CROP PHYSIOLOGY

APPLICATIONS FOR GENETIC IMPROVEMENT AND AGRONOMY

EDITORS

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Cover Photo and Concept by Dr Pablo Calviño. Commercial-scale test of sunflower-soybean intercropping in the Pampas of Argentina. Originally a ″subsistence farming‶ concept, here intercropping is a high-tech solution in one of the world's more technologically advanced agricultural systems. Crop physiology and enabling agronomy are behind this innovative technology, as explained in Chapter 3, Section 5.

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Preface

The problem of agriculture is that it has been too successful

Elias Fereres

As a consequence of the success of post-World War II agriculture, particularly in western Europe, many in affluent societies have taken food for granted for decades. We lack historical perspective to conclude that the gap between the world demand and supply of food is widening or otherwise. Nonetheless, the recent debate on this gap and the role of research and development in agriculture is a positive signal. Nature (2008) has editorialised on this topic, highlighting the need to spend more on agricultural science to overcome food crises, whereas the point has also been made that not only the amount but also the allocation of research efforts is important (Struik et al., 2007).

Current research efforts seem to be under divergent selection favouring either the very large or the very small. On the one hand, legitimate environmental concerns stimulate investments on global-scale issues. On the other hand, the internal dynamics of sciences at the molecular end of the scale, where progress is made at astonishing rates, has become a strong attractor of resources. Crop physiology belongs to the middle ground between these extremes.

There are many hierarchical levels of biological organisation, from molecules to ecosystems. When we search for an understanding of biological phenomena, it is commonly found at levels below that of occurrence. Agro-ecosystem events are explained at the level of the crop, while molecular and cell biology will provide explanations to physiological responses. Besides, crop physiology provides a vital link between molecular biology and the agro-ecosystem.

The peak of crop physiology appears to be in the past. Membership in the Crop Physiology and Metabolism Division of the Crop Science Society of America has declined concurrently with the initiation and rise of the Genomics, Molecular Genetics, and Biotechnology Division (Boote and Sinclair, 2006). This is a worldwide, rather than local, phenomenon, and a clear reflection of the shifts in research perspectives towards, in this case, the small.

The objective of this book is to provide a contemporary appreciation of crop physiology as a mature scientific discipline. We want to show that much unfinished business lies in the domain of crop physiology, and that this intellectually challenging discipline is relevant to agriculture. Progress in agriculture, however, depends directly on progress in agronomy, plant breeding and their interaction. Hence crop physiology can contribute to agriculture only to the extent that it is meaningfully engaged with breeding and agronomy; this is the theme of this book.

V.O. Sadras, Adelaide

D.F. Calderni, Valdivia

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Sustainable Agriculture and Crop Physiology

Victor Sadras, Daniel Calderini and David Connor

> … the herd of cattle was an animal who wanted to be many, or many animals that wanted to be one…
>
> Ricardo Güiraldes

1. INTRODUCTION

A view from space emphasises the areal dimension of agriculture (Loomis and Connor, 1996), which is threefold. First, the spreading of crops across the landscape allows for the effective capture of both aerial (sunlight, CO_2) and soil (water, nutrients) resources that sustain crop growth (Loomis and Connor, 1996; Monteith, 1994). The linkage between spatial distribution of resources and plant growth requirements leads to predictable large-scale patterns of spatial distribution of vegetation (Miller et al., 2007), and competition for resources influences the structure and functioning of plant populations and communities (Benjamin and Park, 2007; Donald, 1981; Dybzinski and Tilman, 2007; Harper, 1977; Tilman, 1990). Second, smaller-scale space-dependent plant-to-plant interactions mediated by a wide array of signals allow plants to differentiate self and no-self, and respond to their neighbours before competition for resources arises (Aphalo and Ballaré, 1995; Aphalo and Rikala, 2006; Ballaré et al., 1990; Djakovic-Petrovic et al., 2007; Dudley and File, 2007; Karban, 2008; McConnaughay and Bazzaz, 1991). Third, there is an areal dimension in the definition of communities and ecosystems where the most significant aspects of agriculture are defined, including yield (Box 1) and resource conservation. A typical cropping field includes a thropic web of primary producers (crop species and weeds), and primary and secondary consumers, including herbivores, pathogens and predators; decomposers play a critical role in the geochemical cycles of major nutrients. Collectively, all these organisms constitute a community, which together with the physical and chemical attributes of the environment form an agro-ecosystem (Loomis and Connor, 1996).

Crop physiology deals with the structure and functioning of crops, and is therefore closely related to plant sciences and ecology. The principles of crop physiology have been reviewed comprehensively, and are therefore out of the scope of this book. Readers interested in these principles are referred to a series of classical and more recent books (Charles-Edwards, 1982; Evans, 1975, 1993; Fageira et al., 2006; Gardener et al., 1985; Hay and Porter, 2006; Johnson, 1981; Loomis and Connor, 1996; Milthorpe and Moorby, 1979; Pessarakli, 1995; Smith and Hamel, 1999).

In this chapter, we outline the paradigm of contemporary agriculture, and the challenge of sustainable production of bulk and quality food, fodder, fibre and energy during the next decades (Sections 2 and 3). We assess critically a range of agricultural aims and practices, including organic farming and production of land-based raw materials for biofuels; the environmental, economic or social flaws of these approaches are

BOX 1 Crop yield: An evolving concept with multiple definitions

Evolution of yield criteria

For birds and mammals, natural selection favours the procurement of food at the lowest energy cost within the phylogenetic constraints of neural architecture (McLean, 2001). Before agriculture, our ancestors were therefore not unlike other animals, for which 'yield' was the ratio between the energy derived from food and the energy invested in obtaining food (Schülke et al., 2006). In the transition from foraging to farming, human populations were exposed to strong selective pressures to capture the full benefit of an energy-dense but initially detrimental food supply, including starchy cereals, roots and tubers, fatty meats, dairy products and alcoholic beverages (Patin and Quintana-Murci, 2008). Although the enzymatic machinery to metabolise these substances was already in place, the basal expression of such enzymes in our ancestors was inadequate to process the massive amounts of food brought about by farming. High levels of amylase in saliva or lactase in the small intestine probably conferred a strong selective advantage to early farmers (Patin and Quintana-Murci, 2008).

Once the sowing of crops was established as a common practice, the definition of yield shifted from an energy ratio to the ratio between seed harvested and seed sown (Evans, 1993). This was particularly important in low-yielding seasons, when farmers had to make the hard decision of allocating seed for food and seed for the next sowing. An important consequence of this measure of yield was that selection possibly favoured highly competitive plant types, that is, abundant tillering, large inflorescences, small grain and weak seed dormancy (Evans, 1993). Only when availability of arable land came under pressure, mass of product per unit land area became a more important criterion. This shift in the definition of yield had a dramatic impact on selective pressures, shifting from the aggressive high-yielding plant (grains per grain) to the less competitive 'communal plant' able to produce more yield per unit area (Donald, 1981). Evans (1993) envisaged the next measure of yield whereby the time dimension is considered explicitly, for example, yield per hectare per year. This measure is particularly important when comparing productivity of systems where the degree of intensification is variable. Intensification of agriculture is a worldwide phenomenon (Caviglia et al., 2004; Farahani et al., 1998; Sadras and Roget, 2004; Shaver et al., 2003; Zhang et al., 2008). In this context, some observations of stabilisation or decline in yield ($\mathrm{kg\,ha^{-1}}$) (e.g. Cassman et al., 2003) could be a consequence of increasing cropping intensity. This is nicely illustrated by Egli (2008), who reported an inverse relationship between the rate of progress of the yield of soybean crops and the intensity of cropping measured as proportion of double crops in the system: the relative rate of yield improvement from 1972 to 2003 declined from 1.51% in counties with little or no double cropping to 0.66% in counties with 70% of land allocated to wheat-soybean double cropping. Paradoxically, the best environments supporting higher cropping intensity could therefore show the lower rate of improvement in the yield of individual crops. Explicitly measuring yield per unit area and time, as proposed by Evans, is therefore of increasing importance.

Yield of individual crops: Definitions

Yields are in a continuum from crop failure to potential (Loomis and Connor, 1996), and several authors have proposed definitions to account for this range (Bingham, 1967; Evans and Fischer, 1999; Loomis and Amthor, 1999; Loomis and Connor, 1996; van Ittersum and Rabbinge, 1997). In this book, we favour the definitions of actual and attainable yield of Loomis and Connor (1996) and the definition of yield potential of Evans and Fischer (1999).

- *Actual yield* is the average yield of a district; it reflects the current state of soils and climate, average skills of the farmers, and their average use of technology. Actual yield also applies to the particular yield of a crop in a given paddock and season.
- *Attainable yield* 'corresponds to the best yield achieved through skilful use of the best available technology'.
- *Potential yield* is 'the maximum yield that could be reached by a crop in given environments' as determined from physiological principles. As such, it is distinguished from *yield potential*, that is, the 'yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting and with pests, diseases, weeds, lodging and other stresses effectively controlled'. In this definition, environment emphasises solar radiation, temperature and day length (Evans and Fischer, 1999). Building on this definition, we propose that diffuse radiation and vapour pressure deficit need explicit consideration, alongside radiation and temperature (Rodriguez and Sadras, 2007). This is based on known phenomena,

(Continued)

BOX 1 Continued

that is, higher fraction of diffuse radiation favours canopy photosynthesis (Roderick and Farquhar, 2003; Sinclair and Shiraiwa, 1993; Sinclair et al., 1992), and high vapour pressure deficit restricts growth of well-watered plants (Bunce, 2006; Gollan et al., 1985; Monteith, 1993; Sadras et al., 1993).

A ranking of yields is expected:

$$\text{Actual yield} \leq \text{attainable yield} < \text{potential yield} < \text{yield potential}$$

Analysis of gaps between successive yield levels allows for identification of constraints and trade-offs.

emphasised (Section 4). In the context of sustainable agricultural systems, we define the aims and outline the structure of this book (Section 5).

2. AGRICULTURAL PARADIGMS

Agriculture started in the Neolithic, about 10,000–12,000 years ago (Childe, 1927; Flannery, 1973). At the beginning and for most of its history, the core objective of agriculture was to harness resources into the most diverse products, from cereal grain and cotton fibre to olive oil and wine. Environmental aspects of crop production have concerned farmers since the early days of agriculture, and from the mid-nineteenth century, scientists have also focused on the links between production and resource conservation.

Many farming practices evolved to account for environmental issues that often led to improvements in both resource protection and production. In early farming systems relying on shifting fallows, one or two seasons of cropping were often followed by regeneration periods of 20–25 years for forest or 6–10 years for bush (Evans, 1993). The four-course rotation developed in Norfolk in the eighteenth century comprised seven elements: enclosures, use of marl and clay, proper rotation of crops, culture of turnips, culture of clover and ryegrass, long leases, and large farms (Evans, 1993). This early technology illustrates two important aspects of agricultural innovation. First, it reinforces the notion that farmers are generally aware of the importance of maintaining their resource base, as shown by the combination of techniques aimed at maintaining soil fertility. Second, it illustrates the principle that substantial improvements in production generally do not result from a single innovation, but rather by the ingenious rearrangement of many, often pre-existing techniques and exploitation of synergies (Evans, 1993, 2005).

The contemporary concept of sustainability accounting for the triple bottom line of economic, environmental and social outcomes has been implicit in agricultural practices and research for a long time, but has only been formalised in the last four decades. The concept of sustainable agriculture raised its profile exponentially in the 1980s and was firmly established in the 1990s (Figure 1). In tune with this trend, a large number of long-term agro-ecosystem experiments were established in the 1980s and 1990s.[1] Food safety and more subtle aspects of the nutritional characteristics of food products (Mayer et al., 2008; Trethowan et al., 2005; Welch and Graham, 1999) are elements of increasing importance that add a fourth dimension to the contemporary paradigm of agriculture (Figure 2).

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[1] Rasmussen et al. (1998) defined long-term agro-ecosystem experiments as ‘large-scale field experiments more than 20 years old that study crop production, nutrient cycling and environmental impacts of agriculture’, and reviewed the features of ‘classic’ (i.e. more than 50 years old) and more recently established experiments in this class. Examples of classic long-term agro-ecosystem experiments include those at Rothamsted (established in 1843) in the United Kingdom; Morrow (1876) and Sanborn (1888) in the United States; Askov (1894) in Denmark; Eternal Rye (1878) and Static Fertiliser (1902) in Germany; Rutherglen (1913), Longerenong (1917) and Waite (1925) in Australia; Skierniewice (1923) in Poland; and Leeethbridge (1911) and Breton (1930) in Canada. In response to the renewed importance of questions in long-term time scales, the number of long-term agronomic experiments raised from less than 30 to more than 240 in recent decades (Rasmussen et al., 1998).

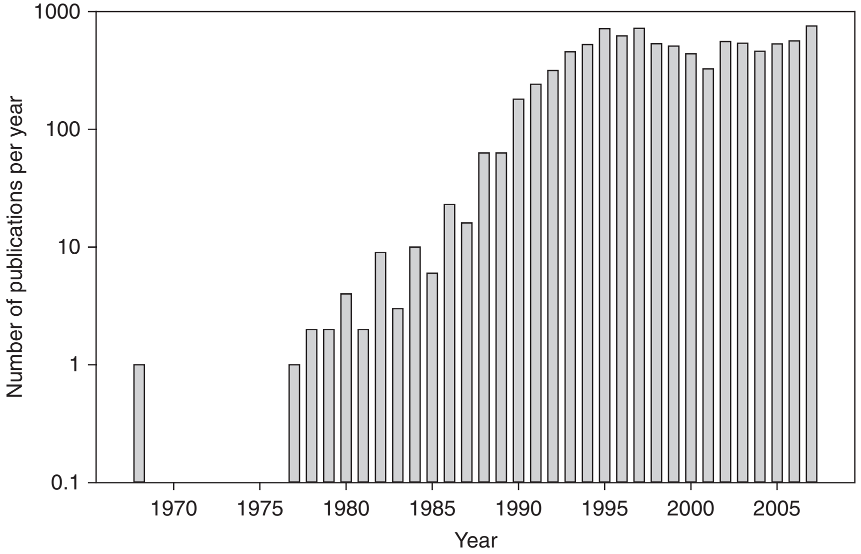

FIGURE 1

Time course of papers retrieved searching for 'sustainable agriculture' in the Commonwealth Agricultural Bureaux (CAB) database (1910–2007). No publications were retrieved for the period 1910–1967. The first paper retrieved with this search criterion was published in 1968, and its focus was on economic sustainability in relation to land price and alternative land uses, that is, agricultural versus industrial or urban (Cervinskij et al., 1968). Biswas and Biswas (1976) challenged the sustainability of high-input agriculture in the context of the energy crisis of the 1970s, and this is one of the first formal accounts, albeit partial, of sustainability in the contemporary meaning of the concept. Bennett and Schork (1979) explicitly considered the environmental, economic and social aspects of sustainability, and theirs is the first publication to feature 'sustainable agriculture' in the title. The concept of sustainable agriculture raised its profile exponentially in the 1980s and was firmly established in the 1990s.

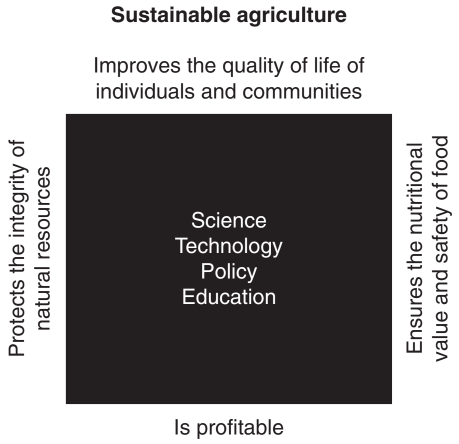

FIGURE 2

Concerted efforts in science, technology, policy and education are required to deliver on the four dimensions of sustainable agriculture.

The link between sustainability and complexity is an exiting theoretical challenge and a point of huge implications for policy makers. It could be argued that the environmental dimension of sustainable development has always been complex, but whether this leads to stasis or collapse is uncertain (Fisk and Kerherve, 2006). In addition, the growing complexity of social and financial systems has been seen negatively, as complex systems risk drifting into unstable domains with no means to steer the system out of its course, whereas the positive side of this problem is a sort of protection against single agents taking control (Fisk and Kerherve, 2006). Finnegan (2003) for instance explained the 2001 outbreak of foot-and-mouth disease in the UK in terms of complexity. Unlike previous outbreaks, this spread faster and farther: 750,000 cattle and 4.5 million sheep were slaughtered, a general election was postponed, and a divide was open between country and city. Finnegan pointed out three elements contributing to the outbreak: (a) economic rationalisation of abattoirs and bizarre EU subsidies that increased the connections between herds to a critical point,[2] (b) changes to reporting rules that may have delayed the identification and isolation of infectious animals, and (c) failure to integrate the economics and the biological components of the system; the variables manipulated to improve economic return also enhanced the rate of spread of the disease.

In the context of sustainability defined along the four axes in Figure 2 and the increasing complexity of world agricultural systems, the major challenges of agriculture in the next decades relate to the increasing demands of food and other agricultural products (Section 3), competing land uses of both agricultural and non-agricultural nature, and misplaced emphasis on ecologically, economically or socially unsound agricultural practices (Section 4).

3. WORLD TRENDS IN POPULATION AND DEMAND OF AGRICULTURAL PRODUCTS

With justified optimism, it was thought that it was a matter of time to completely solve the problem of food shortages after the Green Revolution in the later 1960s. This problem was related to poverty and food distribution as much as it was related to actual production and improved cropping systems. These problems remain for many reasons, including insufficient and poorly allocated investment in research and development in agriculture (Anon., 2008; Borrás and Slafer, 2008; Evans, 1997; Marris, 2008; Struik et al., 2007). Furthermore, naive views of affordable and reliable food supply in affluent societies have been challenged by the convergence of a complex array of factors, including competition for land between food production and alternative uses (Section 4), climate shifts; increasing price of inputs, particularly fertilisers and energy; and increasing food demand resulting from the compounded effect of increasing population and qualitative changes in food demand.

Human population has increased at an impressive pace from 1850 to reach 6 thousand million at the end of the twentieth century (Evans, 1997; UN, 2007). By the middle of the present century, world population is estimated to increase to 9.2 thousand million from the current 6.7 thousand million (UN, 2007). The almost 40% increase in population projected for 2050 will be the most powerful driver of food demand; food consumption is predicted to be 3130 kcal person^{-1} day^{-1} in 2050 from 2789 in 2000 (FAO, 2006). Additionally, qualitative shifts will also influence the demand of agricultural products. In industrialised countries, 73% of cereals are fed to animals in comparison to 37% in developing countries (Pretty, 2008). Only to satisfy the increasing demand for animal products in developing countries, an extra 300 Mt of grain will be needed by 2050 (Pollock et al., 2008). The expansion of agricultural land area was the most important driver of increased production of main crops during the first half of the twentieth century, and the increase of crop yield was fundamental afterwards (Miller, 2008; Slafer et al., 1996; Slafer and Otegui, 2000). The challenge is therefore to further increase production, if anything, with the same or less amount of land and water.

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[2] In a system with *n* elements and *x* random connections between them, the ratio *n/x* is a measure of integration. The size of the connected cluster increases slowly with increasing *n/x* until it reaches a critical point or phase transition, where a giant cluster 'crystallises' (Kauffman, 1995). Beyond this point, important properties emerge that cannot be deduced from the parts of the system.

