lower vascular plants, characterized by end walls that lack sieve plates.

sieve plate: Location on the wall of a sieve tube element that has one or more sieve areas.

sieve tube: In phloem, a column of sieve tube elements arranged end to end and connected by sieve plates.

sieve tube element: Conducting cells of phloem typical of angiosperms, in which the end walls possess sieve plates.

signal transduction: Movement of a chemical signal from one part of a cell, such as the cell membrane, to a different part of a cell, such as the nucleus.

silicle: Type of dry fruit typical of the mustard family. It is short and broad, and divided lengthwise into two compartments.

silique: Type of dry fruit typical of the mustard family. It is elongated and divided lengthwise into two compartments.

silt: Class of mineral particles of soil that has particles with diameters between 0.002 and 0.05 millimeter.

simple diffusion: Movement of a substance from a region of higher concentration of the substance to a region of lower concentration of the same substance. Only the kinetic energy of the molecules is involved.

simple fruit: Fruit that develops from a single pistil.

simple leaf: Leaf that has an undivided blade. Orange leaves are an example.

simple tissue: Plant tissue composed of one type of cell.

single-copy DNA: Nonrepetitive DNA. Most genes are examples of single-copy DNA.
sink: Site to which a substance or energy travels.
siphonostele: Arrangement of xylem and phloem characterized by a column of pith running through the center of the stem or root.
sister chromatids: Result of replication of a chromosome. The two chromatids are held together at the centromere prior to separation during cell division.
smuts: Fungal diseases of plants in which sticky, dark-colored masses of asexual spores form from eruptions in the tissue of the infected plant.
softwood: Species of trees that lack fibers in their xylem. All conifers are softwoods.
solar tracking: Describes a plant whose flowers or leaves follow the sun from east to west during the day.
somatic hybrids: Plants that result from the fusion of two somatic (nonreproductive) cells.
soredia: Reproductive structures of a lichen that consist of tufts of hyphae combined with algal cells.
sorus (*pl.* sori): Cluster of sporangia found on the leaves of ferns.
source: Site from which a substance or energy that is being transported originates.
spadix: In the inflorescence of the members of the *Arum* family, the spadix is a stalk on which many small flowers are tightly clustered.
spathe: In the inflorescence of the members of the *Arum* family, the spathe is a leaflike bract that partially surrounds the spadix.
speciation: The evolution of new species from preexisting species.
species: Group of morphologically and physiologically similar organisms that are potentially capable of breeding with one another and are incapable of breeding with members of other groups.
specific epithet: The second name in the two-part Latin name of a plant species. In *Quercus alba*, the name *alba* is the specific epithet.
sperm: Haploid cells produced by the male gametophyte. A sperm fuses with an egg during the process of fertilization.
spermagonia: Structure in which nonmotile sperm are produced in some fungi and algae.
spermatogenous cells: Cells capable of dividing to form sperm.
spices: Aromatic flavorings derived from the dried seeds, fruits, or barks of a variety of plants.
spike: Inflorescence that has a long axis to which are attached sessile flowers.
spine: Highly modified leaf or part of a leaf that forms a sharp projection.
spirillum: One of the three basic morphological forms of bacteria. These bacteria are elongated, S-shaped, and possess flagella.
spongy parenchyma: Loosely packed, thin-walled photosynthetic cells located next to the lower epidermis in the interior of a leaf; also called spongy mesophyll.
sporangiophore: Small branch on which are formed sporangia.
sporangium (*pl.* sporangia): Plant organ in which are formed reproductive cells that grow directly into new plants without sexual fusion.
spore: Reproductive cell that grows directly into a new plant without sexual fusion. May be either haploid or diploid.
sporocarp: A hard case enclosing the sporangia of water ferns.
sporophyll: Leaf on which sporangia form.
sporophyte: The diploid generation in a plant having alternation of generations.
spring ephemerals: Herbaceous plants that flower in the spring for a brief period of time. In a forest, these appear before the trees leaf out. In a desert, they appear following winter rains.
springwood: Secondary xylem that forms during the first part of the growing season; often contains more and larger vessels and fewer fibers than summerwood.
spur: Elongated projection formed as part of a petal or petals.
stamen: Male reproductive structure in a flower.
staminate: Flower or cone that bears only pollen.
starch: Carbohydrate composed of long chains of glucose molecules. Starch is typically found as the storage product in seeds, roots, and underground stems.
stem: The usually aerial part of a plant on which are formed leaves and axillary buds.
sterile cell: Nonreproductive cell that forms the wall of sporangia and gametangia.
steroids: Class of lipidlike organic compounds characterized by four rings of carbon atoms. Like hormones, they have effects on growth in very small quantities.
sticky ends: Refers to the ends of a piece of DNA that has been cut with a restriction enzyme.

stigma: Receptive top of a pistil where the pollen grains land.
stigmatic tissue: Tissue of a stigma.
stilt root: Adventitious root that grows downward from a branch into the soil and supports the branch. Red mangrove trees form stilt roots.
stinging hair: An epidermal hair that contains an irritating chemical.
stipule: Bladelike projections that usually grow in pairs from the base of the petiole of some kinds of leaves.
stock: Woody plant that receives a graft.
stolon: Rhizome that grows along the surface of the soil and forms roots at its nodes.
stomata (*sing.* stomate): Openings in the epidermis of leaves and green stems that allow gas exchange to occur.
stone cell: Isodiametric cells with extremely thick and hard secondary cell walls. Forms of sclerenchyma are found scattered in the flesh of pears and forming the hard shells of nuts.
stratification: Division of a plant community into layers, such as canopy, shrub, and herb layers of a forest. Also physiological conditioning of seeds or bulbs necessary before germination or flower production can occur. Stratification occurs during a period of a few to several weeks of cool, damp conditions.
stromatolite: Fossilized masses of cyanobacteria that represent some of the first evidence of photosynthetic life on earth.
structural gene: Gene that codes for a protein product.
style: Usually elongated portion of a pistil between the ovary and the stigma.
suberin: Waxlike substance that waterproofs the thick cell walls of cork cells and forms the Casparian strips of endodermis cells.
substrate: The substance, such as soil or bark, on which a plant grows. Also, in biochemical reactions, the chemical compound upon which an enzyme acts.
succession: Orderly progression of plant communities that replace one another over time at a given site.
sucker: Rapidly growing branch from an otherwise unbranched stem.
summerwood: Xylem tissue that forms in the later part of the growing season. It often has fewer and smaller vessel elements and more fibers than does springwood.
sustainable agriculture: Farming methods that do not destroy the ability of the land to produce future crops.
symbiont: Member of a symbiotic relationship.
symbiosis: Relationship involving two unrelated organisms that live together and impact each other. The relationship may benefit both or only one.
sympatric speciation: Evolution of two groups into separate species while living in overlapping geographic locations.
symplast: Interconnected cytoplasm of a plant composed of the cytoplasm of its cells and the plasmodesmata that connect those cells.
symplastic loading: Movement of substances from one cell to another via the symplast.
symplastic pathway: Route taken by substances as they are moved through the cytoplasm and plasmodesmata into other cells.
symport: Movement of two solutes in the same direction at the same time. An example is the transport of sucrose and protons across a membrane.
synergids: Haploid cells at one end of an embryo sac that bracket the egg. The synergids have been found to signal the egg's location to the sperm.
systematics: The study of the naming and classification of plants on the basis of evolutionary relationships.

T-region (T-DNA): Portion of the Ti plasmid that is transferred into a plant cell by *Agrobacterium*. The T-region integrates into the plant genome.
taiga: Biome located across Canada, northern Europe, and northern Asia that consists of forests of spruces, firs, and birches.
tannin: Soluble phenolic substances, brown or black in color, that are produced by plants and used to tan hides or make ink.
tapetum: Nutritive cells found in sporangia.
taproot: A long, tapering root that is an elongation of the primary root of an embryo.
taproot system: Type of root system with one main root and many lateral branches that are much smaller in diameter than the main root.
taxon: Related group of organisms. A taxon may be small (species) or large (order, division).
taxonomy: Study of the relationships of plant groups to one another.
teliospores: Thick-walled resting spores of the pathogenic rust and smut fungi.

telium: Lesion on a plant in which the teliospores of a pathogenic fungus are formed.

telomeres: Areas of repetitive DNA occurring at the ends of chromosomes. The telomeres protect the coding parts of the chromosomes from erosion during cell division.

telophase: The final stage of M-phase of cell division when nuclear envelopes reform around the two groups of chromosomes.

temperate deciduous forest: Biome located in eastern North America south of the taiga, central Europe, and eastern China, characterized by forests of tree species, most of which lose their leaves every autumn.

temperate mixed forest: A subdivision of the temperate deciduous forest in which pines share importance with deciduous trees. These forests are usually found on sandy soils in the southeastern United States.

tendril: Modified leaf or stem that is long, slender, and highly flexible. They coil around objects with which they come in contact to support the tendril-bearing plant.