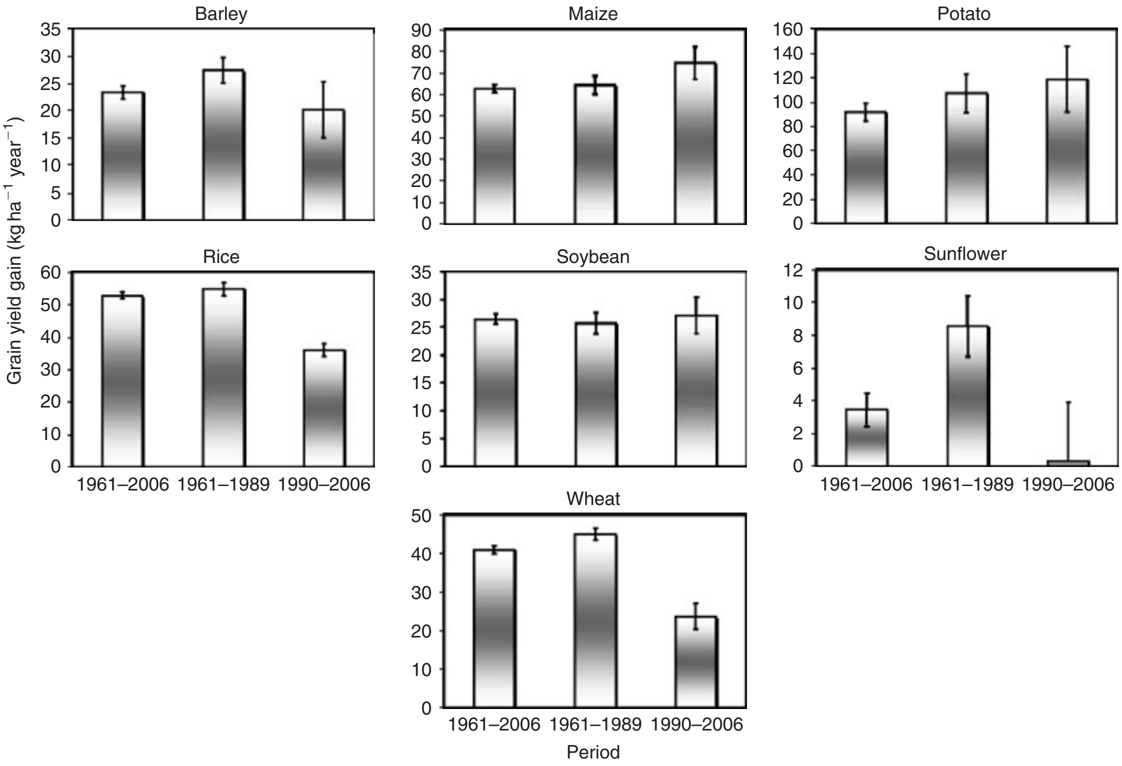


FIGURE 3

Global yield gains of barley, maize, potato, rice, soybean, sunflower and wheat calculated for three periods: 1961–2006, 1961–1989 and 1990–2006. Yield gain is the slope of linear regressions between annual global yield and year; bars are the standard error of the slope.

Figure 3 shows global yield trends of the four more important cereal crops (wheat, rice, maize and barley), the most widely sown grain legume (soybean) and oilseed crop (sunflower) and the largest non-grain food crop (potato). Assuming a population of 8.0 thousand million by 2020–2025 and considering that wheat, rice and maize account for 60% of the human food demand (Tilman et al., 2002), Byrnes and Bumb (1998) calculated the yields necessary to meet this demand: 5.4 t ha^{-1} for wheat, 5.3 t ha^{-1} for rice and 5.8 t ha^{-1} for maize. Projecting the yield trends from the last 17 years (Figure 3) into 2020 indicates 3.3 t ha^{-1} for wheat, 4.8 t ha^{-1} for rice and 6.2 t ha^{-1} for maize, representing gaps of 40, 10 and 8%, respectively.

This type of rate analysis has been the standard to detect shifts in productivity trends and gaps between supply and demand. However, this approach has two drawbacks. First, short-term trends are strongly influenced by local or global temporary phenomena (e.g. widespread drought or political turmoil in major producing countries or unfavourable grain-to-fertiliser price ratio). Evans (1997) coined the term 'plateau spotters' to describe the claims that crop yields are approaching their limit on the grounds of short pauses in yield trends, for example, as seen for wheat and rice in Figure 3. The second reason why yield per unit area and rates derived from it are inappropriate is that farmers are primarily interested in the productivity and profit of their farms, rather than in the production of individual crops. In some cases, for example, in the extreme environments of northern Europe outlined in Chapter 4, yield of individual crops and whole-farm productivity are tightly related. In most of the temperate to tropical regions of the world, the link is more tenuous owing to trade-offs between yield of individual crops and cropping intensity (Box 1). Egli (2008) demonstrated this strong trade-off for soybeans in the USA in a study analysing county yield trends between 1972 and 2003 (Box 1). Likewise in Argentina and Brazil, double-cropped soybean is increasingly important. Interpretation of rates of change in yield per unit area of soybean in Figure 3, therefore, needs to account for the trade-off between soybean yield and whole-farm production and the profit in the three largest world producers (Figure 1 in Chapter 3). The same applies to many other crops including wheat and rice in both dry land and irrigated systems. In the central Great Plains of North America, low and unreliable rainfall has favoured winter wheat-fallow rotations, but greater cropping frequency at the expense of fallow may in some cases improve farmers' profitability despite reduced wheat yields (Lyon et al., 2004, 2007). In the more favourable environment of the Pampas, where continuous cropping has already been established for decades, farmers are stepping up cropping intensity to improve profitability, often at the expense of yield in individual crops (Section 5 in Chapter 3). Part of the apparent 'plateau' or decline in rice productivity perceived in recent analyses (e.g. Chapter 9) is related, as already explained by Evans (1997), to the selection for shorter-season varieties that allow more crops per year: 'four rice crops grown at Los Baños in the Philippines within a period of 335 days yielded 76.7 kg grain per hectare per day, giving a total of 25.7 $\text{t}\,\text{ha}^{-1}$ for the year, 10% more than the world record maize crop'. It is clear that tons per hectare is an inappropriate measure of yield in dynamic systems increasing cropping frequency at rapid rates.

Meeting future world demands of food depend on both improved assemblage of activities (cropping, livestock production) in farming systems and further increases in yield of individual crops through the combination of plant breeding, improved agronomy and their synergy.

4. PRODUCTIVITY IS THE KEY BUT INADEQUATE FOR ALL SOCIETY'S DEMANDS

In a highly populated world, a key to sustainability is large primary production (Section 3). That in turn requires high productivity of limited available land and can only be achieved by efficient use of germplasm, labour, managerial skill, energy, water, fertiliser and other agrochemicals. Without high productivity, it is not possible to provide an adequate and secure food supply for the present or expected world population, while preserving sufficient non-agricultural land for its other services and values. The magnitude of that challenge and the role of technology in its achievement were analysed thoroughly in *Feeding the Ten Billion* (Evans, 1998) and *How much land can ten billion people spare for nature* (Waggoner, 1994). We do not now expect a world population of 10 thousand million (10×10^9), rather 9.2 thousand million by 2050 (UN, 2007); however, the challenge is more daunting because, on the one hand, supporters of low input and organic agriculture promote systems that are inherently unproductive, and on the other hand, supporters of biofuel production require enormous increases in productivity for even a small contribution of liquid fuel to transportation.

Regretfully both movements are widely supported by governments with polemic and subsidies for reasons that defy logic or science. These challenges to productivity are important because there are questions of food and environmental safety, energy security and mitigation of climate change. But the question must be asked if the proposals meet these challenges. Detailed analyses of organic agriculture (Box 2) and land-based biofuels (Box 3) are beyond the scope of this chapter. However, these two industries help to emphasise that a sustainable future can only be achieved by greater productivity underpinned by improved understanding of crops and cropping systems, and careful and comprehensive analyses of their attainable yields and environmental impact. Organic agriculture and biofuel are two currently important agricultural issues with significant implications for society at large. During the lifetime of this book, some of these issues might fade away. A long-lasting lesson is, perhaps, to consider these as a property of human nature searching for naive and easy solutions to complex problems with little regard for their consequences beyond their narrow intended target (Asimov, 1972). The application of the best science and technology are indispensable elements in the search for sustainable food production.

BOX 2 Misleading comparisons of crop production in organic and conventional agriculture

The objective of the organic movement is to produce safe food in a way that preserves the environment; the method adopted to 'ensure' this is avoidance of synthetic chemicals and reliance on natural substances for management of pests, diseases and fertility. Organic agriculture currently occupies 31 Mha of agricultural land, mostly in developed countries (Willer and Yussefi, 2007). Of that total, 15 Mha found in two countries, Australia and Argentina, are mostly extensive zero-input grazing country. Consequently, the part that is farmed to rules administered by various regulating associations is a small proportion (<1%) of the 1500 Mha of world cropland. Misinterpretation of agronomic principles, including crop ratios and yield definitions, have led to unsound recommendations for organic agriculture, particularly as a solution for less developed countries.

Crop ratios

Crops characteristic of subsistence agriculture, including beans, maize and cassava, often show yield ratios relative to current management in excess of 2 (Pretty et al., 2003). Those high ratios are used to promote organic agriculture as the solution to developing country agriculture (Badgley et al., 2007). After all, if yield can be doubled without fertiliser, then why struggle to buy any! The answer is found in yields achieved rather than ratios. Despite the increases, the yields remain small. Increasing yield of maize crops from 0.5 to 1.2 t ha^{-1} (ratio >2), for example, is hardly a long-term solution to hunger when the same gains could be achieved on all fields with small doses of fertiliser, and yields of 5–10 t ha^{-1} with larger applications.

Yield definitions

Crops can indeed be grown to equally high yields when treated with appropriate amounts of inorganic or organic fertilisers, but the environmental 'benefits from reliance on organic N sources have not been established, and the scientific basis for such a perception has not been documented' (Cassman et al., 2003). Whilst carrying no environmental benefit, the task is more difficult with organic nutrients because of the large volumes required and the usually small, and mostly unknown, nutrient content. This equality of yield does not, however, establish that organic agriculture is an equally productive system as alternatives using inorganic fertiliser. Other land is required to provide that organic fertiliser, so the yield of the organic approach *on a system basis,* that is, *per unit area and time*, is smaller. If a crop can be grown in rotation with legumes in an organic system, additional crops can substitute the legumes where nitrogen is supplied by fertiliser. In regions of high food demand, fertiliser is essential for the intensive cropping required to provide adequate food. Thus in Bangladesh, a highly populated country situated on the once fertile delta of the Brahmaputra and Ganges Rivers, the average cropping intensity is 2.5, that is, two or three crops are harvested from each field each year. In the widespread rice–wheat system there, annual yield of 8–10 t grain ha^{-1} would not be possible in an organic system because, other nutrient issues aside, the fixation of the required amount of N (approx. 300 kg N ha^{-1}) would drastically reduce crop area and frequency. In other places where food supply is not so critically short, inefficient use of agricultural land in organic systems requires more land to meet production requirements, so less land can be set aside for nature.

Based on crop productivity of 'organic' systems of medieval Europe and assuming all land is devoted to agriculture, Smil (2001, 2004) estimated maximum carrying capacity of organic agriculture in the range of 3–4 thousand million, well below the present population. Badgley et al. (2007) recently sought to refute those estimates, but their own estimates were badly flawed because they did not account for the severe limitations that the supply of organic manures has on the expansion of organic agriculture (Connor, 2008).

A place for organic farming

In those places where fertilisers are either not available or too costly and subsistence agriculture predominates, application of rotations and fertility management practices can substantially increase the yield of individual crops (Figure 3 in Chapter 5). For these developing country farmers, organic methods should be fairly presented as a valuable start to increasing yields and solving hunger but should not, with their exclusion of fertiliser use, be presented as the sustainable solution. Organic agriculture does not adequately address the most urgent needs of rural poor in developing countries. As in the developed world, it is best implemented as a complementary opportunity to generate additional income in peri-urban areas on land with initial high fertility or where opportunity exists to import organic nutrients, and where consumers are prepared to pay price premiums for the products. Increasingly, however, organic products are faced with competition from 'Good Agricultural Practices' (e.g. EurepGAP) that certify food safety and environmental stewardship using agrochemicals (Hobbs, 2007).

BOX 3 Land-based biofuels

In response to the oil price shock in the 1970s, agriculture was called to provide liquid fuels, bioethanol from sugar and starch crops to replace petrol and biodiesel from oil crops. The resurgent interest in biofuel at the beginning of the twenty-first century is a result of more complex forces. High oil prices caused by increased demand are now combined with concerns over national energy security and targets to mitigate climate change. Biofuel production requires energy to sow, grow and harvest crops, including that for machine construction and operation, production and use of agrochemicals, transport of crop products and finally transformation into biofuel. Important questions are: First, what are the energy benefits of biofuel? Second, to what extent can biofuel mitigate global warming? Third, how much extra primary production can the biosphere accommodate along with food requirements for all creatures great and small?

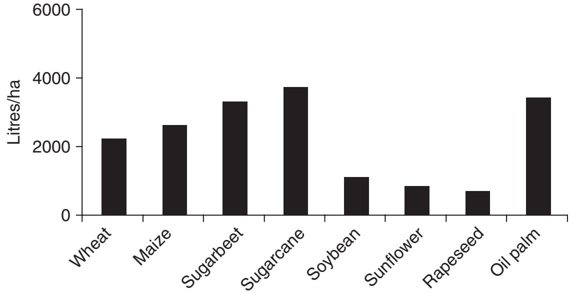
Energy efficiency

This is the ratio of biofuel output to support energy used in crop production and subsequent transformation. Plant physiology provides important explanations of comparative productivity and efficiency through climatic adaptation, including C4 photosynthesis to tropical year-round growing environments (greater production than C3 types in seasonal environments), metabolic costs of product type (decreasing in the order oil, starch, sugar), method of storage (vegetative organs do not depend on successful seed set and can accept assimilate over longer periods of growth), nitrogen fixation in legumes to reduce the high energy cost of nitrogen fertiliser, repeated flowering and fruit set to maintain high sink strength (some crops, e.g. oil palm, flower and set seed throughout the year, while most others just once) and, again related to product type, the energy costs of transformation to biofuel (chemical trans-esterification of vegetable oil to biodiesel is significantly smaller than hydrolysis/fermentation of sugar and starch to ethanol). The productivity of some commonly used crops expressed in gasoline equivalents to account for difference in motive power is presented in the figure below.

The data reveal that various combinations of physiological variables can produce high or similar yield and that perhaps the most important determinant, as seen in both sugarcane and oil palm, is the favourable year-round growing environment of the tropics. Crops restricted to seasonal environments produce less, and except for oil palm, oilseed crops are the least productive. Oil palm biodiesel and sugarcane bioethanol alone have high energy efficiencies in the range 8–10 (Liska and Cassman, 2008) while no other crop consistently exceeds 2. Gnansounou and Dauriat (2005) provided average values for sugar beet (1.83), cereals (1.76) and maize (1.44). While the productivity of soybean is small, its energy efficiency of 1.9 (Liska and Cassman, 2008) is greater than that of maize, presumably reflecting comparative advantages of N fixation and low energy cost of trans-esterification to biodiesel.

Greenhouse gas mitigation

A popular view of biofuel use is that since CO_2 released on combustion was fixed in photosynthesis, impact on the atmosphere is carbon, and hence greenhouse gas, neutral. That is not the case, however, because fossil fuel is widely used to support production and because crop production releases oxides of nitrogen and sulphur, and in moist conditions methane, that are more powerful greenhouse gases than CO_2.



Biofuel productivity (l ha^{-1} of gasoline equivalent, bioethanol × 0.70, biodiesel × 0.91) of various crops based on average yields in countries where they are well adapted. Yields (t ha^{-1}) are 8.0 for wheat in the UK, 9.4 for maize in USA, 78 for sugar beet in France, 74 for sugarcane in Brazil, 2.7 for soybean in Argentina, 2.1 for sunflower in the Czech Republic, 1.7 for rapeseed in Canada and 21 for oil palm in Malaysia (from FAOSTAT http://faostat.fao.org/default.aspx).

(Continued)

BOX 3 Continued

The relatively few analyses of greenhouse gas balance of biofuel production reveal that it is not always significant. While Hill et al. (2006) established a 12% saving over gasoline for bioethanol from maize, Farrell et al. (2006) could find none. In contrast, that study reports a gain of 43% for biodiesel from soybean. The inevitable conclusion is that even without any greenhouse costs associated with land clearing for the expansion of cropping areas to meet the requirements, associated emissions of CO_2 from the decomposition of organic matter and microbial release of nitrous oxides, biofuel does not substantially benefit greenhouse gas mitigation. Where land is cleared for biofuel crops, greenhouse gas emissions may be double those from equivalent gasoline use for 30 years and remain positive for 167 years (Searchinger et al., 2008).

Competition with food production

Marked increases in grain prices in 2007 have revealed the impact of a relatively small diversion of crop production to biofuel. These have found support among farmers and hope in some development agencies for a much required boost to agriculture in developing countries. Consumers, while expressing concern for the environment as forestland is converted to biofuel production, fear the era of cheap food has come to an end. Certainly, competition for crop products for fuel and food between the rich and the poor has the capacity to further increase food prices as the demand for food continues to increase.

Agriculture now provides, with some shortfalls, food for 6.5 thousand million people and is challenged to do better for about 9.0 thousand million by 2050, while conserving the resource base and preserving as much land as possible for nature and its other values. From an agronomic perspective, the doubling of food production during the next 40 years is accepted by international development organisations as an enormous challenge. Biofuel adds a large extra burden. The standard nutritional unit of 500 kg grain equivalent per head per year is a convenient way to express agricultural production in relation to human food supply (Loomis and Connor, 1996). The unit is sufficiently large to allow some production to be used as seed for the next crop, some to be fed to animals, some to be lost in storage, and some land to be diverted to fruit and vegetable crops. Significantly, that same amount of production is sufficient to produce just 200 l of maize ethanol ($2.5\,kg\,l^{-1}$), enough for 2000 km at 10 l per 100 km (Connor and Minguez, 2006). The carrying capacity of land for cars is just too small and increasing population must take precedence for food supply. Even dedicating all US corn and soybean production to biofuel would provide only 12 and 6%, respectively, of the current national demand for gasoline and diesel.

The future

Concern about competition with food production has promoted two reactions to sustain the quest for a biofuel economy: first, utilisation of currently unharvested vegetative parts of crops and forests and, second, use of non-food crops, including woody plants. Most target non-food crops will, as do crop residues, provide lignocellulosic vegetative material. A biomass crop of current focus is switchgrass (*Panicum virgatum*), which has high productivity and wide adaptability (McLaughlin et al., 1999). A biodiesel favourite is *Jatropha curcas* touted to perform well in marginal areas but as yet without evidence. The claims of its productivity on marginal and degraded land (Francis et al., 2005) are unlikely to be established. So far, there are no large-scale production units from which to evaluate energy efficiency or economic viability of biomass crops. Experimental data suggest energy efficiencies of bioethanol from lignocellulosic crops in the range 1.8–5.6 (Gnansounou and Dauriat, 2005). Further, non-food crops always compete with food crops for land, water and nutrients. The hope of using marginal land is fatuous, in a world seeking to increase food production. Land that can grow energy crops could also grow food. There is no essential difference.

Future emphasis on land-based biofuel production is likely to concentrate on residues from agriculture and forestry, and any level of success will await development of commercially efficient technology for transformation to biofuel. It will also require careful site-by-site analyses of how much residue can be removed without deleterious effects on productivity. Residues are not wastes left to rot on the ground but food for domestic animals and a web of consumers and decomposers that play important roles in maintaining the natural environment and the physical and chemical condition of soils. The apparent large net energy benefits of these sources will diminish once they are recognised as part of production systems and appropriate proportions of support energy are allocated to them. Biofuel does not, it seems, generate enough energy to justify the many environmental (Scharlemann and Laurance, 2008; Searchinger et al., 2008) and social impacts of large-scale production. The most likely outcome is that hopes for a land-based biofuel economy will fade. Evidence suggests a modest (+10%) contribution to national motor fuel supply for countries with large cropland resources relative to population size but that biofuel cannot be a major part of a solution in a highly populated and energy-demanding world. The energy now used to generate biofuel, especially natural gas in ethanol production, may well find more efficient use directly in transport.