tepal: One of the units of the perianth that is not differentiated into petals and sepals in flowers such as tulips.

terminal bud: Structure at the tip of a stem or branch consisting of the stem apical meristem, usually covered by bud scales.

terminal bud scale scar: Scar left on a twig when the scales covering the terminal bud are shed at the beginning of the growing season.

terpenoids: Very large and diverse group of organic molecules produced by plants. The group includes carotenoid pigments, latex, and essential oils that give distinctive odors and flavors.

testcross: In genetics, a mating between an organism showing one or more dominant traits with a homozygous recessive organism of the same species.

tetrad: Chromosome configuration formed by synapsis of two replicated homologous chromosomes during Prophase I of meiosis.

tetrasporophyte: Stage in the life cycle of red algae during which meiosis occurs.

thalli (*sing.* thallus): The bodies of algae, fungi, and bryophytes that are not differentiated into stems, roots, or leaves.

theca: Stiff covering of some of the dinoflagellates and other unicellular organisms.

thermophile: Bacterium that lives in very hot water, such as in the hot springs at Yellowstone National Park.

thigmomorphogenesis: Growth pattern found in vines caused by tendrils touching and curling around supporting objects.

thigmonastic movements: Movement of tendrils that occurs until they come in contact with and twine around supporting objects.

thigmotropism: Growth response in a plant resulting from the plant touching other objects.

thorn: Sharp woody projection from a stem.

thylakoids: Chlorophyll-containing membrane sacs in a chloroplast. A granum is a stack of thylakoids.

Ti plasmid: Circle of DNA found in the bacterium that causes crown gall tumor. Genes on the plasmid enable *Agrobacterium* to stimulate cell division and cause the formation of a tumor.

tissue: Group of similar cells that cooperate to carry out a particular function. Epidermis is an example.

tissue culture: Growth of cells in a laboratory container. The cells are supplied with nutrient media and growth factors.

tissue system: A tissue or group of tissues that function together as a unit. The dermal system, vascular system, and the ground tissue system are usually recognized.

tomentose: Covered with dense, woolly hairs.

tonoplast: Membrane that surrounds the vacuole in a plant cell; also known as a vacuolar membrane.

torus: In the pits of tracheids of some conifers, a thickening in the primary cell wall. It may function in the movement of water in and out of a tracheid.

totipotency: Ability of a cell to differentiate into any kind of mature cell in a plant. Cells of the apical meristem are totipotent.

trace element: Chemical element required in very small quantities for plant growth. Examples are molybdenum, boron, copper, manganese, and zinc.

tracheary elements: Any of the conducting cells found in xylem.

tracheid: Conducting cell of xylem whose end walls have pits but not pores. These are found in all vascular plants and are the only kind of tracheary elements in conifers.

tracheophytes: Classification category that includes all plants containing xylem and phloem.

transcription: Transfer of information from DNA to RNA.

transduction: Use of a virus to carry new genetic information into a cell.

transfer cell: Special cells of the phloem that facilitate loading of sugars into sieve tube elements.

transfer RNA (tRNA): RNA that associates with specific amino acids and positions them at the ribosome in the order specified by messenger RNA.

transformation: Uptake of DNA by a bacterium. Transformation usually results in the bacterium acquiring new genetic information, such as that which causes antibiotic resistance.

transgenic plants: Plants that have had their original genetic information altered by the addition of new genes.

transition region: Region in the axis of a plant where the stem changes into the root.

translation: Process by which the information coded in messenger RNA is converted into a protein or other polypeptide product.

translocation: Movement of dissolved substances from place to place in the phloem.

transmembrane proteins: Proteins that are embedded in a membrane and have one terminus outside of the cell and the other terminus inside the cytoplasm. Some signal receptors are transmembrane proteins.

transmitting tissue: Tissue in the style of a pistil through which a pollen tube grows on its way to the ovule in the ovary.

transpiration: Evaporation of water from the leaves and stems of plants. Most transpiration occurs through open stomata.

transpiration stream: Moving column of water through the xylem of stems and leaves. The movement is powered by transpiration.

transpirational pull: Force created by evaporation from the top of a column of water in a plant. This force causes the movement of water up a tree from the roots to the leaves.

transport proteins: Proteins that move specific solutes across cell membranes. Often the expenditure of cellular energy is needed for this transport.

transposon: Mobile segment of DNA that is able to move among the chromosomes in a nucleus.

tree: Woody plant of substantial size, usually consisting of a single trunk and multiple branches.

trichome: Multicellular hairlike structure that grows out from the epidermis of leaves and herbaceous stems.

triglycerides: Lipid composed of glycerol attached to three long-chain fatty acids.

triticale: Allotetraploid grain bred from wheat and rye. It combines the hardiness of rye with the productivity of wheat.

trophic levels: Positions at which specific organisms obtain their nutrition within a food chain. Plants usually occupy the first trophic level.

tropical rain forest: Biome found in tropical regions throughout the world that experience rainfall year-round. These are the most biodiverse ecosystems, often containing thousands of species of plants in a single acre.

tropism: Plant growth response to an external stimulus. The plant may grow toward or away from the stimulus.

tube cell: One of the two cells of a pollen grain. The tube cell elongates to form the pollen tube.

tuber: Large, fleshy underground stem where food is stored. A white potato is an example.

tuberous root: Root that possesses swollen regions containing stored food. Sweet potatoes are an example.

tunica-corpus: Arrangement of the cells of an apical meristem in which the outer two layers of cells, the tunica, are distinct from a mound of cells beneath them, the corpus.

turgid: Describes a cell whose central vacuole is full, causing the cytoplasm and cell membrane to be pressed against the cell wall. The crispness of carrots and celery results from their cells being turgid.

turgor pressure: Pressure of the cell wall against the cell contents that is generated when a plant cell is turgid.

twig: Youngest portion of a branching stem.

tyloses: Projections of parenchyma cells into tracheids and vessel elements that appear as inclusions.

type specimen: Herbarium specimen designated by the author of a new species as being typical of that species.

umbel: Flat-topped inflorescence in which each of the tiny flowers is at the end of its own stalk. Found in the parsley family.

unilocular sporangia: In brown algae, the sporangium in which haploid spores are formed by meiosis.

unsaturated lipids: Lipid molecules in which many of the carbons of the fatty acid chains are connected by double bonds. These contain less hydrogen than do saturated lipids.

urediniospores: Spores produced in the life cycle of a rust fungus that are capable of reinfecting the host plant.

uredinium: In the life cycle of a rust, the orange-colored lesion where urediniospores are formed.

vacuole: Fluid-filled space surrounded by a membrane. In many plant cells, there is a large central vacuole.

variegation, variegated: Refers to leaves that have both green and nongreen areas. Only the green areas are photosynthetic.

vascular bundle: One of the strands of xylem and phloem that run lengthwise in a herbaceous stem.

vascular cambium: Meristematic tissue that forms a cylinder separating xylem and phloem in stems and roots. The vascular cambium divides to form secondary xylem and secondary phloem.

vascular cylinder: All of the xylem and phloem in the center of a root or stem.

vascular plant: Any plant that has xylem and phloem as conducting tissues. Excludes the algae, bryophytes, and fungi.

vascular ray: Flat group of cells, several to many cells high and one to several cells thick, found in woody stems. Rays are oriented in lines running from the center of a stem outward through the xylem and phloem and appear as radial lines in a cross-section.

vascular system: The interconnected network of xylem and phloem throughout a plant.

vascular tissue: Tissue capable of conduction and support, including both xylem and phloem.

vein: Bundle of xylem and phloem that is part of the vascular tissue network of a leaf.

velamen: Outer layer of cells covering the aerial root of an epiphytic orchid.

venter: Swollen base of an archegonium that contains the egg.

vernalization: Physiological process in which a seedling plant is exposed to several weeks of cool temperatures. This exposure is necessary to induce the formation of flowers in that plant.

vesicle: Small, fluid-filled bubble surrounded by membrane and located in the cytoplasm.

vesicle-mediated transport: Movement of substances in vesicles, often from the Golgi body to the cell membrane, where the vesicle releases its contents.

vessel: Hollow tube formed from vessel elements stacked one on top of another. Vessels carry water and dissolved minerals.

vessel elements (also called vessel members): Cells of xylem that are hollow and dead at maturity. They have secondary cell walls with large open pores in the end walls.

viability: The capacity to live and develop; an organism is said to be viable if it can live and thrive.

virion: A virus particle consisting of genetic material surrounded by a protein coat.

viroid: Small, viruslike infectious molecules of RNA without protein coats.

water conduction: Movement of water, usually in xylem, from place to place in a plant.

water-holding capacity: Ability of a soil to hold water against the pull of gravity.

water loss: Evaporation of water from plant surfaces.

water potential: Free energy of water in a substance, such as a sugar solution. The more water relative to dissolved substances, the higher the water potential of the solution. Pure water has the highest possible water potential.

water storage: Retention of water in the vacuoles of parenchyma cells. Succulent plants, such as cacti, retain large amounts of water following rain for later use.

water uptake: Movement of water from soil into a plant.

whorled: Arrangement of plant parts, such as leaves on a stem. A whorl consists of three or more parts in a ring.

wood: Secondary xylem composed of vessels, fibers, and tracheids.

xanthophyll: Type of carotenoid pigment, yellow in color.

xerophyte: Plant adapted to dry habitats.

xylem: Vascular tissue composed of vessels, fibers, and tracheids that is responsible for upward conduction of water and dissolved substances (usually minerals). Xylem is also the supporting tissue of stems.

xylem ray: Vascular ray found in secondary xylem.

yeasts: Single-celled fungi that reproduce by budding. They are able to ferment sugar into carbon dioxide and alcohol and therefore are the foundation of both the baking and brewing industries.

zooplankton: Small animals, often single-celled, that float or swim weakly.
zooxanthellae: Algae that live symbiotically in coral and some other animals.
zygomorphic flower: Flower that is bilaterally symmetrical. Snapdragon flowers are an example.
zygosporangium: In bread molds and their relatives, a structure in which zygospores are formed from the fusion of gametes.
zygospore: Thick-walled spore with multiple nuclei that develops after the fusion of gametes in the life cycle of bread molds and their relatives.
zygote: A fertilized egg formed by the union of a haploid egg and sperm.

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BIBLIOGRAPHY

This annotated, selected bibliography is intended to provide a representative sample of books for supplemental reference, reading, and study on plant life. All of the selected works were readily available at libraries or bookstores at the time of compilation. Most are suitable for general audiences; however, some cover complex topics and require background in the sciences for maximal understanding. Many are illustrated. The books are grouped into broad subject areas and are listed alphabetically by author or by editor.

Jeannie P. Miller

General Reference Works

Allaby, Michael, ed. *A Dictionary of Plant Sciences*. 2d ed. New York: Oxford University Press, 1998. Compresses into one volume both simple definitions and more extensive explanations for more than five thousand terms. Topics covered include ecology, earth sciences, earth history, evolution, genetics, plant physiology, biochemistry, cytology, and biogeography. Descriptions of taxonomic groups of seed plants, ferns, algae, mosses, liverworts, fungi, bacteria, and slime molds comprise one-third of the dictionary.

Brako, Lois, David F. Farr, and Amy Y. Rossman. *Scientific and Common Names of Seven Thousand Vascular Plants in the United States*. St. Paul, Minn.: American Phytopathological Society, 1995. The four sections include scientific names alphabetized by genus, common names followed by scientific name, major synonyms, and the included genera listed under family names.

Brickell, Christopher, and Judith D. Zuk, eds. *The American Horticultural Society A-Z Encyclopedia of Garden Plants*. New York: Dorling Kindersley, 1997. Profiles more than fifteen thousand ornamental garden plants, featuring more than six thousand full-color illustrations. Plants are listed alphabetically by botanical name, with common synonyms cross-referenced. Entries provide information on plant nomenclature and anatomy, cultivation, propagation, and pruning as well as specific growing information for each genus. Includes an in-depth glossary of horticultural terms.

Cole, Trevor, Christopher Brickell, and Elvin McDonald, eds. *American Horticultural Society Encyclopedia of Gardening: The Definitive Practical Guide to Gardening Techniques, Planning, and Maintenance*. New York: Dorling Kindersley, 2000. This definitive guide is organized into four sections, including creating a garden, which discusses garden style, scale, proportion, and use of color and texture; a plant catalog, profiling four thousand plants by plant type, growing season, and color of flowers or foliage; a plant dictionary of more than eight thousand terms; and an index of about twenty-five hundred common names.

Coombes, Allen J. *Dictionary of Plant Names*. Port Jervis, N.Y.: Lubrecht & Cramer, 1985. Main entries for common plants are alphabetically arranged by genus name, with species listed under each genus. Includes references, from common names and synonyms to scientific names. Gives pronunciation, meaning, derivation of scientific name, family, common name, country of origin, and hardiness.

Gledhill, David. *The Names of Plants*. 2d ed. New York: Cambridge University Press, 1989. The first part chronicles how the naming of plants has changed over time and why the changes were necessary. The second part is a glossary of genus and species names with brief definitions.

Huxley, Anthony, and Mark Griffiths, eds. *The New Royal Horticultural Society Dictionary of Gardening*. New York: Nature, 1999. 4 vols. This is an affordable paperback edition of the standard horticultural reference originally published in 1992. Comprehensive in scope, its authority is assured by the credentials of the 250 internationally recognized contributors. Presents botanical accounts of some fifty thousand plants grown worldwide in domestic gardens, commercial operations, or in special collections.

Liberty Hyde Bailey Museum. *Hortus Third: A Concise Dictionary of Plants Cultivated in the United States and Canada*. Originally compiled by Liberty Hyde Bailey and Ethel Zoe Bailey. New York: Macmillan, 1976. Still considered one of the foremost encyclopedias on plants, this compendium presents an alphabetical listing of Latin plant names along with physical descriptions. Includes a common name index and glossary.

Maberely, D. J. *The Plant Book: A Portable Dictionary of the Vascular Plants*. 2d ed., completely revised. New York: Cambridge University Press, 1997. The more than twenty thousand entries combine taxonomic details with English names and uses for every family and genus of flowering plant as well as ferns and other pteridophytes.

Stearn, William T. *Stearn's Dictionary of Plant Names for Gardeners*. Poole, Dorset, England: Cassell PLC, 1996. This technical dictionary includes concise definitions, six thousand botanical terms, and three thousand common names with cross references. Covers plant names, Greek and Latin botanical terms and derivations, and individuals associated with plant nomenclature. Added features are introductory essays on botanical and vernacular names.

Wiersema, John H., and Leon Blanca. *World Economic Plants: A Standard Reference*. Boca Raton, Fla.: CRC Press, 1999. Lists scientific name, synonyms, common names, economic uses, and geographical distribution of some ten thousand vascular plants of worldwide commercial importance. This comprehensive compilation satisfies the information needs of a global economy.

Biotechnology

Bhojwani, S. S., and M. K. Razdan. *Plant Tissue Culture: Theory and Practice*. Rev. ed. New York: Elsevier, 1996. Covers the development of plant tissue culture and its evolution into one of the major components of biotechnology.

Callow, J. A., B. V. Ford-Loyd, and H. J. Newberry, eds. *Biotechnology and Plant Genetic Resources: Conservation and Use*. New York: Oxford University Press, 1997. Discusses development of techniques for manipulating plant genomes and their application to the assessment, conservation, and use of plant genetic variation.

Lurquin, Paul F. *The Green Phoenix: A History of Genetically Modified Plants*. New York: Columbia University Press, 2001. This historical narrative details the development of transgenic plants, including development of biotechnological techniques, scientific controversies, ethical and philosophical issues, and work of individuals and groups of scientists. Includes an extensive bibliography.

McHughen, Alan. *Pandora's Picnic Basket: The Potential and Hazards of Genetically Modified Foods*. New York: Oxford University Press, 2000. Explains in a clear, straightforward style the technologies involved in genetically modified foods and discusses relevant issues such as labeling, popular misconceptions, regulatory issues, safeguards, patenting, and environmental impact.

Martineau, Belinda. *First Fruit: The Creation of the Flavr Savr Tomato and the Birth of Genetically Engineered Food*. New York: McGraw-Hill, 2001. Relates the "rise and fall" of the first whole food produced through genetic engineering that was actually marketed. Assesses the benefits and risks of this new technology.

Tant, Carl. *Plant Biotech: The New Turn-On*. Angleton, Tex.: Biotech, 1991. Features the fundamentals of gene and genome organization in plant cells, basic techniques used in tissue culture and cloning, gene transfer, and molecular markers. Also discusses intellectual property rights.

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Allard, Robert W. *Principles of Plant Breeding*. 2d ed. New York: John Wiley & Sons, 1999. Offers the most recent and detailed information on plant reproduction.

Cassells, Alan C., and Peter W. Jones. *The Methodology of Plant Genetic Manipulation: Criteria for Decision Making*. Hingham, Mass.: Kluwer Academic, 1995. Presents classical breeding methods as well as new techniques based on the integration of plant cell biology and molecular biology. The fifty-five papers also explain how the choice of breeding technique is limited by the breeding system of the crop, the breeding objective, and applicable tissue culture systems.

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Ayensu, Edward S., and Robert A. Defilipps. *Endangered and Threatened Plants of the United States*. Washington, D.C.: Smithsonian Institution Press, 1978. Prepared by the Smithsonian Institute in response to the Endangered Species Act of 1973, which requested both a review of plant species that were or might become endangered or threatened and recommendations or methods of conserving the identified species.