5. AIMS AND STRUCTURE OF THIS BOOK

Agriculture operates in the context of production and profit, environmental and social outcomes and food quality and safety (Section 2). The world faces challenges related to the increasing demand of food and other agricultural products (Section 3), competing land uses, and misplaced emphasis on ecologically, economically or socially unsound agricultural practices (Section 4). Against the twin framework of the current paradigm of agriculture, and the interactions between biophysical sciences contributing to agricultural production, the primary aim of this book is to highlight the value of crop physiology as an interface discipline whose practical benefits are realised by targeted links with genetic improvement and agronomy. Whenever suitable, this book seeks to draw attention to and partially counteract the reductionist views more common in disciplines targeting lower levels of organisation; we will emphasise conserved traits, where definitions at low levels of organisation remain relevant at the crop level (e.g. phenological development, disease tolerance and herbicide resistance), as distinct to those traits that are typical of populations, for which relationships with lower levels of organisation are not straightforward (e.g. grain yield).

This book comprises three parts: Part 1 focuses on selected, contrasting farming systems of the world to sample more specific challenges of agriculture, Part 2 outlines principles of capture and efficiency in the use of crop resources, and Part 3 concentrates in recent and projected advances in breeding and agronomy with emphasis on physiological perspectives, scale issues or both.

5.1. Part 1. Farming systems: Case studies

Whereas, globally, the challenges of sustainable agriculture are similar, the particular drivers and constraints of specific farming systems can be vastly different. Part 1 thus contrasts predominantly rainfed systems – including the cereal-based systems of Australia (Chapter 2), where rainfall patterns constraint and shape farming options; the diverse farming systems of the Pampas of Argentina (Chapter 3), where dramatic intensification of agriculture seeks to improve the capture of resources, chiefly rainfall, dilute fixed costs and maintain the resource base; and short-season, cereal-based systems of Finland, where low temperature and long days are major drivers – whereas EU regulations set strict guidelines for agriculture (Chapter 4). Part 1 closes with an overview of diverse, cereal-based farming systems of Asia, ranging from less than $1\,\mathrm{t\,ha^{-1}\,year^{-1}}$ for sole crops in dry lands to $15\,\mathrm{t\,ha^{-1}\,year^{-1}}$ in irrigated intensive systems, allowing for multiple cropping (Chapter 5).

5.2. Part 2. Capture and efficiency in the use of resources: Quantitative frameworks

The shift from plant growth analysis based on relative growth rate and its components, that is, net assimilation rate and leaf area ratio, to crop growth analysis based on capture and efficiency in the use of resources was a milestone in crop physiology (Monteith, 1994). Part 2 of this book focuses on capture and efficiency in the use of water, radiation and nitrogen with a strong quantitative perspective. Chapter 6 has a dual aim: It considers the challenges of irrigated cropping systems worldwide, hence expanding the focus on rainfed agriculture developed in Part 1, and accounts for water productivity from engineering to crop scales. Chapter 7 outlines the use of radiation-based methods to analyse crop growth in agronomy, breeding and modelling, and Chapter 8 presents a comprehensive physiological perspective of nitrogen nutrition in field crops and pastures.

For updates on other important nutrients not considered in this book, chiefly phosphorus, readers are referred to Lambers et al. (2008), van der Heijden et al. (2008) and Sawers et al. (2008) for recent accounts of nutrient acquisition from evolutionary and ecological perspectives that emphasise the role of mycorrhiza and other soil organisms; Bucher (2007) for a closer look at the biological aspects of phosphorus uptake at the root and mycorrhiza interface; and reviews with an agricultural focus by Ulen et al. (2007) and Hart et al. (2004). Whereas nutrients have generally been considered individually, for example, management of nitrogen or phosphorus, integrated approaches accounting for interactions between nutrients are attracting more attention (Dobermann et al., 1998; Kho, 2000; Sadras, 2006; Saïdou et al., 2003; Yadav et al., 2000).

5.3. Part 3. Crop physiology, breeding and agronomy

The focus of this book is the crop, which biologically is a population with both properties that depend on its constitutive individuals, and emergent properties that are unique to this level of organisation (Donald, 1981). The insightful perspective of Güiraldes opening this chapter highlights the dual feature of the population: It depends on its constitutive individuals, but it is also an entity on its own, with properties that are unique to this level of organisation. Furthermore, relevant attributes of farming systems involve community-level processes where the crop species are primary producers, alongside with weeds, closely interacting with organisms up the trophic chain, including pathogens and decomposers.

A mature crop physiology discipline has grown out of its own, early attempts to increase productivity through a naive, linear scaling up across levels of organisation, but this syndrome is still common in other disciplines (Hammer et al., 2004; Sinclair et al., 2004). Lack of appreciation of both trade-offs and buffering processes involved in scaling up and crop-level attributes that override seemingly sound traits at lower levels of organisation remains an issue and a major source of inefficiency in the investment of research effort (e.g. Vinocur and Altman, 2005; Yamasaki et al., 2005; Zhu et al., 2007). Figure 4 contrasts a general framework of biotechnology and crop physiology. Where biotechnology focuses on very detailed molecular mechanisms at the expense of environmental factors and higher organisation levels, crop physiology focuses on the population level and attempts to integrate across levels of organisation, with greater emphasis on the nuances of environmental drivers of crop growth, development and yield formation.

Part 3 deals with the links between breeding, agronomy and crop physiology against the conceptual framework outlined in Figure 4 (right). Chapter 9 presents an evolutionary perspective that, we propose, provides the theoretical 'glue' for our conceptual model, whereas Chapter 10 updates efforts aiming at its mathematical formalisation. Biological phenomena can be explained by invoking proximal, physiological mechanisms and ultimate evolutionary causes. Both approaches are valuable, and they are not mutually exclusive. The photoperiodic response of flowering plants can be explained physiologically, from gene to phenotype (Chapter 12). However valuable, this explanation is incomplete, as the basic question of why wheat is a long-day plant remains unanswered. The answer to the 'why' question requires evolutionary considerations, which are often speculative but nonetheless illuminating. There is a rich history in crop science demonstrating the insight gained from the consideration of evolutionary aspects of individual plant traits (Denison et al., 2003; Donald, 1968, 1981; Donald and Hamblin, 1983; Evans, 1984, 1993; Troyer, 2006). Chapter 9 explores the notion that trade-off-free options to increase competitiveness (e.g. increased gene expression) have been comprehensively tested by natural selection. This leads to the concept that further genetic improvement of crop yield would therefore involve substantial trade-offs between fitness in past versus present environments, between individual competitiveness and the collective performance of plant communities or between individual and multiple crops, or a combination of these trade-offs.

There is an inherent limitation in adaptive explanations dissecting organisms into unitary traits (Gould and Lewontin, 1979), but recent developments in modelling crops from gene to phenotype allow for integration of individual traits and to capture emergent properties at the individual and population levels (Chapman, 2008; Hammer et al., 2006; Hoogenboom et al., 1997, 2004; Messina et al., 2006). Chapter 10 presents the state-of-the art in this new generation of mathematical models used to explore the links between crop physiology and the critical interaction between genotype and environment, with a proclaimed potential to help integrating molecular technologies in plant improvement. Chapter 11 expands on physiological

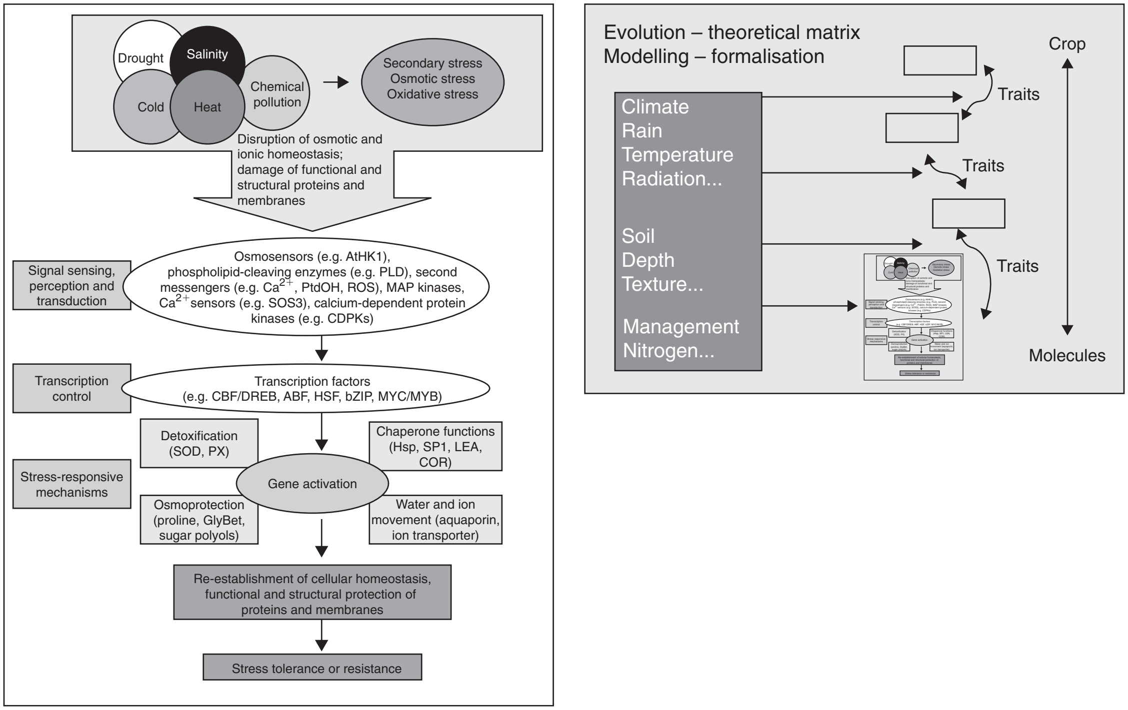


FIGURE 4

Contrast between the conceptual frameworks of biotechnology (left) and crop physiology (right). Biotechnology displays a massive level of detail on processes at molecular level, usually defines stress tolerance at levels of organisation well below the crop and often clumps environmental factors with little consideration of their nature, timing, intensity and duration of stress. Crop physiology scales traits up and down the levels of organisation, explicitly accounts for the environmental complexity of farming systems and ideally uses evolutionary science as a matrix, and modelling as a tool for formalisation. The left figure is adapted from Vinocur and Altman (2005).

perspectives to disentangle complex QTL-by-QTL and QTL-by-environment interactions and trade-offs between agronomically important traits.

Crop phenology is the single most important attribute of crop adaptation (Passioura et al., 1993; Sadras and Trápani, 1999). Chapter 12 uses wheat and soybean as model plants to outline the developmental characteristics of grain crops and the links between phenology and yield, revises the mechanisms of environmental and genetic control of development and explores the possibilities of improving crop adaptation and yield potential through the fine-tuning of developmental patterns.

Root systems remain the ‘hidden half’ (Waisel et al., 1996) of the crop, and Chapter 13 presents recent advances in the quantification of root vigour, that is, the early and fast root extension and proliferation associated with greater root length density and biomass, its value as a trait to improve resource capture and its role as a trait for germplasm improvement. This chapter illustrates the potential for yield improvement through the manipulation of root traits, provided suitable screening techniques are integrated in proper frameworks accounting for the spatial and temporal patterns of resource availability (Manschadi et al., 2008; Schwinning and Ehleringer, 2001).

Chapters 14–16 deal with three aspects of genetic improvement of crops, namely, the role of molecular applications in plant breeding (Chapter 14), physiological perspectives on the improvement of yield potential (Chapter 15) and quality attributes of grains (Chapter 16). The sharp contrast between the successful application of biotechnology to genetically simple traits such as disease tolerance and the difficulties in dealing with more complex traits such as yield potential (Xu and Crouch, 2008) highlights the contrast between the oversimplified approaches to characterise environments and the interaction between genotype and environment G × E (Figure 4, left) and more comprehensive perspectives (Figure 4, right). A bottleneck has emerged from the mismatch between the limited capacity to phenotype large numbers of plants and the massive capacity to characterise traits at molecular and genetic levels (Xu and Crouch, 2008). This mismatch is evident, yet efforts to speed up the phenotyping process may be misplaced if we do not recognise the gap between the crop, where yield and quality are defined, and the plant, the main target of new automated phenotyping systems (left vs. right models in Figure 4). Chapter 16, for example, shows that some quality traits cannot be correctly understood or predicted by extrapolating from the individual plant to the population, for example, oil tocopherol concentration is highly dependent on oil weight per grain, which in turn depends on intercepted radiation by the crop and plant-to-plant competition. Chapters 15 and 16 therefore share a critical focus on the scaling up and down of attributes relevant for the improvement of yield and quality (Figure 4) whereas Chapter 16 further emphasises the interactions between cultivar and agronomy in dealing with the dual objective of high yield and targeted grain quality attributes.

Diseases, weeds and herbivores could cause major yield losses, often reduce grain quality and add a substantial layer of complexity to G × E driven by abiotic factors. Water and nutrient deficit for instance interact in complex, largely unpredictable ways on the fitness of plants and herbivores (Sih et al., 1998, 2004; Waring and Cobb, 1992). In this book, we illustrate crop interactions with diseases (Chapter 17) and weeds (Chapter 18). Chapter 17 outlines pathogen biology at a general level (necrotrophs vs. biotrophs; soil vs. airborne), explains the genetic basis of plant resistance to pathogens, links genetics of resistance with agronomy and discusses epidemiological aspects at continental scale. In common with Chapter 9, Chapter 17 uses an evolutionary perspective to deal with the ephemeral nature of crop resistance to diseases and the agronomic practices to reduce the rate of evolution in agricultural pathogen populations. Chapter 18 discusses the opportunities for improving the inter-specific competitive ability of crops as an approach to complement other weed management practices against the background of the trade-off between intra-specific competitive ability and yield. Readers interested in herbivore pests are referred to literature dealing with specific crops, for example, wheat (Sadras et al., 1999), cotton (Deguine et al., 2008); specific pests, for example, *Nezara viridula* (Knight and Gurr, 2007), thrips (Morse and Hoddle, 2006); principles including the role of chemical (Smith et al., 2008), biological (Khan et al., 2008) and insect-resistant transgenic varieties (Romeis et al., 2008) in crop protection; or higher-order interactions, for example, crop–pest–weed (Schroeder et al., 2005) and insect–virus (Whitfield et al., 2005).

Precision agriculture was born and remains, to some extent, technology driven, rather than science driven. Yield maps and global positioning system (GPS) opened an exciting window of opportunity for the spatial management of crops and to use resources more efficiently. Paradoxically, with these tools, we initially move backwards to a static view of yield at the end of the season, with limited interpretations of the trajectory and subjacent causes leading to final yield. Chapter 19 outlines a more mature technology combining remote sensing, crop- and soil-monitoring tools and rainfall forecasting with principles of crop physiology. This combination yields a more promising proposition involving a more relevant, dynamic view of the key processes underlying the formation of crop yield at paddock and farm scales.

Abatement (i.e. reduction of greenhouse emissions) and adaptation of farming systems to altered climates are two complementary aspects to consider in relation to agriculture and climate change. Chapter 20 deals with the adaptation aspect of climate change. Cropping systems would need to account for changes in climate in terms of species, cultivars, management practices and assemblage of farm activities. Importantly, there are different degrees of certainty on the direction and magnitude of changes in climate. There is agreement on the increasing trends of atmospheric concentration of CO_2 and temperature, but the actual magnitude of these trends is less certain. Even less certain, and very important, are the projected changes in amount, seasonality and size structure of rainfall. Actual responses of crops to the combined effects of changes in CO_2, temperature and rainfall are complex, and simulation models have proved valuable tools for quantitative projections, as shown in Chapter 20.

This book ends with a brief outlook of the contributions, gaps and challenges of crop physiology and its applications with emphasis on the interfaces with modelling, breeding and agronomy (Chapter 21).

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PART 2

Capture and Efficiency in the Use of Resources: Quantitative Frameworks

CHAPTER 2

Farming Systems of Australia: Exploiting the Synergy between Genetic Improvement and Agronomy

Ralph A. Fischer

1. INTRODUCTION

Plant breeding and research in crop agronomy both have contributed to farm productivity progress; developments in other areas are also important for progress, such as input supplies, market access, mechanisation and farmer skill. Of interest in this chapter is how progress has been achieved through breeding and agronomy, and in particular via their interactions, in a water-scarce rainfed cropping environment, namely the Australian wheat belt. Because of this, key aspects of interactions are elaborated in Section 1.1, although subsequent discussion is not confined strictly to interactions: synergy is taken more broadly to imply the inevitable complementation between variety and agronomy that has accompanied agricultural modernisation. Section 1.2 discusses the general aspects of current cropping in Australia. The chapter then deals with what may be loosely called major components of productivity progress. Throughout, results will be related to relevant environments elsewhere, and attention given to the role of applied crop physiology. Finally lessons will be sought and some future innovations canvassed.

1.1. The nature of breeding by agronomy interactions and their relation to progress

Breeding by agronomy interactions can range from simple to complex, while over time usually multiple complex interactions are involved. Box 1 describes the nature of the widespread positive interactions between genetic yield improvement and increased input supplies. Later on, reference is made to the less common crossover interactions with respect to inputs, and it will be noted that some desirable agronomic innovations do not necessarily involve increases in growth inputs (e.g. changed planting date or crop rotation, reduced tillage) but they still may benefit from variety change.

The complexity of progress is evident whenever scientists attempt to disaggregate the causes of past yield progress for a crop and region. Several examples are given in Evans (1993), one of the earliest being maize yield progress in Minnesota (Cardwell, 1982), while another, relevant to this chapter, is the time course of wheat yield in Australia, as initially illustrated by Donald (1965), and more recently by Anderson and Angus (2009; their Figure 2). Throughout such trajectories of yield progress, a series of new varieties are interacting beneficially with a multitude of changes in agronomy, both inputs and practices, as suggested by the labels in Figure 2. Despite these labels, it is actually difficult to disaggregate and quantify all the various causes of

BOX 1 Positive interactions between genetic improvement and crop agronomy

An interaction is defined statistically in its simplest form by the response to one factor depending on the level of a second factor. Here we are considering crop yield (or sometimes gross margin, $\$\,ha^{-1}$) as the response variable, with genotype as the first factor and one of various agronomic factors as the second factor. Commonly we can identify positive interactions when a higher-yielding variety responds more to an agronomic input increase, referring of course to a growth input which generally increases yield within its normal range of use, as is a nutrient like nitrogen (N) fertiliser (Figure 1a, also Figure 5). Statistically, this two-factor example is described as a main effect of modern variety of $630\,kg\,ha^{-1}$, one of nitrogen of $2060\,kg\,ha^{-1}$, and an interaction effect of $420\,kg\,ha^{-1}$. But the synergy is better captured in the small yield response to modern variety at zero N fertiliser level ($+210\,kg\,ha^{-1}$) and the modest response of old varieties to high N ($+1640\,kg\,ha^{-1}$), compared to the large response when modern variety and high N are combined ($+2690\,kg\,ha^{-1}$), which exceeds the sum of the initial responses by $840\,kg\,ha^{-1}$. Thus, there is non-additivity in the responses, which is another way of describing this positive interaction between variety improvement and N fertilisation. Note that it is impossible to separate the effects of variety and N within the interaction; at best we can say the response to variety is smaller than that to N, maybe only a half of it, but even that may change somewhat in favour of variety if the costs are included. Note also that it would be possible to transform the data of Figure 1a such that there is no statistical interaction (e.g. log transformation in case that relative responses are the same), but this is not a useful transformation when dealing with an input like N fertiliser, which must be paid for by extra kilos of grain produced.

Figure 1a illustrates a widespread phenomenon in crops, namely strong positive main and interaction effects on yield for genetic yield potential of a variety, on the one hand, and the supply of a major plant growth resource, on the other. Such interactions are probably impossible without accompanying main effects. Inputs include initial plant population (seeding density), major nutrients, water, carbon dioxide and solar radiation; air temperature and vapour pressure deficit are not growth resources but are important growth determinants that can be affected by management (e.g. sowing date). These positive interactions can be multiple if more than one agronomic factor is involved, and are part of a widespread phenomenon in agriculture, discussed by de Wit (1992). Harking back to the optimum law of Liebscher in the nineteenth century, he concluded that limiting factors in cropping are used more efficiently if other production factors are closer to their optimum, meaning that growth resources are actually used more efficiently as yield increases. This challenges the law of diminishing returns, seen, for example, by following the yield response to N increase alone, as this law has been subverted by the benefits of improvements in other production factors over time in the case of modernising agriculture. It is clear that genetic yield potential behaves like a production factor in this analysis. Higher genetic yield potential means more efficient use of these growth-related production inputs (nutrients, water, radiation), and that the production response to two or more inputs can be better than additive, the response region of the positive interactions. The consequence is that crop yields can increase faster than do individual input levels as agriculture intensifies over time, and the marginal efficiency of use of a particular input (Δyield/Δinput), even the average efficiency (yield/input), can increase: de Wit (1992) and Evans (1993) give several examples. One is maize in USA (Figure 1b): responses to the early use of N fertiliser look like diminishing returns, but after 1980, there has been a remarkable increase in average N fertiliser use efficiency which has now reached $60\,kg\,(kg\,N)^{-1}$. Cassman et al. (2002) argue that soil N in the maize system has likely reached a steady state and ascribe these improved efficiencies with respect to N over time to both genetic improvement in yield potential and improved agronomy, including management of the N fertiliser, higher plant density and conservation tillage.

Physiologically the responses to varietal improvement are not difficult to explain: a higher genetic yield potential arises either because more of the supplied input is captured (input uptake efficiency) and/or because the captured resource is used more efficiently (input utilisation efficiency). In the case of genetic progress and nitrogen, a detailed study with irrigated wheat (Ortiz-Monasterio et al., 1997) showed that both N uptake efficiency and N utilisation efficiency increased with genetic progress in yield potential, the former being more important under low N fertiliser levels and the latter under high levels. The N utilisation efficiency increase was associated with increased harvest index and slightly reduced grain N concentration, but little change in biomass produced per unit N uptake (another measure of N utilisation efficiency); in some circumstances, the greater lodging resistance of the shorter modern cultivars also contributes to the interaction with N fertility.

(Continued)

BOX 1 Continued

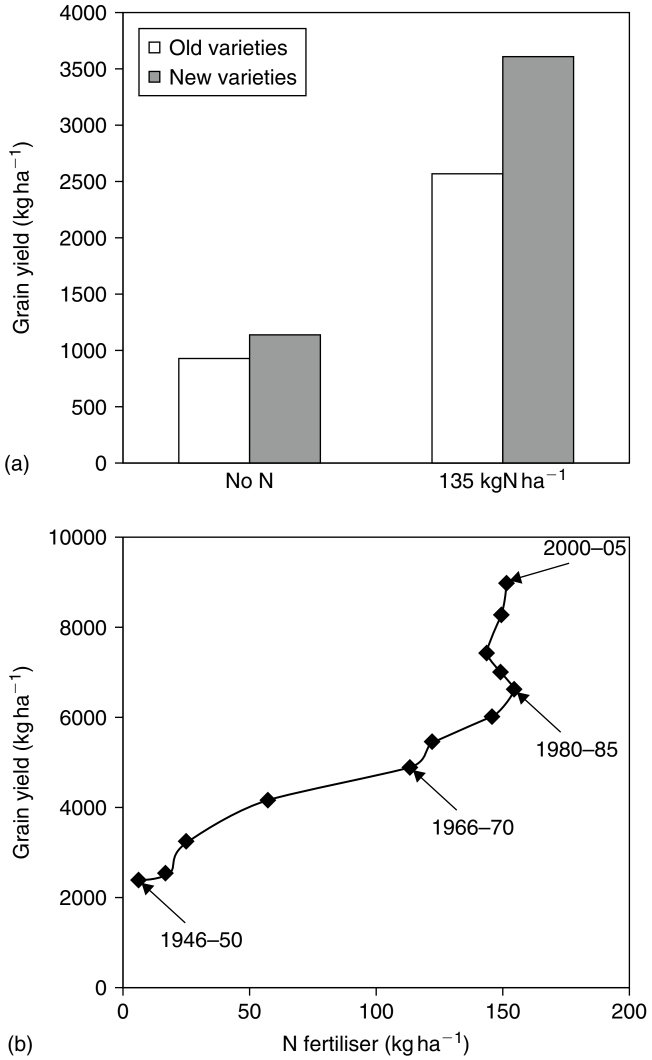

FIGURE 1

(a) Grain yield response of old wheat cultivars (avg of Timgalen and Gatcher) and new semi-dwarf cultivars (WW15 and Condor) to fertiliser nitrogen (at Jondaryan, Qld, 1971), developed from Syme et al. (1976). (b) Progress in average grain yield of all maize in USA plotted against average N fertiliser use on maize in USA; averages for five-year periods; replotting data from de Wit (1992) up to 1960, with data from FAO (yields) and USDA/ERS (N use) thereafter.

the progress. Agricultural economists, using farm survey data, have calculated impressive rates of growth in total factor productivity (outputs/inputs) in the unsubsidised Australian cropping industry over the last 30 years (2–4% p.a. exponential, Kokic et al., 2006); many factors appear to be associated with such growth, and some such as scale of production do not relate to variety and agronomy. Specific attempts to relate yield

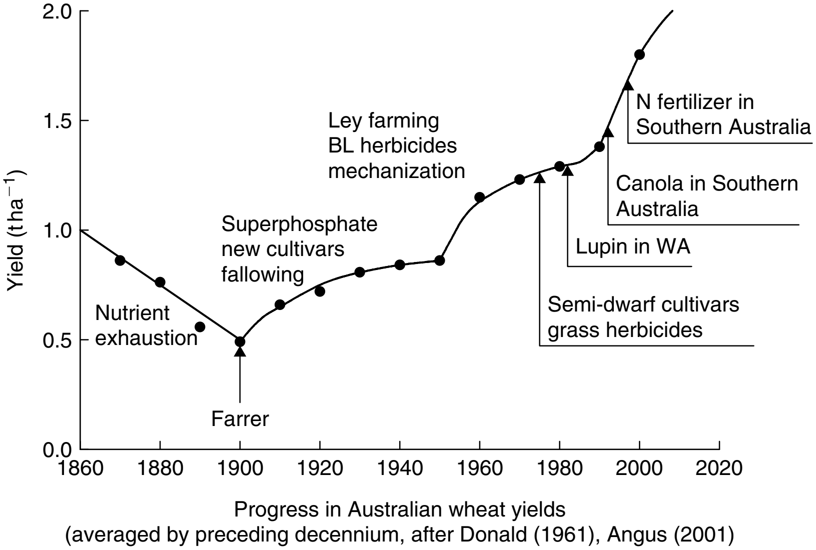

FIGURE 2

Wheat yield change in Australia between 1860 and 2000. (Source: Anderson and Angus, 2009, and derived from Donald, 1967 and Angus, 2001.)

progress to variety and agronomic change across more than 200 local government areas over recent decades have been equally ambiguous, except that they showed that yield growth (kg ha^{-1} year^{-1}) notably accelerated around 1980 and has been generally greater in wetter areas (Hamblin and Kyneur, 1993; Stephens, 2002). This chapter shall nevertheless attempt to elucidate the changes in wheat productivity depicted in Figure 2, as well as give some attention to changes in associated crops.

1.2. Some features of current Australian cropping

The semi-arid to sub-humid livestock-cropping zone of Australia (previously known as the wheat belt or the wheat-sheep zone) comprises the major part of cropping in Australia (Figure 3), and is dominated by winter cereals (wheat, *Triticum aestivum* L. and barley, *Hordeum vulgare* L.). A broad perspective is taken on this rainfed farming system, because of the importance of diverse crop sequences (rotations) and of grazing animals for whole system productivity. The climate ranges from temperate winter-dominant rainfall in the southwest, south and southeast (270–650 mm annual rainfall) to subtropical summer-dominant rainfall in the northeast (500–750 mm annual rainfall). Winter–spring cropping is possible throughout and predominates, with opportunistic summer cropping in the north-east; this amounts to one crop per cropping year, as double cropping is rare because of inadequate rainfall; indeed when long fallow predominated earlier last century it implied only one crop every two years. Climatic factors are described in more detail by Nix (1975) and Freebairn et al. (2006), and recently analysed in greater depth by Rodriguez and Sadras (2007). Based on these studies, it can be estimated that the average evapotranspiration for the wheat crop in Australia is around 300 mm, probably little more than half the potential evapotranspiration for wheat in this region.

Total Australian grain cropping area is shown in the first column of Table 1. More relevant to this chapter is the grain industry as surveyed by the Australian Bureau of Agricultural and Resource Economics (ABARE, 2006). This survey targeted an estimated total population of 30,900 farms, and the data of the survey

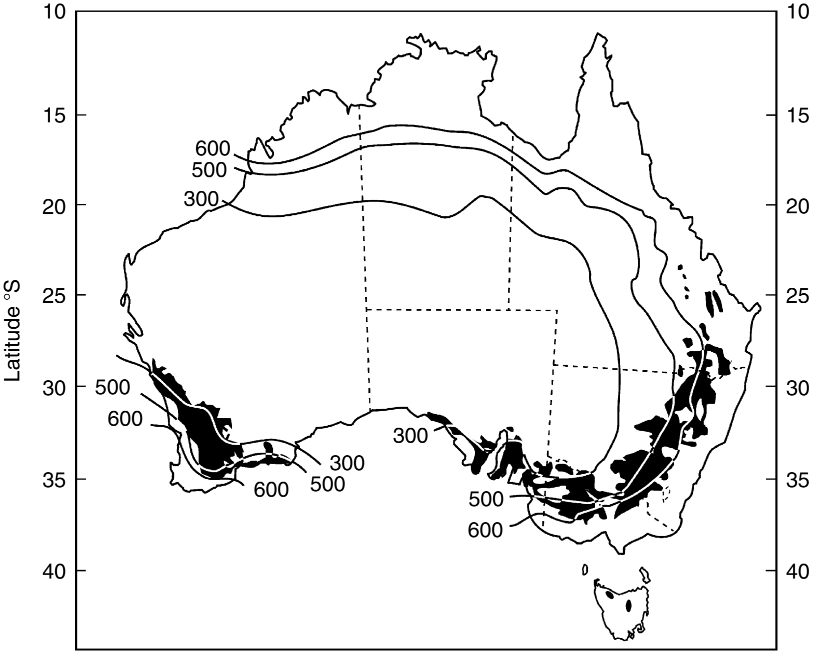

FIGURE 3

The distribution of wheat growing in Australia (solid black) and average annual rainfall in millimetres.

is given in the last two columns of Table 1. This sector currently grows approximately 23 Mha of annual grain crops, almost entirely under rainfed conditions, out of the total 60 Mha of land area operated. Wheat has strongly dominated crop acreage historically, and still is clearly the major crop, followed by barley, and then the broad-leaf crops such as canola (*Brassica napus* L.) and winter pulses (Tables 1 and 3); sorghum (*Sorghum bicolor* L.) is by far the most important summer crop but only occupies about 3% of the total cropped area on average. Of the total land area in the grains industry it is interesting to consider the 37 Mha or so that are not cropped in any year. A little of this land would lie fallow nowadays, although 40 years ago in the year before cropping approximately 40% of the crop land was fallowed (long fallow, plant growth suppression by tillage for more than eight months, Fischer, 1987), but this practice has declined markedly to be replaced, especially in the north, by shorter periods of mostly herbicide-maintained fallow. Thus the 37 Mha non-cropped land is either pasture or non-arable land (uncleared perennial vegetation, degraded land, etc). A 1997–1998 survey by ABARE (2006) indicated that 85% was crop plus pasture; applying this percentage today (i.e. assuming no further land clearing) indicates 28 Mha is pasture, and assuming all pastures are arable, the cropping intensity (crop area over total arable) is close to 45%. Indeed pastures are mostly managed in rotation with cropping, and along with crop stubbles grazed by sheep and cattle, of which there are approximately 70 m sheep equivalents (sheep number + cattle number × 8) on cropping farms in this zone. Of course not all commodities are to be found on each farm, but most farms nowadays would have considerable cropping diversity as well as pasture and ruminants. Farm size is large, and crop yields and input (fertiliser, biocide) levels are low by world standards (Tables 1 and 2), which is largely a reflection of the lack of water. The current cropping system and the associated natural resource base have been more fully described recently by Connor (2004), Freebairn et al. (2006) and Anderson and Angus (2009).

Table 1 Australian Grain Crop Area, Yield and Production Averaged for 2003–2004, 2004–2005, and 2005–2006

Commodity	Area[a] (Mha)	Grain yield[a] (kg ha^{-1})	Production[a] (Mt)	Surveyed Grain Farm Sector[b] Per Farm Average Area Sown (ha) or Livestock Number	% Area
Wheat	13.2	1856	24.4	407	56
Barley	4.62	2023	9.33	140	19
Oats	0.95	1645	1.57	27	3.7
Triticale	0.39	1789	0.73	na	
Sorghum	0.72	2532	1.83	20	2.7
Lupins	0.82	1251	1.02	56	7.6
Other pulses[c]	0.78	1224	0.95		
Canola	1.18	1342	1.56	44	6.0
Other oilseeds[d]	0.10	767	0.08		
Total crops	22.8		41.5	733	100
Total land				1965	
Sheep				1547	
Cattle				77	

Grains industry area sown and livestock number (average per farm over same years) are taken from farm surveys.

[a] *From FAOSTAT.*

[b] *Average across grain specialists and non-specialists cropping farms (total number about 30,900). Source: ABARE (2006) survey of the industry; rice excluded as 100% irrigated.*

[c] *Peas, chickpeas, lentils and faba beans.*

[d] *Sunflower and safflower.*

2. WATER-LIMITED YIELD AND RESOURCE/INPUT SUPPLY

2.1. General picture emerging from progress in wheat yields in Australia

Positive variety by input supply interactions abound under good water supply, but do the ideas given in Box 1 regarding multiple positive interactions still apply under the levels of water limitation common in Australian grain cropping? To try to answer this, the wheat yield progress for Australia shown in Figure 2 is dissected: overall progress and some input changes are summarised in Table 2. In the 100 years after 1891–1900, the national average wheat yield has increased at a rate of 1.3% (all % rates here are per annum calculated on an exponential basis as is common in economic studies). This has occurred even as the wheat area has increased several fold (Table 2), due to crop expansion into generally drier inland regions. This shift has undoubtedly decreased the water supply to the crop and dampened the scope for yield growth (Brennan and Spohr, 1985). As for climate change over the study period, data of Potgieter et al. (2002), who used historical weather records for all Australian shires currently growing wheat and a well-validated weather-based simulation model for wheat yield, suggest that average national wheat yield (for given modern varieties and agronomic practices across all shires) would have changed only about 0.09% due to weather variation over the twentieth century.

Table 2 Changes in the Australian Cropping Industry Over the Last 100 years

Descriptor	1891–1900	1951–1960	1991–2000
Wheat yield (kg ha^{-1})	500	1150	1800
Wheat area (Mha)	1.8	6.0	9.5
Wheat (% total crop area)	84	66	53
Other winter cereals[a] (% total crop area)	10	31	28
Legume (pulse) crops (% total crop area)	<1	<1	9
Oilseeds (% total crop area)	<1	<1	6
Fertiliser use P (kg P ha^{-1})	<1	8	22[b]
N (kg N ha^{-1})	0	0	30[c]
Wheat after legume[d]	0	<10	33

Data are shown by decennial averages, calculated from reports of Commonwealth Bureau of Census and Statistics (before 1961), and the Australian Bureau of Statistics (after 1961). The rate of change in wheat yield in the last 100 years has been 1.3% p.a. exponential.

[a] *Barley + oats + triticale.*

[b] *Calculated from FAOSTAT.*

[c] *Angus (2001).*

[d] *Author estimate of wheat on land that has seen legume pasture or legume crop in previous year or two.*

This slight positive influence upon yield progress just falls below statistical significance ($P < 0.05$) and is more than cancelled by the fact that drier shires were growing less wheat in 1900. However, another possible climatic complication is the increase in atmospheric CO_2 in the last half of the study period (estimated from Tubiello et al., 2007 as equivalent to an annual 0.2% yield increase for the whole century during which CO_2 rose from 295 to 370 ppm). This means that over the century wheat yield progress attributable to technology may be only 1.1%, although the progress on overall water use efficiency would likely have been greater. Chapter 20 further analyses the projected impact of climate change in select Australian farming systems.

Breeding progress for yield over the above-mentioned period can be estimated using a number of comparisons of historic cultivars grown side by side under typical rainfed conditions (Table 3). This suggests that the yield of Australian wheat cultivars has steadily increased by selection and breeding over the last 100+ years, at an average rate of close to 0.5%. The rate was somewhat higher for the period immediately after the introduction of semi-dwarf wheats in the early 1970s. Initially the yield increase was associated with shorter crop duration through phenological adaptation (more on this in Section 3.1), and more recently lodging resistance has been evident, but undoubtedly there have been many other genetic improvements in the efficiency of the plant, in particular harvest index (Siddique et al., 1989). Just as with modern varieties and N use efficiency (Box 1), modern Australian wheat varieties have increased overall water use efficiency because they acquire more water, they have a slightly higher transpiration efficiency for biomass and they have a markedly higher transpiration efficiency for yield because of the higher harvest index (Siddique et al., 1990, also Sadras and Angus, 2006). The rate of yield progress here, about 0.5%, is lower than that for well-watered or irrigated wheat elsewhere, around 1% (see Figure 1 in Chapter 15), but not unusually low for rainfed wheat. Lantican et al. (2003), however, recently reported a higher rate (2–3%) for CIMMYT materials. It should be noted that Australian breeders have also markedly increased and/or maintained disease resistance, and substantially improved grain quality; this is progress not necessarily reflected in yield increase alone.

There appears to be a large difference between overall yield progress of 1.1% and the 0.5% attributable to breeding. Since the 0.5% p.a. figure was measured under relatively modern agronomy (see yields in Table 3,

Table 3 Estimates of the Rate of Breeding Progress for Wheat Yield in Australia

Location	Variety Release Period	Rate of Gain (% p.a.)	Predicted Yield of Latest Variety (kg ha^{-1})	Source
Victoria	1886–1973	0.41	na	O'Brien (1982)
Canberra	1884–1978	0.72	>6000	Richards (1991)
New South Wales 1	1956–1974	1.03	na	Martin (1981)
New South Wales 2	1926–1984	0.60	na	Anthony and Brennan (1987)
New South Wales 3	1956–1984	0.90	na	Anthony and Brennan (1987)
South Australia	1860–1994	0.54	3660	Vandeleur and Gill (2004)
Western Australia	1884–1982	0.44	1780	Perry and D'Antuono (1989)
Western Australia	1894–1986	0.48	3200	Siddique et al. (1989)
Average	Long period	0.54		Excluding NSW 1 and 3

Data are obtained by growing historic sets of varieties side by side in different wheat belt locations, and regressing natural log of yield against year of release (included is the predicted yield of latest cv where available).

also dates of the studies), with varieties which were adopted by farmers, it amounts to a reasonable estimate at the farm level of the breeding plus the breeding by agronomy interaction components of progress. The remaining part of the progress, namely 0.6% p.a., includes not only agronomic change but also any change in the natural resource base of wheat cropping. Climate change has been dealt with, but changes can also occur in the soil resource (soil degradation or soil improvement): it is not possible here to unravel these, and in any case they are the product of farm agronomy. Overall therefore, it appears that the beneficial agronomic change explains 0.6% (1.1–0.5%) of the yield growth, slightly larger than breeding plus interaction. Other Australian reports, using a similar method, attribute a somewhat greater proportion of progress to agronomy (O'Brien, 1982; Turner and Asseng, 2005; Anderson et al., 2005), but these studies did not consider CO_2 rise or the breeding by agronomy interaction. Data of Anderson et al. (2005) suggest that the genotype by management component of variation may be greater than the genotype one, and highlighted a number of the synergisms (e.g. see Section 3.2). It is interesting that in the semi-arid winter rainfall dominant Pacific Northwest of USA, Schillinger and Papendick (2008) show similar yield progress (1.4%) for wheat under wheat-summer fallow (one crop in two years) between 1925 and 2006 (265 mm annual rainfall, projected average yields of 3200 kg ha^{-1} in 2006), but they did not attempt to separate effects of breeding and agronomy.