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Beacham, Walton, Frank Castronova, and Suzanne Sessine, eds. *Beacham's Guide to Endangered Species of North America*. Farmington Hills, Mich.: Gale Group, 2000. Provides basic information on all (about twelve hundred) plants and animals on the U.S. Fish and Wildlife Service list of federally endangered or threatened species as of April, 2000. Entries are arranged by taxonomic group and include both common and scientific names, descriptions, behavior, habitats, distribution, threats, conservation and recovery, contacts, and references. Most entries include color photographs.

Leavell, Chuck. *Forever Green: The History and Hope of the American Forest*. Marietta, Ga.: Longstreet Press, 2001. Discusses progress in forest management and promotes the wise use and conscientious renewal of wood, a critical natural resource.

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Ayala, Francisco J., Walter M. Fitch, and Michael T. Clegg, eds. *Variation and Evolution in Plants and Microorganisms: Toward a New Synthesis Fifty Years After Stebbins*. Washington, D.C.: National Academy Press, 2000. Features papers presented at a colloquium honoring George Ledyard Stebbins, who extended the synthetic theory of evolution to plants.

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Plant Products

Balik, Michael J., Elaine Elisabetsky, and Sarah A. Laird, eds. *Medicinal Resources of the Tropical Forest: Biodiversity and its Importance to Human Health*. New York: Columbia University

Press, 1995. The contributed papers survey the literature on medicinal uses of tropical plants. Coverage includes ethnobotany, biodiversity, ethnomedicine, and pharmacognosy. Regional work covers Africa, Asia, the Caribbean, and Central and South America. This readable work should appeal to the general public.

Buchanan, Rita. *A Weaver's Garden: Growing Plants for Natural Dyes and Fibers*. Mineola, N.Y.: Dover, 1999. Supplies helpful hints for weavers, gardeners, textile artists, and those involved with various crafts. Buchanan, a botanist and weaver, instructs readers on both growing and using plants and their products.

Crackower, Sydney, Barry A. Bohn, and Rodney Langlinais. *Two M.D.'s and a Pharmacist Ask, "Are You Getting it Five Times a Day?": Fruits and Vegetables, Enzymes, Antioxidants, and Fiber*. Rev. ed. Prescott, Ariz.: One World Press, 1999. This is an easy to read presentation on the benefits of fruits and vegetables in the human diet. Sample chapters in the table of contents include free radicals, aging and cancer; beta-carotene, promoter of healthy bodies; vitamin C for support and shape; vitamin E, the most versatile antioxidant; fiber and the digestive system; aging and the retina; the power of garlic; and indoles and breast cancer.

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Anderson, Miles. *The Ultimate Book of Cacti and Succulents*. London: Lorenz Books, 1998. The botany and classification of cacti and succulents, as well as their diversity, is detailed in this comprehensive volume. Features a photographic plant directory and a section on cultivation, including buying and techniques for planting propagation, grafting, and maintenance.

Armitage, Allan M. *Herbaceous Perennial Plants: A Treatise on their Identification, Culture, and Garden Attributes*. 2d ed. Champaign, Ill.: Stipes, 1997. Describes ordinary and rare perennials, with a limited number of photographs and other illustrations.

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Botanica's Annuals and Perennials. San Diego: Laurel Glen, 1999. A comprehensive alphabetic guide to more than two thousand flowering plants, including annuals, biennials, and perennials. Features some twenty-five hundred color illustrations as well as a handy reference table and an index of common names and synonyms.

Botanica's Trees and Shrubs. San Diego: Laurel Glen, 1999. Identifies more than two thousand plants and provides information on cultivation in different climates and soil conditions. Format and added features are similar to the work on annuals and perennials.

Brown, Lauren. *Grasses: An Identification Guide*. Boston: Houghton Mifflin, 1992. The first popular book on grasses that focuses on plant color, shape, and texture while avoiding technicalities. Presents the history, ecology, and uses of 135 grass species.

Bruneton, Jean. *Toxic Plants: Dangerous to Humans and Animals*. Andover, England: Intercept, 1999. Meets the needs of physicians, pharmacists, and veterinarians for reliable information on managing accidental ingestion of toxic plants. Describes risks, plant identification, symptoms, toxin identification, toxic doses, toxic mechanisms, and medical treatments. The specifics of animal poisoning, concentrates on pets.

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Dirr, Michael A. *Dirr's Hardy Trees and Shrubs: An Illustrated Encyclopedia*. Portland, Oreg.: Timber Press, 1997. This illustrated guide describes the best trees and shrubs for cooler climates, that is, U.S. Department of Agriculture Hardiness Zones 3 to 6. Includes more than five hundred species, some seven hundred additional cultivars, and more than sixteen hundred color photographs.

Heywood, V. H., ed. *Flowering Plants of the World*. New York: Oxford University Press, 1993. Includes more than three hundred entries on angiosperms (flowering plants), taxonomically arranged and generously illustrated. Covers distribution, diagnostic features, classification, and economic uses. Main entries are supplemented by an extensive glossary and an introduction to the forms, structure, ecology, and classification of flowering plants.

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Jones, David L. *Encyclopedia of Ferns*. Vol. 1. Portland, Oreg.: Timber Press, 1992. The botanical information and descriptions of more than seven hundred ferns are intended for a general audience. Worldwide in scope, the volume covers both tropical and temperate ferns. Includes color plates, line drawings, glossary, and an international list of fern societies and study groups.

Jordan, Peter, and Steven Wheeler. *The Practical Mushroom Encyclopedia: Identifying, Picking, and Cooking with Mushrooms*. Mount Carmel, Conn.: Southwater, 2000. Describes mushrooms and their anatomy and describes the where, when, and how of mushroom collecting as well as differentiating between edible and poisonous mushrooms. Supplemented with recipes, glossary, and indexes.

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Nicholson, Barbara. *The Oxford Book of Flowerless Plants: Ferns, Fungi, Mosses and Liverworts, Lichens, and Seaweeds*. London: Oxford University Press, 1996. Surveys nonflowering plants, such as ferns, mosses, and liverworts as well as lichens.

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Sajeva, Maurizio, and Mariangela Costanzo. *Succulents: The Illustrated Dictionary*. Portland, Oreg.: Timber Press, 1997. Catalogs succulent varieties from 195 genera. Contains twelve hundred excellent photographs to aid in accurate identification, with captions covering description, size, origin, alternate names, and endangered status.

Schenk, George H. *Moss Gardening: Including Lichens, Liverworts, and Other Miniatures*. Portland, Oreg.: Timber Press, 1997. A color-illustrated treatise on gardening with moss species. Includes fifteen chapters covering topics including transplanting, propagating, and uses as ground covers, in containers, and bonsai.

Shaw, A. Jonathan, and Bernard Goffinet. *Bryophyte Biology*. New York: Cambridge University Press, 2000. Presents an overview of the morphology, systematics, ecology, and evolution of hornworts, liverworts, and mosses. Text is comprehensive yet succinct and contains good illustrations.

Symonds, George W. *The Shrub Identification Book*. New York: William Morrow, 1980. An aid to visual identification and recognition of shrubs, vines, and ground covers. The 3,550 photographs of leaves, flowers, twigs, and bark are true to size.

Thomas, Peter. *Trees: Their Natural History*. New York: Cambridge University Press, 2000. Written for a nontechnical audience, this book presents a comprehensive introduction to all aspects of tree biology and ecology.

Van Gelderen, D. M., with Will Smith. *Conifers: The Illustrated Encyclopedia*. Updated ed. 2 vols. Portland, Oreg.: Timber Press, 1996. Volume 1 contains brief descriptions of the sixty-five genera of *Ginkgophyta*, *Coniferophyta*, and *Gnetophyta*. The second volume consists of photographs and short captions for individual species, alphabetically arranged by scientific name. Additional features are hardiness-zone maps for Europe, North America and China, and indexes of common names and synonyms.

Processes and Structures

Agrios, George N. *Plant Pathology*. 4th ed. Orlando, Fla.: Morgan Kaufmann, 1997. This comprehensive text covers identification, treatment, and prevention of diseases caused by fungi, viruses, bacteria, and nematodes. Discusses epidemiology, genetics of resistance, and modern management practices.

American Horticultural Society. *Plant Propagation*. Edited by Alan Toogood. New York: Dorling Kindersley, 1999. This practical, beautifully illustrated guide details reproduction of plants by seeds, cuttings, grafting, division, and other methods of propagation. The extensive introduction explains the botany and physiology involved in propagation, while the encyclopedic, alphabetical entries describe appropriate techniques for propagation of more than one thousand plants.

Bowes, Bryan G. *A Color Atlas of Plant Structures*. Ames: Iowa State Press, 2000. Focusing on structure at the anatomical, histological, and fine-structure levels, this fundamental guide deals with developing and mature forms of plant life. The 380 illustrations that accompany the concise scientific text include color photographs as well as line drawings.

Dickinson, William C. *Integrative Plant Anatomy*. New York: Academic Press, 2000. Information on the developmental and comparative study of plant cells and tissues is consolidated into a single volume. Highlights the importance of understanding plant anatomy in order to solve present and future problems.

Druse, Ken. *Making More Plants: The Science, Art, and Joy of Propagation*. Toronto: Crown, 2000. Addresses all of the components of propagation, including sowing, vegetative reproduction, layering, leaf and stem cutting, bulb division, and grafting. The text is accompanied by more than five hundred full-color illustrations.

Fenner, Michael, ed. *Seeds: The Ecology of Regeneration in Plant Communities*. 2d ed. New York: Oxford University Press, 2001. The sixteen chapters written by international experts cover various pertinent topics, such as seed size, seedling establishment, fire and fire gaps in regeneration, maternal effects in seed development, the role of temperature in dormancy and germination, and the influence of seedling regeneration on plant communities and ecosystems.

Galston, Arthur W. *Life Processes of Plants: Mechanisms for Survival*. Gordonsville, Va.: W. H. Freeman, 1993. The preface describes this work as a plant physiology text "for the intelligent lay public." Written in a direct and conversational style, the book describes how plants live, react to stresses, and adapt when necessary. Includes illustrations, bibliographies for each chapter, and a general index.

Glass, Anthony. *Plant Nutrition: Introduction to Current Concepts*. Sudbury, Mass.: Jones & Bartlett, 1989. This text introduces the topic of plant nutrition to undergraduate students in botany, biology, soil science, or agriculture.

Hall, David O., and Krishna Rao. *Photosynthesis*. 6th ed. New York: Cambridge University

Press, 1999. This is an advanced treatise, providing a clear and concise introduction to a complex process. Includes line illustrations and color plates.

Hartmann, Hudson T., Dale Kester, Fred Davies, and Robert Geneve. *Plant Propagation: Principles and Practice*. 7th ed. Old Tappan, N.J.: Prentice Hall PTR, 2002. This extremely successful text covers the art and science of both the sexual and asexual aspects of plant propagation. This edition includes new information on advances in biotechnology and their revolutionary impact on plant propagation.

Horst, R. Kenneth, ed. *Westcott's Plant Disease Handbook*. 6th ed. Boston: Kluwer Academic, 2001. Gardeners, botanical gardens, landscape architects, florists, nurserymen, seed and fungicide dealers, pesticide applicators, arborists, cooperative extension agents, pathologists, diagnostic laboratories, and consultants should benefit from the newly revised edition of this authoritative reference. Provides diagnostic and disease control information on about twelve hundred host plants and twenty-four thousand plant diseases. The scope is worldwide but emphasizes the continental United States.

Ingram, David S., and N. Robertson. *Plant Disease: A Natural History*. Rev. ed. New York: HarperCollins, 1999. Covers all aspects of disease of plants, both cultivated and growing in the wild. Examines the causes of plant diseases and the methods of pathogenicity and disease resistance in plants. Symptoms of diseases caused by fungi, viruses, and bacteria are discussed.

Lyndon, Robert. *Plant Development: The Cellular Basis*. Florence, Ky.: Thomson Learning, 1990. Explains the genetic and molecular control of vegetative development in higher plants.

Raven, Peter H., Ray F. Evert, and Susan E. Eichhorn. *Biology of Plants*. 6th ed. New York: W. H. Freeman/Worth, 1999. The plant kingdom is discussed, with emphasis on plant growth and development, evolutionary relationships, and the dependence of humans on plants.

Special Adaptations

Anderson, Roger B., and James S. Fralish, eds. *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. New York: Cambridge University Press, 1999. Summarizes the available technical information on these plant communities and organizes it by eastern/southeastern, central/Midwestern, western/southwestern, and northern regions. Discusses climate, geology, and soil as well as current and historic vegetation.

Chapman, A. R. *Functional Diversity of Plants in the Sea and on Land*. Sudbury, Mass.: Jones & Bartlett, 1986. Introduces the plant taxa and examines the history of plant life from an aquatic environment to various land types. Topics include phytoplankton in the sea, seaweeds, terrestrial conditions and plant life, mechanical properties of land plants, water absorption and loss, carbon dioxide exchange and vascular transport, drought avoidance in desert plants, reproduction in vascular plants, systematic survey, and evolutionary history of vascular plants, bryophytes, and fungi.

Crow, Garrett E., C. Barre Hellquist, and Norman C. Fassett. *Aquatic and Wetland Plants*. Rev. ed. 2 vols. Madison: University of Wisconsin Press, 2002. A revision of the 1940 classic, this illustrated guide to native and naturalized vascular plants growing in aquatic and wetland habitats covers 1,139 species and includes six hundred pages of black-and-white drawings.

Dawes, Clinton J. *Marine Botany*. 2d ed. New York: John Wiley & Sons, 1998. Discusses the diversity and ecology of marine wetland plants and habitats, algae, sea grasses, mangroves, salt marshes, phytoplankton, and benthic communities. Focuses on abiotic, biotic, and anthopogenic influences on marine-plant life.

Duffield, Mary Rose, and Warren Jones. *Plants for Dry Climates: How to Select, Grow, and Enjoy*. 2d ed. Boulder, Colo.: Perseus, 2001. Offers complete descriptions of more than three hundred species of low-maintenance and drought-resistant plants. Includes 430 color photographs as well as useful charts to assist in selection of appropriate plants.

Eleuterius, Lionel N. *Tidal Marsh Plants*. Dunlap, Ill.: Firebird Press Books, 1990. Describes four hundred vascular plants that grow in the salt marshes along the Gulf and Atlantic coasts of the United States. Entries include drawings of plants, their location, scientific and common names, and identifying traits.

Redington, Charles B. *Plants in Wetlands*. Dubuque, Iowa: Kendall/Hunt, 2000. Considers the biological interactions among plants and the full range of animal groups in wetlands. Describes more than one hundred plant species and includes a simple wetlands delineation method and a key to wetland communities as well as appendices on spiders, community interactions, and human and economic uses.

Smith, Stanley D., Russell K. Monson, Jay E. Anderson, and S. D. Smith. *Physiological Ecology of North American Desert Plants*. New York: Springer-Verlag, 1966. Characterizes the physical and biological aspects of the four North American deserts and provides a comprehensive review of the primary adaptation patterns of desert plants to environmental stress.

Zwinger, Ann H., and Beatrice E. Willard. *Land Above the Trees: A Guide to American Alpine Tundra*. Rev. ed. Boulder, Colo.: Johnson Books, 1996. The first section of this work details the nine biological zones encountered at 12,000 feet and above: tree limit and krummholz, boulder fields, talus and scree slopes, fell fields, alpine meadows and turfs, snowbed and snow communities, and alpine heath communities. The second section describes the alpine areas in the United States: the Southern Rockies, the Presidential Range in New England, the Great Basin ranges, the Northern Rockies, Northern Cascades, Olympic Mountains, Southern Cascades, and Sierra Nevadas.

Miscellaneous Texts

Musgrave, Toby, Christina Gardner, and William Musgrave. *The Plant Hunters: Two Hundred Years of Adventure & Discovery Around the World*. London: Ward Lock, 1999. Details the adventures of daring explorers as they gathered plants from all over the world and introduced some seven thousand plant species into habitats that they would never have reached naturally. Features Sir Joseph Banks, who established a "systematic, worldwide plant hunting program" during the eighteenth century at Kew Gardens, London, as well his protégé Francis Mason and seven others who carried this work into the nineteenth century.

Pollan, Michael. *The Botany of Desire: A Plant's Eye View of the World*. Westminster, Md.: Random House, 2001. An original and entertaining narrative that tells the story of four domesticated species—the apple for sweetness, tulips for beauty, marijuana for intoxication, and potatoes for control—from the viewpoint of the plant.

Tomkins, Peter, and Christopher O. Bird. *The Secret Life of Plants*. New York: Harper Trade, 1989. Treats the relationship of plants to humankind, as revealed through scientific discoveries.

WEB SITES

The sites listed below were visited by the editors of Salem Press in March of 2002. Because URLs frequently change or are moved, their accuracy cannot be guaranteed; however, long-standing sites—such as those of university departments, national organizations, and government agencies—generally offer links when sites move or otherwise may upgrade their offerings and hence remain useful. Moreover, sites often provide lists of links to other useful resources on the Internet. Sites with an affiliation of N/A are, to our knowledge, unallied, mounted by an individual person, or "uncredited."

Roger Smith

GENERAL

AgNIC Plant Science Home Page
http://www.unl.edu/agnicpls/agnic.html
Affiliated with: University of Nebraska, Lincoln
- An information resource that fields questions from users and posts information about genetics, taxonomy, plant protection, and crop products, with links and directions to e-journals and e-newsletters.

The Biota of North American Program
http://www.bonap.org/
Affiliated with: North Carolina Botanical Garden, University of North Carolina, Chapel Hill
- Maintains a database of taxonomic, nomenclatural, and biogeographical data on North American vascular plants (and vertebrates) in order to develop a unified digital system for assessing the continent's species (north of Mexico).