The broad nature of the important agronomic changes last century is fairly clear, and increased inputs were a big part of this (Table 2, Figure 2). Australian soils were mostly notably deficient in phosphorus (and often trace elements) in their native condition, such that soil fertility had become completely depleted of available phosphorus in cropped areas by 1890; superphosphate use was only just beginning in 1900, while no other agricultural chemical inputs were used then. Thus phosphorus fertiliser use (Table 2) has been a major part of the beneficial agronomic change since 1900. There may have been small benefits also from specific targeting of minor element deficiencies (Zn, Cu, Mn, Mo) that came later in the first half of the century (to some extent these, and sulphur, deficiencies would have been inadvertently alleviated by impurities in the single superphosphate which was the exclusive source of P until the 1970s). Other major management contributions

Table 4 Changes in Annual Inputs and Outputs for a Typical Wheat–Sheep Farm in Southern New South Wales from 1964 to 2005 (at Boree Creek, additions to Fischer, 2006)

Farm or Crop Attribute	Period for Which Attribute was Averaged				
	1964–1974	1975–1984	1985–1988	1989–1995	1996–2005
May–October rain (mm)	244	239	293	270	248
Cropping intensity (%)	45	44	41	48	50
Cereal (% crop area)	99	98	81	64	71
Liming (% farm area)	0	0	0	0	2.4
All wheat crops:					
Average sowing date	15 May	16 May	13 May	22 May	21 May
Semi-dwarf cultivars (%)	1	89	100	100	100
Cultivations per crop (No)	3.5	5.4	1.9	1.3	1.3
Biocides per crop (No)	0.3	0.9	1.5	1.9	3.1
Fertiliser N (kg ha^{-1})	0	0	3	12	33
Fertiliser P (kg ha^{-1})	8.5	10	11	17	21
Yield after long cultivated fallow (kg ha^{-1})	2048	2468	3534	–	–
Yield after wheat (kg ha^{-1})	1597	1936	2635	–	2739
Yield after canola (kg ha^{-1})	–	–	3408	3157	2923
WUE[a] after wheat (kg ha^{-1} mm^{-1})	8.9	9.7	12.8	–	14.1
WUE after canola (kg ha^{-1} mm^{-1})	–	–	16.4	14.2	15.0
Barley yield (kg ha^{-1})	1920	1745	2293	2471	2862
Canola yield (kg ha^{-1})	–	–	1442	1752	1132

[a] *WUE = grain yield/(estimated ET − 100).*

to yield were, in chronological order, improved timeliness of cropping operations with mechanisation, higher general soil fertility through legume pastures, better weed control with herbicides, break crop benefits arising from more rotation with broad-leaf crops, such as canola and pulses, in the last 20 years, as Figure 2 indicates, and most recently modest use of lime and N fertiliser, as reported by many authors (Donald, 1967; Hamblin and Kyneur, 1993; Angus, 2001; Stephens, 2002; Connor, 2004; Turner and Asseng, 2005; Anderson et al., 2005; Anderson and Angus, 2009).

It is difficult to get accurate national statistics on all the above-mentioned agronomic changes (some are shown in Table 2), but detailed data from a typical wheat-sheep farm in southern New South Wales (NSW) where annual rainfall averages 425 mm gives a good indication of the more recent changes and of the improvement in water use efficiency (Table 4). Over the period shown in Table 4 the cropping phase sequence changed from cultivated long fallow, wheat, wheat, barley, followed by several years subterranean clover pasture, to herbicide-maintained long fallow, canola, wheat, then another wheat, a pulse crop, and finally barley, followed by a longer pasture phase with lucerne as well as sub-clover; this is reflected in the increase in non-cereal crops, with little change in cropping intensity. Table 4 confirms that the overall progress in wheat yield is also progress in productivity per unit of water supply, which appears to have doubled in 40 years (rate of progress 1.8%). There is little doubt that the genetic increase in yield (about 1.0% for this 40-year period which covered the introduction of semi-dwarf wheats, Tables 2 and 4) has permitted exploitation of the improved inputs such that the efficiency with which the most limiting resource, namely water, is used by the crop has increased even more. It looks like another case of Liebscher's law in which multiple factor interaction, between variety and agronomic inputs, especially N and P supply, is an integral component.

The importance of water supply to the crop for exploiting other input interactions is seen when recent Australian wheat yield progress is disaggregated into adjacent higher and lower rainfall regions in the traditional wheat belt of southern NSW, with average annual (and seasonal, May–October) rainfall totals of 650 (350) and 480 (240) mm, respectively (Figure 4). Progress over the last 50 years was 2.4% in the wetter shires and 1.7% in the drier ones. With respect to further increases in yield potential in the face of water limitations, one might expect positive variety versus agronomic input interactions to continue to play a role, as breeding continues to raise yield (see also Section 2.3), but with the proviso that the water limitation itself probably constrains the size of other positive responses and interactions, as seen in Figure 4; besides, lower rainfall means greater risk in cropping which could inhibit the adoption of innovations (Stephens, 2002). Since yield increases more in higher-yielding modern varieties as water supply is increased to the crop (Figure 4, plus underlying physiological considerations discussed in the preceding text), any other agronomic practices which can increase water supply (e.g. conservation tillage, better nutrition and root systems) will exploit this positive interaction with variety; this could include supplemental irrigation which unfortunately is of minor importance in Australia due to lack of water.

The low fertility that prevailed in 1900 in Australian wheat soils is not unlike that more recently seen in much of the semi-arid crop lands of the developing world. For example, in the semi-arid barley areas of Syria, conventional wisdom had decreed that the barley zone (<300 mm annual rainfall) was too dry for fertiliser responses, and P fertiliser use had actually been proscribed (not unlike the early resistance to P fertiliser in Australia). ICARDA scientists however showed good yield responses of modern barley varieties to N and especially P (Cooper et al., 1987; Shepherd et al., 1987). They could explain these in terms of greater transpiration due to greater early ground cover leading to the substitution of transpiration for soil evaporation, somewhat higher transpiration efficiency and, finally, greater harvest index because of greater earliness with P and inherently higher harvest index in modern varieties. Bolstered by this understanding, recommendations were changed for the barley zone of Syria. Similar thinking was incorporated into simulation models for improved maize varieties in the sub-humid tropical parts of southern Africa, giving International Centre for Research in the Semi-Arid Tropics (ICRISAT) and national scientists confidence to recommend small amounts of N and P fertiliser for modern maize varieties, even

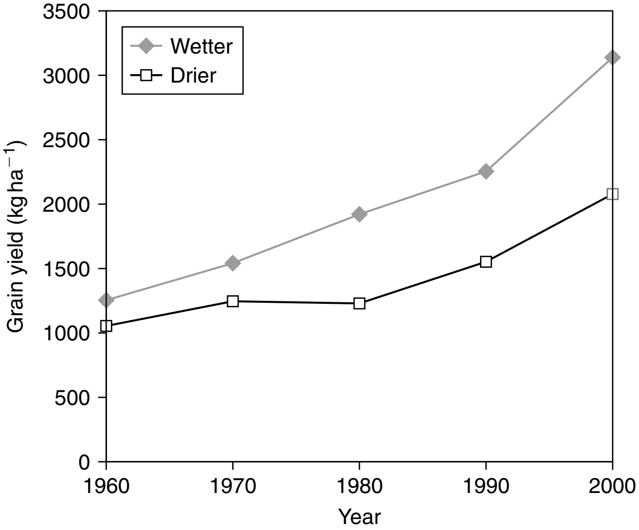

FIGURE 4

Change in decennial wheat yield in adjacent higher and lower rainfall shires of southern New South Wales over period 1950 to 2000: higher rainfall shires (Harden, Cootamundra, Young); lower rainfall ones (Bland, Lachlan, Urana).

in the driest cropping zones (Dimes, 2005). Not in the Australian case, but in both these recent examples, it is likely that crop physiological understanding, coming out of conceptual modelling in the former case (Fischer, 1981) and incorporated into a sound tropical maize simulation model in the latter (Keating et al., 2003), played an important underpinning role.

2.2. Genotype, seeding density and row spacing

Greater seeding rates and narrower rows has been one general aspect of the increase in agronomic inputs for higher-yielding varieties overseas; for example, maize improvement for favoured environments has exploited a positive population density by genotype interaction (Evans and Fischer, 1999), such that modern hybrids are clearly high-density responsive. Generally, however, such an evolution in this agronomic practice has been less evident for crops other than maize (with a laterally borne yield organ, maize is likely to respond uniquely to crowding). When Australia grew taller wheat cultivars, seeding rates tended to be quite low (20–50 kg ha^{-1}, Anderson and Angus, 2009) as might be expected from the low water supply and yield expectations. As yields improved through semi-dwarf varieties and higher fertility, an approximate relationship between optimum population density and expected yield, as influenced largely by moisture supply, has been recognised. At least in Western Australia extensive experiment suggest that in the absence of weed competition and at normal sowing dates, the optimum density is about 40 plants m^{-2} (20–25 kg seed ha^{-1}) for each ton per hectare of expected yield (Anderson et al., 2004). However few interactions between seeding rate and variety have been reported. As is common everywhere with winter cereals, the yield response curve to population is quite flat and differences amongst current varieties in the optimum population are quite minor and rarely significant. Similarly, with pulse crops in the Australian system, differences between varieties in optimum plant density are generally not recognised.

It is interesting to note that in the history of Australian crop improvement there was one notable attempt to exploit a hypothesised interaction between genotype and plant density. Donald (1968) proposed a uniculm wheat ideotype, efficient in the use of light and water (e.g. no waste due to unproductive tillers), but obviously requiring a higher optimum plant density for per hectare performance. He subsequently attempted to validate this concept, using barley, for which non-tillering types were then available. Initial results were promising, with a clear positive interaction between absence of tillering and plant density, and the revelation of considerable plasticity in spike size in the uniculms (Donald, 1979); later tests failed to confirm the promise of the barley uniculms (McDonald, 1990). In wheat, pre-breeders in Australia and elsewhere are now exploring the use of the reduced tillering via the tiller inhibition gene (*tin*), derived from a uniculm source. Looking at *tin* in four isogenic backgrounds under terminal drought, Duggan et al. (2005) showed that *tin*, which causes an early cessation of tillering and substantially less shoots, did reduce fertile spike number by 11%, while increasing kernels per spike and kernel weight; nevertheless, *tin* affected grain yield little, although there was a tendency for increased yield at higher planting density. It remains to be seen whether these novel plant types can deliver higher yields via a positive interaction with population density.

Where water supply is adequate, rows need to be narrow enough for full interception of radiation during the critical seed number determination period just before flowering (Andrade et al., 2002; Fischer et al., 2005). In Australia, small grained cereals have been sown in relatively narrow rows (traditionally 18 cm, nowadays up to 22 cm), as have most pulses and canola; only sorghum and sunflower (*Helianthus annuus* L.), and sometimes pulses like chickpeas (*Cicer arietinum* L.) growing on stored soil water, are sown in much wider rows. However, several management factors are currently favouring wider rows: most important is that it facilitates seeding into crop residue; also along with precision guidance, it facilitates seeding in the inter-row of the past crop (e.g. Simpendorfer et al., 2005 showed that in wheat after wheat this can reduce the incidence of crown rot disease); and finally, in several crops, such as chickpeas and sorghum, planting in wide rows is a way of appropriately metering out subsoil water in situations where most transpiration comes from that source. With wheat, at least in Western Australia, yield tends to decline as row spacing increases above 18 cm, and especially over 24 cm (Amjad and Anderson, 2006), but variety by row spacing interactions appear small. With high-input irrigated wheat, yield does not fall until spacing exceeds around 40 cm, and this depends on the variety's ability to capture light (Fischer et al., 2005). The sensitivity to row width in Western Australia can be readily explained in this winter rainfall environment with frequent small rain events, in terms of the expected increase in the wasteful soil evaporation component of evapotranspiration as row width increases (weed competition also tends to increase with wider rows). Varieties adapted to wider rows could become important in small grained crops such as winter cereals, canola and lentils (*Lens culinaris* Medik), for the agronomic advantages of seeding into residue offered by rows spaced at 25 cm and more are significant; such cultivars would need to cover the inter-row space rapidly unless amounts of residue were enough to substantially lessen soil evaporation and suppress weeds.

2.3. Selection for performance under low inputs

The broad picture just outlined with higher-yield potential varieties favoured by greater physical inputs to cropping might be expected to change where there are limits to a key input (e.g. water), and/or where these inputs are expensive (e.g. fertiliser P) while being present in the soil in poorly available forms. These are discussed here briefly.

Much has been written about the possibility of a crossover interaction with water limitation, whereby genotypes selected for performance under poor water supply are superior, but outranked by contrasting higher-yield potential genotypes when the water supply increases (e.g. Section 2 in Chapter 15): surely this is an exception to the above-mentioned notion of positive genotype by input interactions. Some physiological traits can even be envisaged that, if constitutive, might favour crossover, such as low tillering, or low stomatal conductance, or earliness for the low water supply–adapted cultivar (Blum, 2005). Products of the barley breeding programme at ICARDA are probably the best illustration of such crossover interaction (Ceccarelli et al., 1991). However, this programme has targeted very dry environments (mean plot yield below $1.5\,\mathrm{t\,ha^{-1}}$), and there is little evidence of such crossovers in Australian breeding. One reason is that water supply inevitably varies greatly from year to year at any location, and that the very low supply situations (say <150 mm) are not so common and anyhow contribute little to across-year average grain production. Besides, it is likely that breeding based on performance in multilocational testing across a range of water supplies can lead to the accumulation of traits which aid performance right across this range and/or are at least not detrimental under any such conditions; high harvest index would be one such trait and high resistance to stress-induced oxidative processes might be another. It is worth noting that with maize, both temperate varieties in USA (Duvick, 2005) and tropical ones in Mexico (Srinivasan et al., 2004), modern higher-yielding cultivars have an absolute yield advantage that is little affected by reduced water supply (and hence the relative yield advantage markedly increases). Overall, therefore, it would appear that specific adaptation to low water supply has not been delivered, nor indeed sought, and does not complicate the general conclusion regarding inputs and positive interactions, when, for example, agronomy manages to increase water supply (e.g. through conservation tillage).

Phosphorus fertiliser is an essential and expensive input for cropping. Typically the interaction between varietal yield potential and P fertiliser is similar to that shown in Figure 1a for N fertiliser, as reflected in Figure 5 and related again to the high harvest index and high P utilisation efficiency for grain of modern cultivars. Since soils often have high amounts of unavailable inorganic and/or organic P, but low levels of available P, there has been some interest in genotypes that may be able to source this unavailable P. Such genotypes, with high uptake of native soil P, would also contradict the general notion depicted in Figure 4 of a positive interaction with P supply, when compared to a normal variety with lower uptake at low P but similar yield potential at high P. McLachlan (1976) showed big species differences in P uptake efficiency in Australian soils, with buckwheat (*Fagopyrum esculentum* Moench) being superior to rye (*Secale cereale* L.), and rye in turn superior to two *Trifolium* spp. Batten (1993) reviewed differences between hexaploid wheat genotypes: there were genotypic differences in P use efficiency and they tended to be related to differences in P utilisation efficiency for grain, which in turn was associated with harvest index and with grain P% (as with N use efficiency above). Such genetic differences actually point to a positive interaction between yield potential and P supply. The magic wheat variety which is able to take up more native or applied P, such as

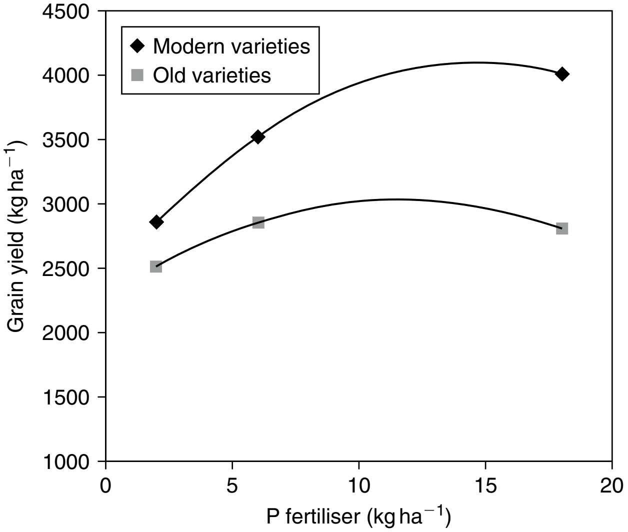

FIGURE 5

Grain yield response of old and modern varieties to P fertiliser under rainfed conditions at Wagga Wagga in 1979. Old cultivars: Olympic and Gamenya; new cultivars: WW33G and Egret. (Source: Batten et al., 1984.)

buckwheat or lupins (*Lupinus* spp.), has not been found, yet one would have imagined strong natural selection (Chapter 9) and substantive selection pressure to its advantage in breeding programmes which tended to apply sub-optimal rates of P fertiliser (Batten, 1993). Work in Mexico (Manske et al., 2001) comprising over 30 modern but diverse wheat genotypes did find a good association between P uptake and grain yield under both P deficiency and abundance, and a modest correlation between P utilisation efficiency and yield under P abundance on a calcareous soil; P utilisation efficiency was strongly associated with harvest index. It is possible that genotype by P supply crossover interactions could be found in this group of cultivars, and more importantly, cultivars profitably adapted to low P supply might be identified. Some primitive wheats and old varieties appear to have root features (e.g. many long root hairs) that might favour P uptake efficiency (E. Delhaize, personal communication) and efforts are being made to genetically engineer into wheat root, enzymes which break down insoluble soil P (Richardson et al., 2006). Although dealing with root traits has inherent difficulties, the successful incorporation of shallow branch roots angle in bean to improve capture of surface phosphorus is an example of the potential rewards from ex ante physiological thinking (see Section 5 in Chapter 13).

2.4. Varieties tolerant to soil toxicities

Soil toxicities are constraints on resource availability to the crop. Toxicities in the subsoil seem to operate by restricting root growth, the major consequence of which in the Australian environment is reduced yield because of reduced water availability to the crop (Dang et al., 2008). There appear to be no agronomic interventions to alleviate serious subsoil toxicities found widely in parts of southern Australia (e.g. salinity, sodicity, acidity, alkalinity, boron); genetic tolerance to these toxicities is therefore very useful and has been exploited with some success in the case of wheat tolerant to subsoil boron (Millar et al., 2007). Primer plants for making the hostile subsoil more accessible to roots of subsequent crops may also play a role (e.g. *Lotus corniculatus* thus benefited wheat in the study by Nuttall et al., 2008). Topsoil toxicities (Al, Mn, associated with acidity, salinity), to which waterlogging can be added, also inhibit crop root systems and access to inputs, but are more amenable to agronomic solutions: liming will be discussed later in Section 6.2; landscape water management affects salinity, and raised beds are being used against waterlogging in some wet regions; useful genetic variation in response to salinity and waterlogging exists and is currently the target of pre-breeding, but it has yet to be deployed against these problems to lessen the need for major agronomic intervention.