Botanical Ecological Unit
http://www.fs.fed.us/biology/plants/beu.html
Affiliated with: U.S. Forest Service
- A virtual office with information on rare and threatened U.S. plants and environmental initiatives and with links to similar sites, experts, and publications.

Botanical Electronic News
http://www.ou.edu/cas/botany-micro/ben/
Affiliated with: N/A
- A professional e-journal covering a different topic in botany each month.

Botanical Glossaries
http://155.187.10.12/glossary/glossary.html
Affiliated with: Centre for Plant Biodiversity Research
- A list of links to online glossaries of botanical terms contained on Web sites in Australia and the United States.

Botany
http://www.nmnh.si.edu/departments/botany.html
Affiliated with: Department of Systematic Biology, Smithsonian Institution
- An extensive directory of online and print resources devoted to all aspects of botany, maintained by America's premier natural history institution. Contains a catalog of more than three thousand botanical illustrations.

Botany.com
http://www.botany.com/
Affiliated with: N/A
- An online encyclopedia for gardeners maintained by an e-commerce company. The site offers information about common and botanical names, pests and diseases, leaf shapes, and a botanical dictionary.

Botany Online: The Internet Hypertextbook
http://www.biologie.uni-hamburg.de/b-online/
Affiliated with: University of Hamburg, Germany
- A comprehensive online information source featuring the Internet Library, which teaches users about topics in botany and related subjects, directions about how to use the World Wide Web productively, and links. Designed for university students.

Centre for Plant Architecture Informatics
http://www.cpai.uq.edu.au/
Affiliated with: University of Queensland, Australia
- A sophisticated site containing images, virtual plants, and animations created by a collaboration of biologists, mathematicians, and computer scientists in order to aid research in the three-dimensional dynamics of plants.

Delta
http://biodiversity.uno.edu/delta/
Affiliated with: CSIRO, Australia
- A site for scientists involved with the DEscription Language for TAxonomy, or Delta, which records taxonomic descriptions of plants for computer analysis. Offers information on plants, lichen, soil, and some insects, primarily species in Australia and North America.

Electronic Sites of Leading Botany, Plant Biology, and Science Journals
http://www.e-journals.org/botany/
Affiliated with: e-journals.org
- Lists links to 750 journals from throughout the world devoted to plant sciences or related topics.

Food and Agriculture Organization
http://www.fao.org/
Affiliated with: United Nations
- Extensive informational resources, including texts, photos, and statistics, concerning agriculture and forestry, among other topics, for all users, in English, French, Arabic, and Chinese.

GardenNet
http://gardennet.com/
Affiliated with: N/A
- An information and shopping resource for gardeners listing plants by species and equipment, garden types, and events.

Index Nominum Genericorum
http://rathbun.si.edu/botany/ing/
Affiliated with: The Smithsonian Institution and the International Association for Plant Taxonomy
- Provides a search engine for a database of the generic names of all recorded plants. The database offers information about their classification and nomenclature and bibliographical citations.

Integrated Taxonomic Information System
http://www.itis.usda.gov/
Affiliated with: U.S. Department of Agriculture
- Guides users to taxonomic information, focusing especially on North American species but also with links to resources worldwide. Its search engine supports searches by common or scientific name.

International Organization for Plant Information
http://iopi.csu.edu.au/iopi/
Affiliated with: International Union of Biological Sciences
- Affords general botanical information through databases and links to similar sites and hosts three projects: the Global Plant Checklist, Species Plantarum Project (concerning publications about plants of the world), and Database of Plant Databases. Designed with scientists in mind.

The International Plant Names Index
http://www.ipni.org/
Affiliated with: The Royal Botanic Gardens, Kew; Harvard University Herbaria; Australian National Herbaria
- Contains a database of the names and bibliographical references for all recorded seed plants, continually updated, for general use.

Internet Directory for Botany
http://www.botany.net/IDB
Affiliated with: SHL Systemhouse, Edmonton, Canada
- Offers alphabetical and subject category searches for botanical information in Web sites of arboreta, botanical gardens, herbaria, botanical societies, and botanical research institutes. Created and maintained by scientists in the United States, Finland, and Canada primarily for colleagues worldwide.

MedBioWorld
http://www.medbioworld.com/bio/journals/plants.html
Affiliated with: N/A
- Provides links to more than one hundred journals about the plant sciences from throughout the world and has search engines for abstracts, articles, and images.

Natural Perspective
http://www.perspective.com/nature/index.html
Affiliated with: N/A
- For general users, a site describing the characteristics of organisms in four taxonomic kingdoms, including one for plants and one for fungi.

Plant Facts
http://plantfacts.ohio-state.edu/
Affiliated with: Ohio State University
- Hosts two search engines: one that guides users to university and government sites in the United States and Canada for answers to plant-related questions; a second helps prospective students obtain admissions and degree information from forty university departments in the United States.

Plant Information Systems
http://www.wes.army.mil/el/squa/cdroms.html
Affiliated with: Army Corps of Engineers
- Access page to two repositories of information: one covering identification and management of more than sixty aquatic and wetlands plant species; another concerning more than sixty noxious and nuisance species.

The Plants Database
http://plants.usda.gov./topics.html
Affiliated with: Natural Resources Conservation Service, U.S. Department of Agriculture
- Performs searches of the PLANTS database for taxonomy, life form and nativity, legal status, images, and conservation plant characteristics, all for the general public. Also informs farmers and homeowners about alternative crops; provides the taxonomic hierarchy for any vascular plant, North American nonvascular plant, or lichen; discusses the usage, management, and importance of culturally significant plants; and lists hundreds of links.

Species 2000
http://www.sp2000.org
Affiliated with: Global Biodiversity Information Facility
- Part of the attempt to catalog all species of life on earth, this site offers a species locator, catalog of life, checklist, and name location service and explains the initiative's technical plan. Also, lists links to mirror sites.

The Virtual Library of Botany
http://www.ou.edu/cas/botany-micro/www-vl/
Affiliated with: University of Oklahoma
- Lists hundreds of Web links and newsgroups worldwide that treat topics in botany, agriculture, and other biosciences.

W3 Tropicos
http://mobot.mobot.org/W3T/search/image/imagefr.html
Affiliated with: Missouri Botanical Gardens
- Hosts a search engine for information on plant species and a large resource list, arranged by plant taxa, of drawings, photos of living plants, and photos of specimens in the holdings of museums and libraries.

AGRICULTURE, FORESTRY, AND HORTICULTURE

AGRICOLA
http://www.nal.usda.gov/ag98/
Affiliated with: National Agricultural Library, U.S. Department of Agriculture
- The online catalog for the National Agricultural Library's holdings—including books, serials, and audiovisual materials—about plants. The holdings themselves are not available online but can be delivered by mail.

Center for Subtropical Agroforestry
http://cstaf.ifas.ufl.edu/
Affiliated with: University of Florida
- A research resource for scientists and landowners developing the technology of raising trees as crops, with links and a newsletter.

CPM Magazine
http://www.crop-net.com/cpmmagazine/Rooms/Home Page
Affiliated with: N/A
- Collects and posts information for the agricultural industry about weeds, diseases, and insects affecting crops.

4Plants.com
http://4plants.4anything.com/
Affiliated with: 4Anything Network
- Maintains information about gardening and medicinal and poisonous plants for the general public.

Hortiplex
http://plants.gardenweb.com/plants/
Affiliated with: Garden Web
- A search engine dedicated to browsing the entire Web for information about plants that filters out nonplant-related hits. Designed for nonspecialists, with a glossary of botanical terms.

Internet Guidepost for Plant Production
http://www.fb.u-tokai.ac.jp/plant/production
Affiliated with: Tokai University, Japan
- A search engine for resources about agriculture, horticulture, botany, and gardening worldwide, with an emphasis upon Japan, for plant sciences researchers.

National Agroforestry Center
http://www.unl.edu/nac/
Affiliated with: U.S. Department of Agriculture
- Instructs public on agroforestry, which combines agriculture and forestry technologies for sustainable land use.

National Plant Germplasm System
http://www.ars-grin.gov/npgs/
Affiliated with: U.S. Department of Agriculture
- Supports a cooperative effort of federal, state, and private organizations helping scientists preserve the genetic diversity of crop plants. Offers search engines concerning crop science, plant variety, and taxonomy and accepts requests for germplasm (genetic material) for research.

Plant Search
http://www.ag.auburn.edu/landscape/database/search.php3
Affiliated with: Auburn University
- Provides a database allowing users to type in common names and call up color photos, descriptors, and information about the horticultural use of plants.

Plants for a Future
http://www.scs.leeds.ac.uk/pfaf/index.html
Affiliated with: N/A
- Contains articles, fact sheets, links, and a database of about seven thousand plants, all to promote research and provide information on ecologically sustainable horticulture. Maintained by a British charitable organization.

BOTANICAL GARDENS AND COLLECTIONS

Botanical Garden and Botanical Museum Berlin-Dahlem
http://www.bgbm.fu-berlin.de/
Affiliated with: Free University, Berlin, Germany
- An extensive collection, begun more than three hundred years ago, and among the world's largest today. This home page tells users about its plants, events, the affiliated museum, and research at the site.

Botanique
http://www.botanique.com/
Affiliated with: N/A
- A guide to gardens, arboreta, and nature sites for the public. It lists more than 2,300 in North America, with a search program by type of facility or by state, and has a list of events and links.

Desert Botanical Garden
http://www.dbg.org/
Affiliated with: N/A
- A Phoenix, Arizona, facility that opened in 2002. The site covers the garden's collection and events and has information about desert gardening in general, research, and conservation.

Lady Bird Johnson Wildflower Center
http://www.wildflower.org/index.html
Affiliated with: N/A
- Although concerned primarily with wildflowers in Texas, the Web site for the former first lady's botanical center is well designed and offers information on species and a special page for children.

Missouri Botanical Garden
http://www.mobot.org/
Affiliated with: N/A
- A leading American botanical garden, located in St. Louis. The Web site presents information about the collection as well as help to gardeners and pages devoted to its history, horticulture, the Shaw Nature Reserve, images, and a schedule of plants in bloom.

Montreal Botanical Garden
http://www2.ville.montreal.qc.ca/jardin/en/menu.htm
Affiliated with: N/A
- A well organized Web site, listing information about the collection, activities, and scientific programs and with images of particularly lovely specimens, although some of the related text is available only in French.

The National Garden
http://www.nationalgarden.org/
Affiliated with: United States Botanical Garden
- Located in Washington, D.C., the oldest continuously operated botanical garden in the United States. The Web site is devoted to the collection and its associated facilities.

National Tropical Botanical Garden
http://www.nthg.org/
Affiliated with: N/A
- An association of three preserves and four gardens in south Florida and Hawaii. The site contains information about the location, collections, and events schedule for each facility, a generous summary of each issue of *Plant Talk*, the organization's magazine, and pages featuring news stories and research.

The New York Botanical Garden
http://www.nybg.org/
Affiliated with: N/A
- Describes the extensive gardens, located in the Bronx, New York City, and activities there but also maintains pages about gardening and data on plants.

Royal Botanical Gardens
http://www.rbg.ca/
Affiliated with: N/A
- Located in Ontario, Canada's premier botanical garden. The home page concerns the collection, activities, and educational resources.

Royal Botanic Gardens, Kew
http://www.rbgkew.org.uk/index.html
Affiliated with: RBG, Kew
- Home page of one of the most prestigious and scientifically successful botanical gardens in the world, offering database resources consonant with its mission to develop worldwide collections, foster research, support conservation, and inform the general public. Major categories of information include science and horticulture, botanical collections, conservation and wildlife, education, and data and publications.

University of California Botanical Garden
http://www.mip.berkeley.edu/garden/
Affiliated with: University of California, Berkeley
- Introduces users to the extensive botanical collection and its history.

What Are Herbaria?
http://www.rom.on.ca/biodiversity/herbaria/herbwhat/html
Affiliated with: Centre for Biodiversity and Conservation Biology
- Explains the history and nature of collections of labeled, preserved plant specimens and offers extensive information about those in the Centre's collection.

FLORA

Bryophytes
http://bryophytes.plant.siu.edu/index.html
Affiliated with: Southern Illinois University at Carbondale
- Teaches about mosses, liverworts, and hornworts and gives information to those interested in studying them at Southern Illinois University in Carbondale's Department of Plant Biology.

Checklist of World Ferns
http://homepages.coverock.net.nz/~bj/fern/
Affiliated with: N/A
- Maintains well-ordered lists of information about the classification and description of ferns and their distribution worldwide.

Dendro Home
http://www.snr.vt.edu/dendro/dendrology/main.htm
Affiliated with: Virginia Polytechnic and State University
- Displays basic facts and photos of trees and tree structures for North American species and encourages users to ask questions of Dr. Dendro, the resident tree expert.

Find Wild Flowers
http://www.reticule.co.uk/flora/
Affiliated with: N/A
- A Web site for British flora. It enables users to identify wildflowers they have found by filling out a questionnaire that a computer program analyzes. It also offers a checklist of plants to be found in specific habitats.

Grassland Index
http://www.fao.org/ag/AGP/AGC/doc/Gbase/Default.htm
Affiliated with: Food and Agriculture Organization, United Nations
- Searches database by genus, Latin name, or common name for information on grasses and legumes. Includes a bibliography and photos of selected species.

Lichen Information System
http://lis.freeweb.supereva.it/index.htm?p
Affiliated with: N/A
- A collection of links to sites with information on lichen biology, collections, professional meetings, and organizations.

Manual of Grasses for North America North of Mexico
http://herbarium.usu.edu/GrassManual/default.htm
Affiliated with: Utah State University
- Supplies range maps, illustrations, and text descriptions of grasses.

Silvics of North America
http://www.na.fs.fed.us/spfo/pubs/silvics_manual/table_of_contents.htm
Affiliated with: U.S. Department of Agriculture
- An online manual reprinting edited research papers describing the characteristics of 127 trees, both hardwoods and conifers.

Vascular Family Plant Access Page
http://www.botany.hawaii.edu/faculty/carr/pfamilies.html
Affiliated with: University of Hawaii
- Intended to aid instructors, this site offers basic information, images, and diagrams concerning plant families and their phylogenetic relationships.

Wildland Shrubs of the United States and Its Territories
http://www.fs.fed.us/global/iitf/wildland_shrubs.htm
Affiliated with: U.S. Forest Service
- Contains downloadable files describing shrub species.

World Gymnosperm Database
http://www.botanik.uni-bonn.de/conifers/topics/big_index.htm
Affiliated with: University of Bonn, Germany
- A database containing extensive information, images, and range maps about conifers worldwide.

IMAGES

Cal's Plant of the Week
http://www.plantoftheweek.org/
Affiliated with: N/A
- Displays an image of a new species of plant each week, followed by information about its habitat, cultivation, propagation, and care.

Grass Images
http://www.csdl.tamu.edu/FLORA/image/poacr2ba.htm
Affiliated with: Texas A&M University and Hunt Institute for Botanical Documentation
- Preserves approximately 6,500 images of grass species, scanned from drawings.

Natural Resources Conservation Service Photo Gallery
http://photogallery.nrcs.usda.gov/PhotoGallery.asp
Affiliated with: U.S. Department of Agriculture
- Shows color photographs of plant species in the United States, searchable by category or state.

The Plant Kaleidoscope
http://www.biologie.uni-ulm.de/systax/dendrologie/index.html
Affiliated with: N/A
- Offers 665 color photos and 331 descriptions of rare and unusual plants cultivated in Europe.

U.S. Department of Agriculture Forest Service Collections
http://huntbot.andrew.cmu.edu/USDA/USDA.html
Affiliated with: Hunt Institute for Botanical Documentation
- Offers 2308 scanned ink drawings from the archives of the U.S. Forest Service, covering species in the continental United States, Puerto Rico, and the Virgin Islands.

FOR K-12 STUDENTS AND TEACHERS

Dragonfly
http://miavx1.muohio.edu/dragonfly/
Affiliated with: Miami University of Ohio
- An award-winning science Web site for children that includes articles on plants, the web of life, and trees. Also offers workshops for teachers.

The Mining Company's Botany Site
http://botany.miningco.com/cs/botany
Affiliated with: About.com
- Offers explanations of botanical concepts for students, teaching aids for teachers, images, an index of plants and herbs, and links.

Photosynthesis, Energy, and Life
http://www.ftexploring.com/photosyn/photosynth.html
Affiliated with: Flying Turtle
- Displays articles explaining how photosynthesis works and its importance to the environment, as well as links. A science site for grammar school children.

Tree World
http://www.domtar.com/arbre/english/start.htm
Affiliated with: Domtar and the Minister of Education of Québec
- Articles about the uses and conservation of trees, designed both for schoolchildren and their teachers.

The Tulip Project
http://www.uwlax.edu/faculty/gerber/
Affiliated with: University of Wisconsin, La Crosse
- Contains guidance for the improvement of K-12 education about plants by providing information and suggesting activities for teachers, with links to similarly dedicated sites.

USDA for Kids
http://www.usda.gov/news/usdakids/index.html
Affiliated with: U.S. Department of Agriculture
- Among other topics, offers children information about agriculture, food, gardening, and conservation.

ORGANIZATIONS

American Bryological and Lichenological Society
http://www.unomaha.edu/~abls/
Affiliated with: N/A
- Mainly offers information and activities for members of the society, which is made up of scientists interested in mosses and lichens, but has a large listing of links to other resources about bryology and botany in general.