3. CROP PHENOLOGY

3.1. General phenological adaptation to the Australian environment

Adapting the duration of all crops to the growing environments predominating in Australia was important, since most crop introductions came from cooler temperate higher-latitude environments. In autumn-sown crops,[1] selection for earliness was essential for their adaptation to the drier Australian environment (Figure 1 in Chapter 12) and escape from stem rust (Section 5.1.2 in Chapter 17). This process of adaptation fitted the crop into the relatively short period of favourable moisture availability and high crop transpiration efficiency (through low vapour pressure deficit) between the late autumn and spring (Fischer, 1979). An added constraint was the need for flowering in many crops to be late enough to reduce the risk of spring frost damage around flowering to acceptable levels. Frost, and its converse, heat and declining moisture availability later in spring, defined an optimum flowering period for each location (Nix, 1975). Ideally sowing was in the late autumn, meaning soon after the "winter" rains were expected to arrive at least in the South; thus, the crop duration from sowing to flowering was approximately defined for each location. This varietal adaptation was achieved largely empirically over the last 120 years in the case of wheat (and more recently achieved for newer crops) as cropping spread from the cooler and wetter coastal and upland fringe into the drier interior. Siddique et al. (1990) studied wheat varieties released between 1860 and 1986 in Western Australia and found that days to flowering was reduced 0.143 days per year (of release). This move towards earliness in wheat, which appears to be ending now, makes an interesting contrast with wheat improvement in Argentina (see Figure 1 in Chapter 12): there, days to flowering did not change over much of the last century as yield improved markedly (Slafer and Andrade, 1989), possibly because early farmers came from Mediterranean countries of more similar latitude and temperature. Manipulating the phasic development of wheat was aided somewhat in the last 40 years or so by a growing understanding of the major vernalisation and photoperiod genes controlling crop phenology (Pugsley, 1983; Table 1 in Chapter 12): generally adaptation of the winter crops for Australia required a reduction in the need for long days, and for vernalisation, to initiate flowering. It is interesting to note that this is a rare case when the physiology and genetics of a trait at the plant level strongly reflected upon how the trait was expressed in the field crop (Section 5 in Chapter 1). This is a simplistic picture of the very important synergy achieved by matching variety duration with sowing date, but there are many intriguing variations and complications on this theme, as discussed here and in Chapter 12.

3.2. Fine-tuning crop duration to sowing options

Delayed sowing depresses the yield of current varieties (4–5% per week delay) yet it is often unavoidable because of the late arrival of the rains. On other occasions when the rains do arrive on time, late sowing could even be desirable, for example permitting better pre-sowing weed control or leading to less root disease, such as take-all, or smaller canopies and possibly less foliar disease. Such conditions could benefit from varieties earlier than those currently available. And even when rains and agronomy permit normal sowing, the question arises as to whether further shortening of the vegetative period (and hence later sowing) can be tolerated without loss of yield potential. Fischer (1979) suggested that there is an optimum amount of crop growth at anthesis depending on the water supply. Further, he argued that even very early varieties, especially

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[1] In Australia seasons are defined such that autumn is from 1 March to 30 May.

if selected for early vigour and ability to grow and photosynthesise under the generally sub-optimal winter temperatures, and if soil fertility is high, should be able to reach this optimum by anthesis in average or drier parts of the Australian wheat belt. The earliness, vigour and yield of barley alongside wheat (Siddique et al., 1990; Lopez-Castañeda and Richards, 1994) would seem to support the pursuit of a barley-like wheat. A possible trade-off in investment in roots and in stem-stored carbohydrate at anthesis with greater earliness could challenge this notion, but it is worthwhile noting that the highest-yielding wheat varieties currently available in the east seem to be amongst the earliest ever grown.

The current penalty for delayed sowing has encouraged ways of guaranteeing optimal sowing dates. In some regions, in particular Western Australia, the advent of widespread direct drilling (seeding without prior cultivation often aided by the use of knock-down herbicide) in the last 25 years has permitted, on average, earlier sowing and as might be expected, there is evidence that this especially suits varieties of longer-cycle, higher-yield potential (Anderson and Smith, 1990). The advent of effective herbicide-tolerant varieties (e.g. of canola, perhaps one day, wheat) might also call for longer-cycle varieties, by favouring reduced tillage and even permitting direct seeding into dry seedbeds. Better soil engaging sowing tools, and perhaps varieties to suit, may also help such a trend, by reducing soil moisture needed for sowing and/or germination and/or permitting deeper moisture-seeking seed placement.

The presence of grazing animals in many Australian cropping farms and the common shortage of forage in the autumn and winter in most regions have conspired to maintain an interest in very early sown (late summer–autumn, moisture permitting) long-duration crop varieties which can be grazed in the late autumn and winter and, if appropriate, then allowed to produce grain. This is the grazing-grain option, to be found in the wetter southern and eastern margins of the wheat belt, using long-cycle varieties of wheat, oats (*Avena sativa* L.) and triticale (*T. aestivum* L. × *S. cereale* L.). Vernalisation sensitivity is needed to prevent flowering before or during the winter. For many years, breeders have produced cereal varieties to meet the needs of the various early sowing niches, utilising appropriate degrees of vernalisation as is permitted by multiple vernalisation alleles (Table 1 in Chapter 12); in the highest, coldest locations true winter wheats are actually used for grazing-grain, as is also the case in the southern Great Plains of USA. Notwithstanding common periods of post-sowing moisture stress, early sowing usually provides substantial and nutritious forage within two to three months because good ground cover is reached by late autumn when water is usually available and transpiration efficiency is high. As expected the final rooting depth of these long-cycle varieties is greater (P.M. Bremner, unpublished), and this can be advantageous. A novel development in south-eastern Australia, partly stimulated by the appearance of wheat streak mosaic virus on early-sown wheat, is the use of long-cycle vernalisation–requiring canola varieties for the grazing-grain option (Kirkegaard et al., 2008b); canola not only produces high-quality forage but also brings rotational advantages (Section 6.1). Another consequence of grazing animals on the farm is worth noting: in a bad spring drought, failing crops can deliver more value through salvage grazing (as sometimes also used in West Asia and North Africa) or cutting for silage or hay. Varieties of wheat without awns are advantageous in these cases.

Lately there has been a trend towards increased grain cropping in the southern high-rainfall zone (>500 mm annual rainfall), where cropping originally began in Australia only to be replaced by fertilised leguminous pastures and limited fodder cropping. In this region, the greater moisture supply should support much higher yields, and it is estimated that crop area could increase by 50% on the 2.7 Mha already cropped (Zhang et al., 2006). This move is driven by several factors such as lower relative prices for livestock products, a build-up of soil fertility as a result of the many years of pasture improvement, along with better tillage options for water erosion control on sloping lands and better herbicides for weed control, and wheat and canola cultivars with a higher-yield potential. In the case of wheat, even greater crop yields are predicted by simulation models (6–8 $\mathrm{t\,ha^{-1}}$) once adapted longer-cycle cultivars become available – cultivars that would be grown purely for grain (Zhang et al., 2006). This requires the breeding of new winter varieties with the right phenology, disease resistance and grain quality; tolerance to, or agronomic measures against, waterlogging is also needed.

4. CROP PROTECTION: WEEDS AND DISEASES, INCLUDING SOIL BORNE

It is generally suggested that modern high–yield potential cultivars are more susceptible to biotic stresses, in particular weed competition, and foliar disease and certain insects. To some extent this may be due to the pest organisms that flourish more under the higher nutritional level (soil, leaf) to which these varieties respond; in other cases, characteristics of the genotypes themselves play a role in increasing susceptibility (for example a greater harvest index, representing a greater investment in yield organs and often less in leaves and stem, makes the crop less competitive and less well buffered against loss of leaf area). Either way, as a result of this, three-way positive interactions can be seen between modern varieties, and fertiliser and biocide inputs. This is especially so where water supply is high, for example in cropping regions of Central and Northern Europe (Chapter 4) and South America (Chapter 3), and under favourable conditions in parts of Australia in some years. But it is clear that weeds are potentially damaging in almost all situations. The importance of water supply in Australia means that managerial decisions on these agronomic practices are often tactical such that they are adjusted as the crop develops and season unfolds, with the water supply and biotic stress potential becoming clearer, and as a function of varietal susceptibility. It is an excellent example of the increased use of another input, namely managerial skill, in order to improve the efficiency of biocide use. But there are breeding opportunities and complications to be found behind this simple overview. Chapter 17 focuses on diseases and Chapter 18 deals with crop–weed interactions in detail. Here we deal briefly with these abiotic factors to highlight the synergies between agronomy and breeding.

4.1. Dealing with weeds

Weeds probably make up the most costly biotic stress in Australian cropping. Their control nowadays depends very much upon the use of herbicides, to such an extent that some weed species, in particular annual ryegrass (*Lolium rigidum* L.), have evolved resistance to important herbicides. This is especially so in continuous reduced tillage systems. Integrated weed management is seen as the way forward, and competitive crops and cultivars could be part of this. Oats and barley are seen as more competitive than wheat and canola, and pulses are generally the least competitive (Lemerle et al., 2001). Amongst wheat varieties, it is of special concern that some modern ones appear to be less competitive against weeds (e.g. rye grass, wild oats) than some older ones (Vandeleur and Gill, 2004). With canola, one study clearly showed that a low early vigour variety (associated with genetic triazine resistance) had markedly increased yield loss and weed biomass in the absence of weed control, compared with a more vigorous normal variety (Lythgoe et al., 2001).

Thus considerable attention has recently been given to the genetic basis in wheat of low yield loss in the presence of weeds (using rye grass or wild oats, sometimes wild turnip) and of good weed suppression (Lemerle et al., 2001). In wheat, competitiveness was positively, though weakly, associated with plant height, which is a problem because yield is negatively associated with height, at least down to a mature (unstressed) height of about 90 cm (Figure 1 in Chapter 14). Attention has therefore been paid to early traits which may not carry a weed-free yield penalty, such as early vigour, early leaf size, leaf area index and light interception at the end of tillering, tiller number and low tiller angle. Most of these show negative correlations with per cent yield loss and/or weed growth in certain genetic backgrounds, under certain conditions of season and weed infestation (Lemerle et al., 2001; Coleman et al., 2001; Vandeleur and Gill, 2004). However, none of these associations have yet proved strong enough to be taken up as selection criteria by breeders, who are reassured by the fact that despite trade-offs, under most circumstances weedy yield is positively correlated with weed-free yield (Lemerle et al., 2001). A simple scoring system has been developed which at least could be useful in classifying varieties (Lemerle et al., 2001). In a related effort to help farmers, many new varieties have been screened for the absence of herbicide susceptibility, a problem that arose with some varieties and herbicides in the past (Lemerle and Hinkley, 1991). Little attention has been paid to underground competition, despite its likely importance under rainfed conditions, although work continues on genetic variation in allelopathy which, measured as ryegrass root growth suppression, can be substantial in seedlings of some wheat cultivars (Wu et al., 2000). Given the threat of growing resistance to herbicides in key weed species of cropping in Australia, research to enhance the competitiveness of cultivars, including exploitation of allelopathy, will continue.

The advent of herbicide-tolerant cultivars has had big impacts on crop agronomy, most notably in the case of glyphosate-tolerant cultivars of soybeans in USA and in South America (Chapter 3) where their advent gave a major boost to reduced- and zero-tillage crop establishment methods. More relevant to Australia, which has only a few thousand hectares of soybeans, is the Canadian experience with genetically modified (GM) canola. Adoption of both glyphosate- (Roundup Ready) and glufosinate-tolerant (Liberty Link) GM varieties was fast, driven by ease of weed control, and also involved reductions in tillage (Stringham et al., 2003). Australia has extensively adopted Roundup Ready cotton, a largely irrigated crop not considered here, and has a few varieties of non-GM herbicide-tolerant canola and wheat: the former suffers yield disadvantages but is widely grown because of the magnitude of weed problems with canola. The complementary interaction between cultivars, and reductions in tillage and expensive herbicides, is however likely to be substantial, when, for the first time in Australia, GM herbicide-resistant canola varieties reach farmers in NSW and Victoria in the 2008 growing season. The impact could be even greater than that in Canada given the greater problems Australian farmers face with inadequate soil moisture for germination. This in turn will lead to greater pressure for, firstly, herbicide resistance in other crops (especially the less-competitive pulses) and, secondly, better integrated weed management to avoid build-up of herbicide resistance in weeds. Researchers were poised to release GM glufosinate-resistant lupins more than a decade ago in Western Australia but it was thwarted by unnecessary caution, with long-lasting negative consequences.

4.2. Dealing with diseases

Agronomic inputs do not always increase: sometimes input reduction is the key part of a desirable genotype by agronomy interaction. One of the best examples of this is the replacement of disease control using fungicide by control through genetic resistance: rust resistance breeding in wheat is the most striking case (e.g. Figure 6a; Sayre et al., 1998), while Figure 6b shows an example of canola from Australia (Marcroft et al., 2003). Only a (partial) gross margin calculation properly reveals such desirable interactions, which involve the substitution of an expensive agronomic input by a low-cost genetic trait.

Diseases have caused considerable yield losses in Australia. Brennan and Murray (1988) calculated the actual losses in wheat amounting to 18% of gross crop value. About half of this is foliar disease and the other half root and lower stem pathogens; without genetic resistance the former would have been much higher. Fungicide as seed dressing kept the third type of disease, namely inflorescence and kernel diseases, at a low level. The disease loss percentage is likely to be higher in the newer broad-leaf crops such as pulses and oilseeds, where some insect problems also arise. Traditionally wheat breeders in Australia have always placed great emphasis on genetic control of foliar diseases; they have been successful with respect to the major biotrophic diseases (the rusts, *Puccinia* spp.) of cereals. However, since these data were compiled, there has been an increase in fungicide use for foliar diseases as more effective fungicides have become available and as disease pressure has mounted. For example, there has been tactical use against stripe rust, and strategic seed and fertiliser dressing with new more powerful systemic fungicides against many diseases is common. Susceptible cultivars are often grown in these situations precisely because they have higher-yield potential, leading to a crossover cultivar by level of fungicide interaction. Chapter 3 (Section 3.1) discusses the tradeoff between disease tolerance and yield potential of wheat in the Pampas.

Necotrophic foliar diseases of cereals such as yellow leaf spot (YLS, *Pyrenophora tritici-repentis*) and septoria (*Septoria tritici*, *Stagonospora nodorum*) on wheat, and scald (*Rynchosporium* spp.) on barley, have proved more difficult to completely control with host plant resistance; their incidence is more dependent on season and situation (e.g. YLS is favoured by low N, whereas septoria and scald is favoured by high N). The level of varietal resistance substantially influences variety recommendations and farmer choice, especially when conditions are expected to be favourable for the disease (e.g. stubble retention favours YLS, whereas early planting favours septoria, as it does the major foliar diseases of most pulses). An excellent example of this comes

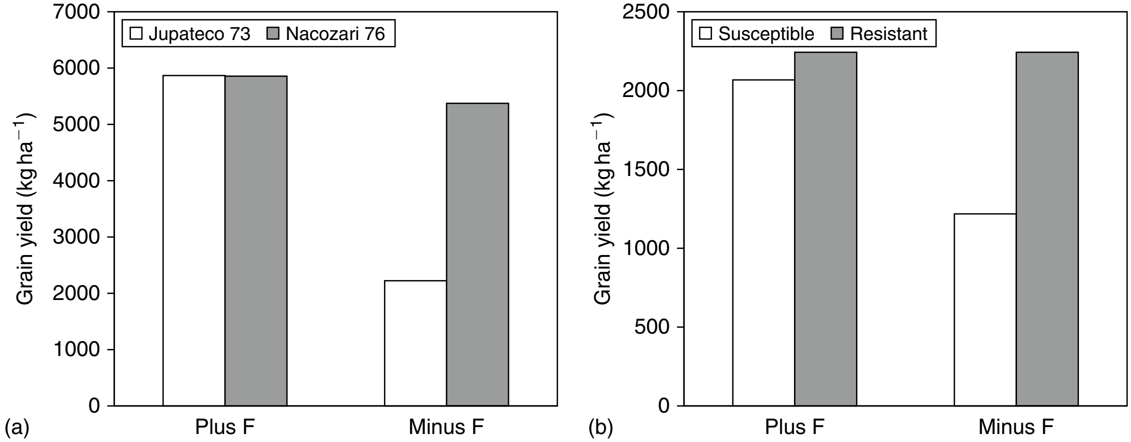

FIGURE 6

(a) Grain yield of susceptible and resistant wheat varieties (Jupateco 73 and Nacozari 76, respectively) in the presence of leaf rust (Puccinia recondita) with and without fungicide protection (Plus F and Minus F, respectively); data from Sayre et al. (1998). (b) Grain yield response to seed fungicide protection (Plus F, Minus F) against blackleg (Leptosphaeria maculans) in susceptible and resistant canola varieties (Karoo and Surpass400, respectively). Data from Marcroft et al. (2003).

from chickpea in the semi-arid winter rainfall areas of West Asia: breeding *Ascochyta* blight resistant varieties has permitted early winter sowing which gives an average 70% yield increase over the traditional spring sowing so as to avoid the disease (Singh et al., 1997), because the winter planting sees a much more favourable climate for growth and grain filling.

Soil diseases (including nematodes) contribute about one half of the wheat yield losses calculated above, and would be considerably higher were it not for cultural and crop rotational control measures (see Section 6.1). Wherever genetic resistance is available (e.g. cereal cyst and root lesion nematode, *Fusarium* crown rot) breeders are trying to use this. However, this is rarely adequate and is not even possible with many soil biotic stresses. Therefore, the different propensity of different crop species (and sometimes varieties within species like wheat; Rovira and Simon, 1982) to tolerate and/or suppress soil pathogens remains the major control strategy through crop rotation (see Section 6.1), which is sometimes complemented by seed treatment. A major new research initiative by Australia's Grains Research and Development Corporation (GRDC) is attempting to better understand the complex interactions in the rhizosphere between crop genotypes and microbes, including the use of microbial additives to control soil pathogens.

5. CROP ATTRIBUTES FOR REDUCED TILLAGE SYSTEMS

As in many parts of the world, Australian farmers have shifted towards reduced tillage, including direct drilling (seeding without prior tillage), with varying degrees of soil disturbance and of retention of residue of the prior crop or pasture. Late burning of the prior crop residue is still common with direct drilling, but gradually with the newer tillage machines and systems, there is greater retention of residue on the soil surface, a practice commonly known as conservation tillage. In the early twenty-first century well over half of farmers were practicing some form of conservation tillage in Australia (Lyon et al., 2004); the figure is closer to 100% in Queensland (Thomas et al., 2007), where it is often accompanied by controlled traffic (confining all vehicles to fixed tram lines across the field). Reductions in tillage and increases in surface residue have many potential implications for crops and cultivars; most are positive, some are negative, and some justify the attention of breeders.

5.1. Implications arising from increased soil water capture and storage

A steady abandonment of the traditional long (>eight months) cultivated fallows has been part of the equation, and these have often been replaced by more efficient herbicide-maintained non-cultivated fallows of usually lesser duration. The net effect of these reductions in tillage, and retention of crop residue, is probably greater available soil moisture at the time of sowing in many situations due to less runoff and less soil evaporation in the albeit often shorter fallow period (Fischer, 1987; Lyon et al., 2004). This has also been accompanied by a greater awareness amongst farmers of soil-stored water at the time of sowing as an important element in crop management, such that crop and variety choice are now more influenced by this input. For instance, farmers in the northern cropping areas tend to crop opportunistically, sowing either a winter or summer crop only when the available soil water at sowing time has risen to a predetermined quantity, as discussed in Chapter 19 (Section 4). Another consequence in the western region in particular has been faster and earlier sowing, favouring slightly longer-cycle cultivars as already mentioned. Greater implications for breeding from improved water storage efficiency are seen, for example, in the Great Plains of USA, where stored moisture is more important, and where extra moisture from conservation tillage has permitted the replacement of traditional wheat fallow using conventional tillage (one crop in two years) with more intensive cropping systems that approach one crop per year and combine the winter wheat with other crops including sorghum, maize, millet and sunflower (Lyon et al., 2004), and has favoured the use of longer duration varieties (Nielsen et al., 2005). In the semi-arid Mediterranean Pacific Northwest of USA, conservation tillage has permitted continuous spring wheat cropping to compete economically with traditional winter wheat–summer fallow where annual precipitation is more than about 300 mm (Schillinger and Papendick, 2008), but not where it is only 152 mm (Schillinger and Young, 2004); the latter wheat-growing region is probably the driest in the world!