The American Fern Society
http://www.amerfernssoc.org/
Affiliated with: N/A
- Provides information to its international membership and arranges exchange of specimens. Also has links and a forum where members post remarks on topics of current interest.

American Forests
http://www.americanforests.org/
Affiliated with: N/A
- The home page for an environmental organization encouraging the planting and preservation of trees. Includes history, information about purchasing and planting trees, images, and resources for children.

The American Society for Horticultural Science
http://www.ashs.org/
Affiliated with: N/A
- Provides information, links, and publications for members of the society, which include scientists, educators, growers, and field agents.

The American Society of Plant Biologists
http://www.aspb.org/
Affiliated with: N/A
- Offers information about the society and its publications and activities to the university students and scientists that make up its membership. Also

has a large list of links to related academic and government sites.

American Society of Plant Taxonomists
http://www.sysbot.org/
Affiliated with: N/A
- Provides information on the society's activities for scientists, including its journal, newsletter, and monograph series, all addressing topics in taxonomy.

APSnet
http://www.apsnet.org/
Affiliated with: The American Phytopathological Society
- Displays society information about activities, research, educational and job opportunities, and links for its international membership of scientists who study plant diseases.

ASC Web
http://www.nscalliance.org/
Affiliated with: Natural Science Collections Alliance
- Site of a nonprofit organization, formerly called the Association of Systematics Collections, for the international community of museums, botanical gardens, herbariums, and institutions with natural science collections. Offers society news, links, information about collections, and databases.

Botanical Society of America
http://www.botany.org/
Affiliated with: N/A
- Maintains pages that support the purpose of the society: to foster formal and informal education about plants and research, to supply expertise for issues connected to ecosystems, and to expand communications among scientists and between scientists and the public. Directs visitors to print publications, conferences, career opportunities, and links. Offers eight hundred botanical images for instructional use.

The Botanical Society of the British Isles
http://www.rbge.org.uk/Introduction.php
Affiliated with: N/A
- In addition to society news, provides information and atlases about British and Irish flowering plants and ferns, along with links.

California Native Plant Society
http://www.cnps.org/
Affiliated with: N/A
- Provides information about the society's programs, including plant inventory and conservation campaign, but also has a photo gallery and a site for kids that explains botanical concepts.

The Ecological Society of America
http://www.esa.org/
Affiliated with: N/A
- Offers information, links, and notice of the nonprofit society's activities, which are to help ecologists share information and raise public awareness about biotechnology, ecosystem management, species extinction and habitat destruction, and sustainable systems.

The Herb Society of America
http://www.herbsociety.org/
Affiliated with: N/A
- Information resources, links, and descriptions of projects and meetings for a nonprofit organization dedicated to the cultivation of herbs and study of their history and uses.

International Association for Plant Taxonomy
http://www.botanik.univie.ac.at/iapt/
Affiliated with: N/A
- Fosters projects by systematic botanists, especially those related to classification and nomenclature, and acts as a repository of information to be shared by scientists worldwide.

International Oak Society
http://www.saintmarys.edu/~rjensen/ios.html
Affiliated with: N/A
- Informs members about the status of the society's efforts to advance scientific knowledge about oaks and their preservation.

International Palm Society
http://www.palms.org/
Affiliated with: N/A
- In addition to society business, contains images, links, a bulletin board, and online articles about palm trees.

The Mycological Society of America
http://www.erin.utoronto.ca/~w3msa/
Affiliated with: N/A

- Updates members on society news and publications and offers a bulletin board and links.

National Arbor Day Foundation
http://www.arborday.org/
Affiliated with: N/A
- An rich home page with information about the name, habitat, and care of trees in the United States; Arbor Day activities; resources for children; and images.

National Gardening Association
http://www.garden.org/
Affiliated with: N/A
- A nonprofit organization. The site guides gardeners to information resources, maintains a bulletin board for members, and offers an online newsletter.

The Phycological Society of America
http://www.psaalgae.org/
Affiliated with: N/A
- A professional organization devoted to the study of algae. The site primarily concerns society affairs but has links to related resources.

Plant Conservation Alliance
http://www.nps.gov/plants/index.htm
Affiliated with: N/A
- A Web site supported by ten federal agencies and more than 145 nongovernmental contributors, including organizations of biologists, botanists, habitat preservationists, horticulturists, and soil scientists working to prevent native plant extinction and habitat restoration. Lists ongoing projects, publications, meetings, and links.

Society for Economic Botany
http://www.econbot.org/home.html
Affiliated with: N/A
- A professional organization dedicated to scientific research and education regarding the uses of plants and the relationship between people and plants. The site concerns society business, but its online journal is downloadable.

Society of American Foresters
http://www.safnet.org/index.shtml
Affiliated with: N/A
- A professional organization's site that fosters exchange of information about forestry science, posts the latest news about forestry and ecology, and offers aids to education.

SPECIALTY SITES

The Arabidopsis Information Resource
http://www.arabidopsis.org/home.html
Affiliated with: A consortium of university departments and government agencies
- Supplies the means for plant scientists to search a database containing the completely decoded genome of the weed *Arabidopsis thaliana*, a widely used model plant and the first plant species to be genetically sequenced.

Atlas of the Flora of New England
http://www.herbaria.harvard.edu/~rangelo/Neatlas0/WebIntro.html
Affiliated with: Harvard University Herbaria
- A repository of basic ecological information and range maps of ferns, mosses, flowering plants, gymnosperms, and grasses in New England.

Carnivorous Plant Database
http://www2.labs.agilent.com/bot/cp_home
Affiliated with: Agilent Labs
- Presents slide shows, photographs, and a database with taxonomic, descriptive, and habitat information about more than three thousand plants that eat insects.

Center for Aquatic and Invasive Plants
http://aquat1.ifas.ufl.edu/
Affiliated with: University of Florida
- Contains images, drawings, basic information, and a bibliographic database, with links to full-text articles, concerning freshwater and wetland plants (about 55,000 citations in all). Also has links and articles about plant management.

ESA Panel of Vegetation Classification
http://esa.sdsc.edu/vegwebpg.htm
Affiliated with: Ecological Society of America
- Affords access to information about the program for experts and organizations that are part of an effort to develop a science-based national classification system, which is intended to aid research and conservation.

Exotic and Invasive Weeds Research Unit
http://wric.ucdavis.edu/exotic/exotic.htm
Affiliated with: U.S. Department of Agriculture
- Provides technical information and cites professional articles about plants introduced into the United States from other environments, along with photographs and links to other resources. Geared to botanists and agricultural scientists.

Herbal Information Resource
http://www.stevenfoster.com/education/index.html
Affiliated with: Steven Foster Group
- Collects monographs and links regarding plants that can be used as food, medicine, flavoring, or fragrance in order to promote their use among the public.

Invasivespecies.gov
http://invasivespecies.gov/
Affiliated with: National Biological Information Infrastructure
- The federal government's gateway to agencies and nongovernmental organizations worldwide that work with invasive species identification and control. Contains articles about the impact of, means of spreading, response to, and laws concerning invasive species, as well as databases.

Manual of Leaf Architecture
http://www.peabody.yale.edu/collections/pb/MLA/
Affiliated with: Peabody Museum, Yale University
- A downloadable PDF manual of the morphological descriptions and categorization of leaves of angiosperms.

Native American Ethnobotany Database
http://www.umd.umich.edu/cgi-bin/herb
Affiliated with: University of Michigan, Dearborn
- Provides information on foods, drugs, dyes, and fibers that is derived from the practical knowledge of plants accumulated by native North American peoples. Compiled by an anthropology professor for general use and provides citations of the source of information about each plant cited.

Native Plants Network
http://www.nativeplantnetwork.org/
Affiliated with: N/A
- Shares information on how to propagate native American plants, with a database devoted to species, links to government and university members, and the *The Native Plants Journal*.

The Parasitic Plant Connection
http://www.science.siu.edu/parasitic-plants/
Affiliated with: Southern Illinois University at Carbondale
- A repository of information about the taxonomy, phylogenetic relationships, and molecular data of parasitic plants for researchers and educators, with links and a glossary of terms about parasites.

Poisonous Plant Database
http://vm.cfsan.fda.gov/~djw/readme.html
Affiliated with: U.S. Food and Drug Administration
- Contains a list of plants worldwide that are harmful to animals and humans and citations of scientific articles that can be e-mailed upon request.

Ultimate Tree-Ring Web Page
http://web.utk.edu/~grissino/
Affiliated with: University of Tennessee
- Supplies explanations of tree-ring dating methods (dendrochronology) and links to other sources, designed for public school students and the general public. With a gallery of images and software related to dendrochronology for downloading.

The Weed Hall of Shame
http://www.blm.gov/education/weeds/hall_of_shame.html
Affiliated with: Bureau of Land Management
- A cleverly designed site about scourges of public lands—exotic plants, such as purple loosestrife and spotted knapweed—that are crowding out native species. With images and informative narratives.

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