Sometimes, especially in the eastern and northern wheat areas of Australia, good available soil water at sowing time is accompanied by a dry surface, encouraging deep seeding into moisture: wheat cultivars with longer coleoptiles are needed to guarantee emergence under such conditions (and under normal moisture conditions when, not uncommonly, there is poor seeding depth control), and one pre-breeding programme is pursuing this (Rebetzke et al., 2005). The original semi-dwarf wheat cultivars in Australia were based on Norin 10 dwarfing genes (*Rht1* and *Rht2*); these have short coleoptiles and emerge poorly from depth, especially if the soil temperature is high. New dwarfing genes are being tried (e.g. *Rht*8) with which the coleoptile is long but the stature remains optimally short (Rebetzke et al., 2005). Successful breeding here should facilitate an agronomic innovation to better guarantee timely crop germination, namely deep moisture-seeking seeding. Seeding into deep moisture (at 15 cm!) ahead of the winter rains is especially critical for maximum yield in the winter wheat–summer fallow rotation practiced in the Pacific Northwest (and in the climatically similar Anatolian Plateau of Turkey); this is where deep-furrow drilling of wheat originated and where varieties with long coleoptiles are also sought (Schillinger and Papendick, 2008).

5.2. Increased mechanical impedance

The most significant of the other physical changes with conservation tillage and direct drilling appears to be related to the greater topsoil physical impedance, which was widely shown to reduce early vigour in wheat, with variable effects on grain yield depending on the spring rains (Cornish, 1987). Later the phenomenon was related to the slowing of seedling root growth that interacted with certain inhibitory *Pseudomonas* spp. to reduce early seedling vigour (Simpendorfer et al., 2002). Cultivar interactions with direct drilling have been found but are complicated by whether the reduction in vigour and the general level of vigour of the cultivar are appropriate for the water supply of any particular growing season and location (Cornish, 1987). This led to the conclusion that breeding wheat specifically for direct drilling (without crop residue retention) was not warranted, because of the variable yield response to early vigour. Subsequently, cultivar differences in vigour response to direct drilling have not been widely explored, although one study compared a highly vigorous experimental line (Vigour 18) with the less vigorous cultivar, Janz. It found that the more rapid root growth (and top growth) of Vigour 18 was unaffected by growth in uncultivated soil, while that of roots and shoots in Janz was substantially reduced; possibly the rapidly growing roots were able to escape the inhibitory pseudomonads (Watt et al., 2005). Other studies suggest that greater early vigour is good for water use efficiency in winter rainfall environments (South and Western Australia) and can help with weed suppression. Therefore, a pre-breeding programme has pursued the considerable genetic variation which exists in this trait in wheat (Richards and Lukacs, 2002); this could be especially beneficial in situations where direct drilling reduces early vigour. Section 4 in Chapter 13 analyses the agronomic value of root vigour in relation to no-till and capture of nitrogen and water.

5.3. Implications of other physical conditions of soil

Surface soil changes affected by reduced tillage also include small changes in soil temperature (lower minima above residue and smaller diurnal fluctuations below it), but unlike higher latitude environments, or lower ones, these are not very significant for cropping in Australia's temperate latitudes. Crop residue on the soil surface, if in sufficient quantity, can impair seedling emergence in the case of wheat and especially small-seeded crops such as canola. In the case of wheat, the problem is not unlike excessively deep seeding with Norin-10 semi-dwarf wheats, and the solution could lie in short wheat cultivars with longer coleoptiles (Rebetzke et al., 2005). For canola sown into wheat residue, the solution seems to be agronomic, involving sweeping the stubble away from the seeded row (Section 5.2 in Chapter 3; Bruce et al., 2006).

5.4. Retention of crop residue and disease

It is widely recognised that crop residue retention can affect the amount of inoculum for certain diseases. With reduced tillage in Australia this is especially relevant in wheat, with a tendency for increased incidence of certain root rots (bare patch, *Rhizoctonia*, and *crown rot*, *Fusarium pseudograminearum*) and of the foliar disease YLS. No-till with residue retention is absolutely essential in the north-eastern wheat belt for erosion control, and brings yield benefits. More than 50% of this region is thus cropped, and for this to become more widespread, agronomic solutions including diverse crop rotations have become critical, while wheat breeders must now place more emphasis on resistance to both YLS and to crown rot in varietal selection (Thomas et al., 2007). Also it is recognised that in reduced tillage situations, crown rot–susceptible durum wheat is less appropriate than crown rot–tolerant bread wheat (Kirkegaard et al., 2008a).

6. FARMING SYSTEM DIVERSITY

6.1. Crop diversity and crop rotation

Traditionally wheat has dominated rainfed cropping in Australia, with small amounts of other cereals (barley, oats, sorghum), but since the 1980s some broad-leaf crops (canola, winter pulses, summer mung beans) and triticale have appeared and steadily increased in area; the broad-leaf crop area has now reached around 15% of total cropping area (Tables 1 and 4). This diversification into broad-leaf crops, which are inevitably grown in rotation with cereals, has brought reduced production and marketing risks as well as several rotational benefits. Summarising 135 site years of Australian data, Angus et al. (2001) reported that the yield of wheat following a broad-leaf crop, relative to that of wheat following wheat, was 40–50% higher after grain legumes and 20% higher after canola. Kirkegaard et al. (2008a) recently reviewed these rotational benefits as including disease control, via underground effects and via non-host residue so important in conservation tillage, improved residual nitrogen and sometimes more phosphorus and water, easier weed control, and better soil structure and facilitated root access. The point here is that the diversification has been dependent on substantial efforts in the fields of plant introduction, selection and breeding. In the extreme case of narrow leaf lupins (*Lupinus angustifolius* L., about 800,000 ha now planted), the breeding commenced with domestication of the wild species, from which the first non-shattering short and early cultivar was selected and released in 1967, to be followed by continuous improvement through local breeding (French and Buirchell, 2005). Major breeding has also been undertaken, especially in the last 30 years, for canola and peas (*Pisum sativum* L.), and more recently broad beans (*Vicia faba* L.), chickpeas, lentils, soybeans (*Glycine max* L.), mung bean (*Vigna radiata* L.), and the latest addition, Indian mustard (*Brassica juncea* L.). Initially in some cases, reasonably well-adapted varieties could be directly introduced from overseas (e.g. chickpeas and lentils), but the future of all these new crops now depends upon ongoing local breeding targeting in particular drought and disease resistance (as does that of all the cereals).

Even with more rotational options, growing two or more wheat crops in succession is not uncommon, and growing a long sequence of wheat has actually been shown to lead to suppression of some of the serious root diseases seen in the early years of continuous wheat, for example *Rhizoctonia solani* (Roget, 1995). Wheat variety rotation may be important in such situations, with certain varieties not showing the common 10–20% yield depression associated with a second wheat crop, a response linked not to well-known wheat root pathogens but to lower populations of cophiotrophic bacteria in the rhizosphere (Gupta et al., 2004). There is also evidence from these workers that the effect of the second-crop wheat variety interacts with tillage (cultivated vs. direct drill), while the yield depression is markedly lessened when the first cereal is barley.

6.2. Ley farming: crop–pasture rotation

After the Second World War, cropping in rotation with P-fertilised leguminous pasture grew rapidly in popularity, because of the soil N benefits for pastures and crops alike and the attractive prices for wool. All of the leguminous pasture species were from overseas but most released cultivars nowadays are the product of intensive local selection and breeding programmes; the latter is especially so for the most dominant pasture legumes, namely subterranean clover (*Trifolium subterranean*), annual medic (*Medicago* spp.) and lucerne (*Medicago sativa*), with breeding for low oestrogen content and pest resistance (mites and aphids) as unique features. Pasture rotation has been adopted for a number of reasons, with the gross margins from grazing for wool or meat production during the pasture phase being important initially; subsequently, there have been periods when prices and weather have not favoured attention to pasture quality (Hamblin and Kyneur, 1993). Restoring soil organic matter and nitrogen fertility, and soil structure, to the benefit of subsequent crops, having animals for crop salvage grazing and fallow management, having more options for weed control, and minimising overall risk are all other important reasons. Having a deep-rooted perennial pasture plant such as lucerne for limiting deep soil drainage (and thus reducing the risk of dryland salinity build-up) is lately considered another advantage in some situations. More speculative is a possible role of perennial pastures (lucerne, *Phalaris*) in making the dense subsoils of the duplex soils common in Australia more accessible to the roots of following annual crops (McCallum et al., 2004; Nuttall et al., 2008). Overall, the crop–leguminous pasture rotation remains important, leading to substantial reductions in the N fertiliser demands of the system (Angus, 2001; Anderson and Angus, 2009), and its future depends inter alia on continuing efforts to genetically improve the pasture species. At the same time, certain conditions (high N prices and low animal ones) could boost the current incipient interest in leguminous green manure crops (e.g. *Vicia* and *Lathyrus* spp.).

Leguminous pastures are not without problems. Invasion by aggressive annual grass weeds (e.g. ryegrass, barley brass and brome grass, some being hosts to wheat root diseases) as fertility builds up is one, and the gradual acidification due to nitrate leaching is another. Only with the advent of selective grass herbicides could the former problem be dealt with. This has permitted over the last 30 years a shift of cropping back to the wetter fringes of the cropping zone, which traditionally had not been cropped in the last 60 years or so, in order to take advantage of the huge build-up in soil fertility: with good weed control, it was here that the high–yield potential semi-dwarf wheat and adapted canola varieties were able to cause a veritable revolution in grain yields (see wetter shires in Figure 4).

Legume-based pastures, fuelled by superphosphate fertilisation over many years, have, because of nitrate leaching, caused serious acidification of low–exchange capacity soils in the wetter parts of the cropping zone of Australia. This has resulted in significant aluminium and manganese toxicity for certain important agricultural species, in particular barley, wheat, canola, *Phalaris* and lucerne. Liming these soils is the only long-term solution, but genetic adaptation to acid soils has, in the last 30 years, become a goal for breeders of crops targeting these regions, while other species, more tolerant to acidity (especially triticale), have become more common. Such crops and cultivars can buy time and generate income to cover the cost of liming.

7. ADOPTION OF IMPROVED VARIETIES AND PRACTICES BY FARMERS

To exploit the synergy between variety and agronomy, farmers must adopt the improved technologies. Therefore, some attention to adoption is relevant here, especially because Australia has had several recent important innovations in this field, along with the more traditional and important agricultural extension activities of the public sector. One innovation came from agronomists taking a physiologically based look at actual and attainable wheat yields and the apparent large gap separating them (Fischer, 1979; French and Schultz, 1984). It is the approach of French and Schultz (1984) which most successfully illustrates the point: plotting grain yields for many seasons and locations against crop water use (Figure 7) revealed a clear upper yield boundary, the limit imposed by water supply given best practice management, and a large number of points well below this limit because of one or other failure in management and/or variety. The authors claimed that the slope of the upper limit (20 $\mathrm{kg\,ha^{-1}\,mm^{-1}}$) and the abscissa intercept (110 mm) represent transpiration efficiency for grain and soil evaporation, respectively. This is a simplification, pointed out by the authors and subsequently by several others, but the strength of the approach lay in both its simplicity and its sound physiological basis, as set out earlier in an acclaimed conceptual model of water-limited crop yield (Passioura, 1977). The points on Figure 7 were from experiments but they may well have been farmers' fields as Cornish and Murray (1989) and Angus and van Herwaarden (2001) later showed. The rule of thumb for water-limited yield contained within Figure 7, and certain derivations from this, including ones for other

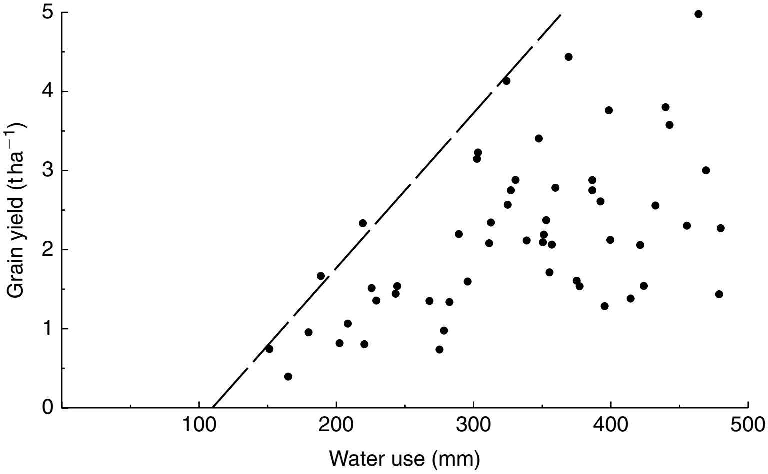

FIGURE 7

The relationship between grain yield of wheat and water use (soil water plus rainfall). The line (slope 20 kg ha^{-1} mm^{-1}) indicates the attainable yield from the water in excess of the soil evaporation (110 mm of water). (Source: French and Schultz, 1984.)

crops such as winter grain legumes (Siddique et al., 2001) and canola (Robertson and Kirkegaard, 2005), has subsequently been accepted as a very valuable benchmark for good farmers and most advisers as they strive to improve profitability. Awareness of the size of the yield gap between actual and water-limited potential yield stimulated much interest in the rapid identification of yield constraints in the field – essential simple metrics for in-season benchmarking such as stage of development, plant number, tiller number, ground cover, spike number, green leaves at flowering, root condition, etc., which were popularised through farmer groups and tabulated in guidebooks labelled as Crop Check or Top Crop, pointing Australian advisers and farmers towards practical solutions. The model reflected in Figure 7 has been very useful in examining wheat yields in rainfed dry environments around the world (Sadras and Angus, 2006).

Parallel to the above-mentioned developments, we have seen a fascinating evolution of the thinking of the agricultural economics profession in Australia with respect to the provision of management advice for farmers (McCown and Parton, 2006). Initial excitement about the quantification of relationships between profit and agronomic management, and then profit and enterprise mix, using increasingly complex computer models, led to disappointing impact and ultimate disillusionment with the approach. The advent of simulation models of crop and pasture growth (e.g. Keating et al., 2003) based on steadily increasing knowledge of the underlying physiological and environmental relationships, and remarkable increases in computer power, seemed to offer new hope for crop physiologist–economist teams, under the banner of decision support systems for crop and farm management. Again farmer and farm adviser acceptance of the new tool was limited. McCown and Parton (2006) argue that the problem lay in the formulation of the results of such modelling. An innovative and more participatory approach, involving the farmers and their actual biophysical situations, in which the models deliver expected outcomes for likely specified scenarios (governed by, for example, measured planting soil water and N, the seasonal climate forecast, variety and practice) is showing promise. In one endeavour (Carberry et al., 2002), such simulations, based on actual varieties and weather, have recently become available as online guides for wheat management tactics (for example, whether to apply supplemental nitrogen or fungicide) and as a physiologically-speaking sounder way of benchmarking yield possibilities in any particular situation compared with the simpler approach of French and Schultz (1984) outlined in Figure 7. Such modelling also permits crop, variety and management decisions to be tested in advance, taking into account the best available seasonal climate forecasts at the time. It becomes another tool in smart decision-making by agronomists and farmers, such skill being a socio-economic input of increasing importance for progress, leading to smarter exploitation of the synergy between variety and management. Section 4 in Chapter 3 illustrates the successful adoption of modelling tools by large cropping companies in the Pampas, and Section 4 in Chapter 19 illustrates the application of modelling to integrate spatial management and rainfall forecasting in a risk framework in northern Australia.

8. LESSONS AND NEW OPPORTUNITIES

This review has pointed to numerous beneficial interactions between varietal change and agronomic management; inevitably they are linked to advances (main effects in the terms of Box 1) in either or both fields. Before looking for future opportunities, it is useful to ask how past advances came to be recognised: were they anticipated and consciously sought after, and by whom, or were they recognised in retrospect? Table 5 attempts to summarise this for the key interactions, following approximately the order in which they were presented in the preceding text.

Many of the above-mentioned innovations and associated processes were discussed thoroughly by Donald (1967), at least those operating up to around the mid-1960s plus some of the later ones (but not all) already anticipated by this famous Australian agronomist and crop physiologist. From Table 5, it can be seen that advances range from new agronomic techniques creating opportunities for breeders (e.g. cheap N fertiliser and reduced tillage) right through to advances driven initially by breeding (e.g. disease-resistant cultivars and broadleaf crops). Early ideas have almost always arisen overseas (not surprising, since less than 2% of world agricultural research is done in Australia), followed by essential adaptive research in Australia;

also progress has been slow, although speeding up somewhat in the last 50 years as research investment has increased. Few efforts have been, or are, anticipatory; examples that were anticipatory would be the search for broadleaf crops for diversification, and the current selection for wheats with long coleoptiles and early vigour, and GM crops with herbicide resistance. Many examples were reactive, seizing opportunities created by enhanced yield potential or solving problems that arose from other desirable changes (e.g. from retention of crop residue with reduced tillage).

In Table 5, there is an apparent lack of examples of farm level impact where the innovation derives from ex ante physiological or crop physiological thinking, particularly Australian thinking (a powerful example would have been the initial development of selective herbicides, but this came from plant physiological research overseas). Yet Australia prides itself in having developed early on a strong standing in crop physiology, starting, for example, with the landmark papers of C.M. Donald and colleagues (Donald, 1968; Donald and Hamblin, 1976), and reflected in works of Evans (Evans, 1975, 1993). Specifically in the area of rainfed agriculture we had seminal papers by Fischer and Kohn (1966), Nix and Fitzpatrick (1969), Greacen and Hignett (1976), Passioura (1977) and Fischer (1979) which, stimulated by several key works from overseas (de Wit, 1958; Hanks et al., 1969), caused water use and transpiration efficiency to assume the central role in thinking about water-limited yield. Subsequently crop physiology blossomed, being well supported by various funding agencies, recently in particular by national organisations such as CSIRO and GRDC, and farmers themselves, with the implicit expectation that there would be an impact. Sound and often innovative physiological thinking permeated much of the subsequent literature focusing on advances in crop performance in Australia, many examples of which have been cited in this chapter. But the role of crop physiology in these examples has been much more facilitating, particularly through the establishment of biophysically realistic frameworks within which possibilities of progress can be evaluated. Passioura (2002), in commenting on the rapid advances in wheat yield in the last 30 years (see Figure 1), argues that 'all these advances are reflections of better understanding of the environmental biology of crops, especially in terms of "real" environments (farms) … … understanding mostly … at the levels of ecology and crop physiology'. His paper also gives many examples of ex ante crop physiological thinking about future advances, some of which have been realised in the last decade (see also Richards et al., 2002). Perhaps therefore the contradiction raised at the outset of this paragraph was explained by the time needed for crop physiological thinking to penetrate the initially separate areas of plant breeding and agronomy. This time might seem to be unnecessarily long possibly because of conservatism or institutional barriers or imperatives to deliver quick impacts, but cannot it seems be blamed on an unsympathetic national research funding environment. Another point is that any impact at farm level is inevitably the result of collaboration amongst many disciplines, including breeding and agronomy, and it is hard to attribute progress to any one discipline such as crop physiology. A somewhat similar situation has prevailed at CIMMYT with respect to the input of crop physiology into wheat and maize breeding and agronomy (Fischer, 2005), where collocation of physiologists in the crop teams should have eliminated any institutional barriers: initial enthusiasm for physiology in the early 1970s waned, as did support in the face of competing imperatives, but the work never quite ceased and lately has permeated much thinking by breeders and agronomists at CIMMYT, as well as delivering some specific impacts (e.g. drought-resistant maize for the tropics – Srinivasan et al., 2004; see also Chapter 15). It is probably fair to conclude that crop physiology has come to be accepted as an essential part of any breeding or agronomy team (just as had more specialist disciplines such as plant pathology and cereal chemistry). The integrating power of crop physiology in fact now becomes essential if new understanding at lower levels of plant organisation, such as functional genomics, is ever going to deliver yield increase, whether under water limitation or not (Passioura, 2002; Fischer, 2008; Chapters 11 and 14).

Finally, some examples of a more proactive crop physiology are canvassed, firstly under the heading of agronomy. Management tools based on computer simulations of crops and cropping systems, and taking advantage of currently weak but steadily improving seasonal climate forecasts, are being used (Hammer et al., 2002) and will improve. Obviously this will facilitate tactical management of crop inputs. However, it also has implications for the choice of crops, and varieties within crops, ahead of any particular sowing period, taking advantage of existing varietal diversity, and perhaps stimulating breeders to produce more

Table 5 Key Beneficial Breeding and Agronomy Advances and Interactions in Australia Over the Last 100 Years and Their Origin

Advance/Interaction	Source of Idea	Realization in Australian Research and Farmers Fields
Yield potential and nitrogen supply	Japan, USA, Mexico, Western Europe	Legume leys boosted fertility, after which semi-dwarf varieties beginning in 1970s realised the benefit; N fertiliser came even later, with Australian Wheat Board campaign targeting $2\,\mathrm{t\,ha^{-1}}$ and 10% protein in late 1980s; see also Angus (2001)
Yield potential and P supply	UK where first chemical P fertiliser developed	P fertiliser use began in mid 1890s at about $10\,\mathrm{kg\,P\,ha^{-1}}$; higher yields in 1970s and beyond demanded higher P rates. Specific P use efficiency to save P input is now sought in pre-breeding
Yield potential and planting density/arrangement	Western Europe	No major interaction in Australia, but zero till now driving wider rows, with possible breeding implications
Early drought–tolerant varieties permit cropping in drier interior	India, William Farrer, and others	Early Australian wheat selectors and breeders deliberately sought earliness; this and new mechanisation aided farmers to open up interior
Winter cereals for grazing and grain	Breeders S.L. Macindoe, R.H. Martin, A.T. Pugsley	Presence of sheep on farms and autumn shortage of feed drove this innovation from middle of twentieth century
High rainfall zone cropping with long-cycle varieties	Western Europe, J.L. Davidson	Winter wheat breeding programme of CSIRO began in 1980s; some European cultivars and agronomy imported. Full realisation incomplete
Disease-resistant cultivars to avoid fungicides	Farrer, Minnesota State University, W.L. Waterhouse, I. A. Watson, R.A. Macintosh	Started early in twentieth century before fungicides were available, continued due to economic imperatives driving wheat farming, and due to strong public funding
Yield potential and weed management by herbicides	UK basic plant research, then private Northern companies	Herbicides readily adopted from 1950s, short cultivars came later, later still was evolution of weed resistance pushing some pre-breeding on ‘competitiveness’
Cultivars for reduced and zero tillage	UK, USA, South America	Agronomic revolution began in early 1970s with knock-down herbicides, and continues; breeding against residue diseases followed, but to realise other synergies (e.g. early vigour) incipient
Herbicide-resistant cultivars to save herbicides and facilitate direct seeding	Major ag chemical companies USA, Canada, South America	Adopted in cotton in 1990s, canola 2008, but transgenic approach for others crops currently constrained by regulations
Legume pastures for soil fertility and diversification	Norfolk rotation with origins in the seventeenth century Flanders and the eighteenth century United Kingdom	Accidental introduction of annual legumes, followed in mid-twentieth century by better management (P fertiliser, trace elements especially Mo), and then targeted introduction and legume breeding

(Continued)

Table 5 Continued

Advance/Interaction	Source of Idea	Realization in Australian Research and Farmers Fields
Pulse and oilseed crops for diversification of cereal rotation	Europe, Canada, and various farsighted Australians (e.g. J.S. Gladstones)	Introduction, selection and then breeding for local adaptation are the essential first steps, agronomy followed. Lupins is a special case
Adoption of improved varieties and appropriate agronomic packages	Largely Australian agronomists, crop physiologists and agricultural economists	Attainable yield as a simple function of rainfall or water supply, and the FARMSCAPE approaches, arose in Australia, as did the notion of crop checking. Crop simulation modelling was a truly international effort, but Nix and Fitzpatrick (1969) were one of the first to simulate wheat yields, then J.T. Ritchie's CERES had a big influence in 1980s

or different genetic options. Precision agriculture (Chapter 19), which in Australia means satellite-based centimetre-accurate tractor guidance and/or field map–based variable-rate technology, has been adopted gradually; a precursor has been controlled traffic under manual guidance with fixed wheel bases for all field operations. Inter-row sowing to reduce contact with root disease inoculums from the previous crop has been mentioned. In Argentina, with better water supply, precision guidance has opened up possibilities for mechanised relay cropping (e.g. soybeans into wheat) and new varieties suited to this and other novel systems (Chapter 3). In Australia, it is possible that short-cycle winter cereals planted into the inter-rows of a lucerne variety, which is selected to be weakly competitive in the topsoil, could provide an integrated crop–pasture system to better manage deep drainage and dry land salinity (Humphries et al., 2004). Currently there is significant basic research on soil and rhizosphere microbiology, which is a relatively new field, and some applied research on microbiological soil additives. Gupta et al. (2004) point to fascinating varietal interactions, such that further research in this difficult area may reveal exploitable synergies. Hostile subsoils often limit water extraction and hence the yield of crops in Australia; crop rotational solutions via the primer-plant concept need further attention. Another avenue for increasing water available for crops may be the reduction of soil evaporation using low-cost inter-row nano-films (reflective or not, biodegradable or not), bearing in mind that in semi-arid parts of China significant areas of crop such as wheat, groundnut and canola use inter-row plastic film. It should be remembered that any management innovation that increases water supply to the crop reaps extra synergy from varietal improvement and from most other inputs.

What initiatives could come from the breeding side of the equation, noting that biotechnology, and in particular genetic engineering, open up many new possibilities? Diversification into triticale, a new crop now grown on 400,000 ha of acid soil in eastern Australia, is the product of biotechnology, while ultra-narrow row cotton, with desirable earlier maturity and easier weed control, is the product of genetic engineering for glyphosate resistance. Glyphosate-resistant soybean and imidazolinone herbicide–resistant sunflower allow for previously unimagined intercropping opportunities in the Pampas (Section 5.1 in Chapter 3). Looking forward, any trait that facilitates weed control brings substantial management benefits: allelopathic cultivars would seem a difficult but worthwhile objective, while a new mode-of-action broad-spectrum herbicide accompanied by engineered resistance for crops, which is very difficult and expensive to achieve, is surely needed globally. Varieties, the phenology of which adjusts perfectly to changes in sowing date to always give optimum flowering, would eliminate the need for farmers to carry several varieties in face of inevitable uncertain sowing dates. Genetic resistance to spring frosting would likely permit earlier flowering and higher yields; at the same time, it would place more emphasis on agronomic techniques to ensure early sowing. Genetic modifications to change the composition of crop residue (e.g. to facilitate microbial fermentation) could make residue more suitable as a feedstock for biofuel production, placing much more pressure on careful soil management. Residue for local pyrolysis plants and the simultaneous production of bio-oil, syngas and charcoal for returning to the soil (Laird, 2008) must surely have breeding implications. Breeding could produce new crops for the rainfed Australian environment, creating further agronomic opportunities: drought-resistant maize and tropical legumes (e.g. pigeon pea) represent possibilities for the north-east; perennial wheat to lessen dryland salinity would be the most extreme example, but even this is now being sought (Bell et al., 2008). Environment benefits could arise from altered N fertiliser tactics that would accompany improvements in nitrate uptake efficiency, as genetic engineering now promises (Shrawat and Good, 2008). Nitrogen management could also benefit from crops and varieties whose roots have the ability to inhibit nitrification, recently identified in, for example, the tropical grass genus, *Brachiaria*. The production of more F1 hybrid varieties of crops, perhaps facilitated by genetic engineering, with their likely higher seed costs, would place a special premium on seed processing and sowing machinery for accurate spaced seeding and reliable germination. As in many other potential areas of interaction, it is useful to note that it is one thing to seek interactions amongst current modern varieties, but quite a different result can arise if wider gene pools such as old varieties, land races and wild species are examined. This assumes that appropriate traits for screening can be specified. Wheat examples where useful trait variation is coming from such sources include the extra early vigour found in the line Vigour 18, the *tin* gene for low tillering, new salt tolerance genes in durum wheats and roots with more and longer root hairs as a possible avenue to high P uptake efficiency.

The uncertain but generally negative implications of future climate change for cropping in an already dry continent like Australia are beyond the scope of this chapter (but see Chapter 20). It suffices here to point out that the need to adapt to this will serve to intensify the challenges and opportunities for crop breeding and agronomy research, while not necessarily changing much the nature of the challenges, for these are already seen within the normal spatial and temporal variation faced by farmers and field researchers. Also, some developments already referred to, such as reduced tillage and more efficient nutrient use, will be relevant to mitigation of greenhouse gas emissions.

9. CONCLUDING REMARKS

This chapter has identified many synergies between breeding and agronomy, such that it is hard to imagine agricultural progress without advances in both fields, and frequent specific interactions. Evans (1993), writing extensively on the subject, concluded that the ongoing synergy between genetic and agronomic change is the essence of productivity improvement and the undiminishing returns to inputs in agriculture. It is also evident that it is difficult to be predictive about breeding by agronomy synergies, for they often result from unanticipated advances in one field or the other; it would be unwise to assume they have been exhausted. Again quoting from Evans (1993), 'many futures for agriculture await invention, and our responsibility is not to foreclose the options and opportunities'. Only sometimes can crop physiology be seen as driving synergies that have had impact on farmers' fields, but it has always bolstered understanding and thereby aided ongoing exploitation. More recently, as such understanding continues to improve, and challenges and opportunities multiply (e.g. functional genomics, seasonal forecasting, climate change and precision agriculture), physiology plays a more predictive role (e.g. in pre-breeding and simulation modelling), and this is likely to continue, with more examples of ex ante input into impact ensuing. It is important that it continues to be supported nationally and attention be given to institutional structures which facilitate synergy between the whole range of research areas which must come together for full exploitation of the synergies in farmers' fields.

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CHAPTER 3

Farming Systems of Argentina: Yield Constraints and Risk Management

Pablo Calviño and Juan Monzon

1. INTRODUCTION

In non-subsidised agricultures, farm income depends primarily on commodity prices, crop productivity and production costs. Prices are a major source of uncertainty and risk, and farmers have only a small degree of control of this variable in terms of risk management, for example future trading. Increasing productivity is the key to sustaining and increasing farm income, hence its critical role for agricultural sustainability. High productivity is the result of the best combination of management variables that influence crop production in a given paddock, and how paddocks and whole-farm activities are organised and integrated (see Section 4 in Chapter 19).

Cropping area in Argentina is around 31 million ha; major crops are wheat, sunflower, soybean and maize (Figure 1a). Barley, rice, peanut and sorghum have a narrower regional spread. There are some remarkable characteristics of current Argentinean agriculture: (i) around 56% of acreage is rented to their owners (Cloquell et al., 2005); (ii) 70% of the agricultural land is under no-till (Gonzalez Montaner, 2004); (iii) soybean is the main crop occupying more than half of the total cropped area (Figure 1a); (iv) 99% of soybean is transgenic glyphosate resistant and (v) around 30% of the soybean is sown as double crop after harvest of winter crops (mainly wheat). Since 2005, the aggregated soybean production of Argentina and Brazil exceeded the production of USA, making South America the largest world producer and exporter of soybean and derived products (Figure 1b).

Leading farmers and consultants in the Pampas are familiar with basic concepts of crop physiology, including the notions of capture and efficiency in the use of resources (Chapters 6–8) and the notion of critical periods for grain number and yield determination (see Section 5 in Chapter 12 and Section 3.2.2 in Chapter 15). The books by Andrade and Sadras (2002) and Satorre et al. (2003) are examples of popular resources dealing with management practices for individual crops formulated from a physiological perspective. Using these principles and a range of models, the main drivers and biophysical constraints of yield and yield responses to management have been identified for the main grain crops in the Pampas (Sadras and Hall, 1989; Magrin et al., 1993; Andrade, 1995; Calviño and Sadras, 1999, 2002; Mercau et al., 2001; Calviño et al., 2002, 2003a, 2004; Menendez et al., 2008). A physiological perspective has also been applied to estimate yield gaps and identify yield constraints for other crops such as potato (Caldiz et al., 2001), and for identification of drivers of grain quality (Chapter 16). Although agriculture in the Pampas has benefited from crop physiology to manage individual crops, less attention has been paid to the application of these

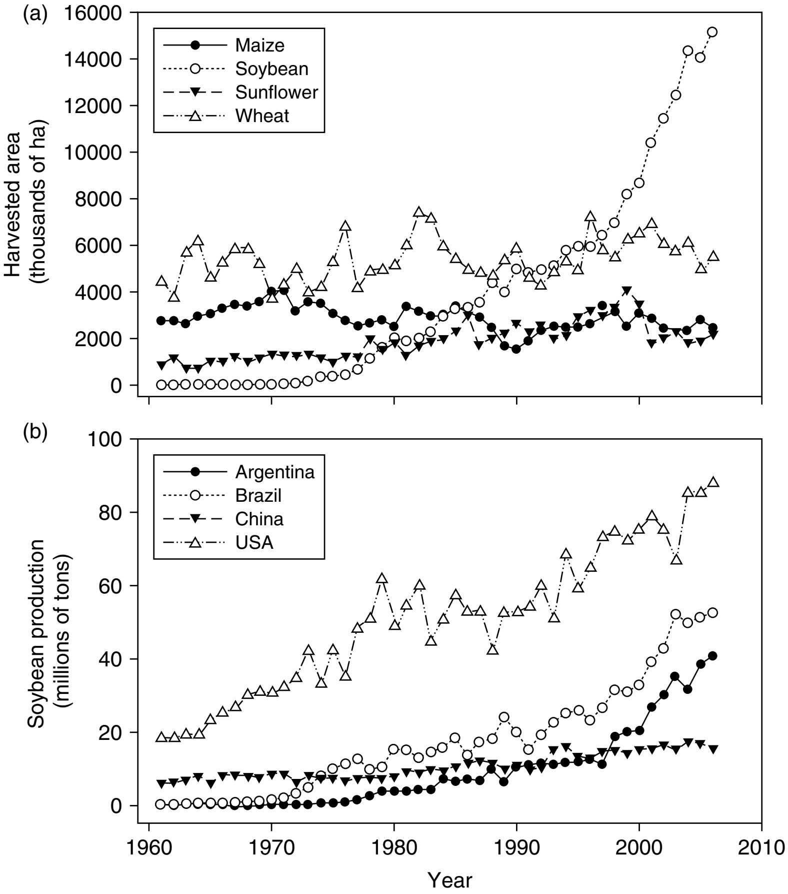

FIGURE 1

Time trajectories of (a) area allocated to main grain crops in Argentina and (b) soybean production by major producing countries worldwide. In 2005, the aggregated production of Brazil and Argentina exceeded that of USA for the first time. Source: FAOSTAT (http://faostat.fao.org/default.aspx).

principles for integrating of individual crops in cropping systems and risk management (Messina et al., 1999). The aims of this chapter are to highlight the application of physiological principles to elucidate and overcome environmental constraints to yield of individual crops, and to illustrate how a commercial company utilises principles of crop physiology and modelling to whole-farm risk management with a focus on productivity and environmental outcomes.

2. THE PHYSICAL ENVIRONMENT

The physical characteristics of the Pampas relevant for agriculture have been described by Hall et al. (1992). For the purposes of this chapter, we selected three locations in a south–north (S–N) transect (Figure 2) with contrasting soils (Table 1) and climates (Figure 3). Balcarce (37°50′S) is a temperate-cool, typical wheat

Table 1 Typical Soils at Three Locations in Argentina

Location	Soil Type	Soil Series	Soil Depth (cm)	Plant Available Water (mm)	Organic Carbon (%, 0–30 cm)
Balcarce	Typic Argiudol	Tandil	80	102	3.5
			140	190	3.5
Pergamino	Typic Argiudol	Rojas eroded	160	208	1.0
		Rojas	210	274	1.6
Las Breñas	Durustalf	Pampa	80	101	1.6
	Udic Argiustol	Capdevilla	180	256	1.4

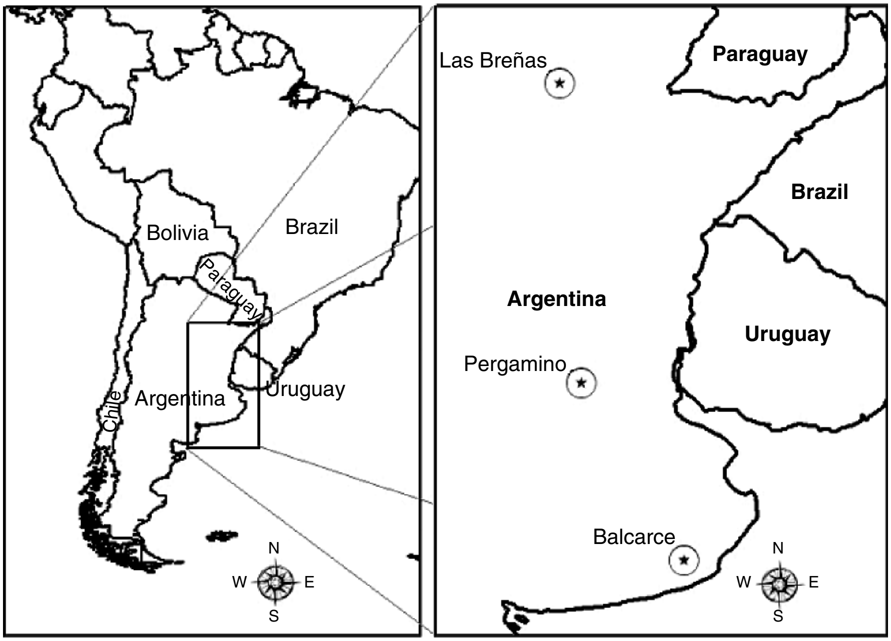

FIGURE 2

Location of Balcarce, Pergamino and Las Breñas, three contrasting environments for the case study in this chapter.

growing area. Pergamino (33°53′S) is a temperate location at the core of the former maize-belt of the Pampas; it is one of the most productive areas of Argentina. Las Breñas (27°05′S), in the Chaco region, has a subtropical climate with a dry season. Mean annual rainfall for these locations is similar, that is from 900 to 1000 mm but the seasonal distribution is quite contrasting (Figure 3). Balcarce has a very even seasonal distribution of rainfall, Pergamino has a more marked seasonality with low winter rainfall and Las Breñas has a strong seasonal regime with 80% of the annual rainfall between November and April. Mean annual reference evapotranspiration is 950 mm in Balcarce, 1133 mm in Pergamino and 1360 mm in Las Breñas. A coarse climatic water balance indicates water deficits occur in all three sites mainly during summer, with the more critical situation in Las Breñas (Figure 3). Temperature increases northwards and frost-free period ranges from 217 days in Balcarce to 284 days in Las Breñas.

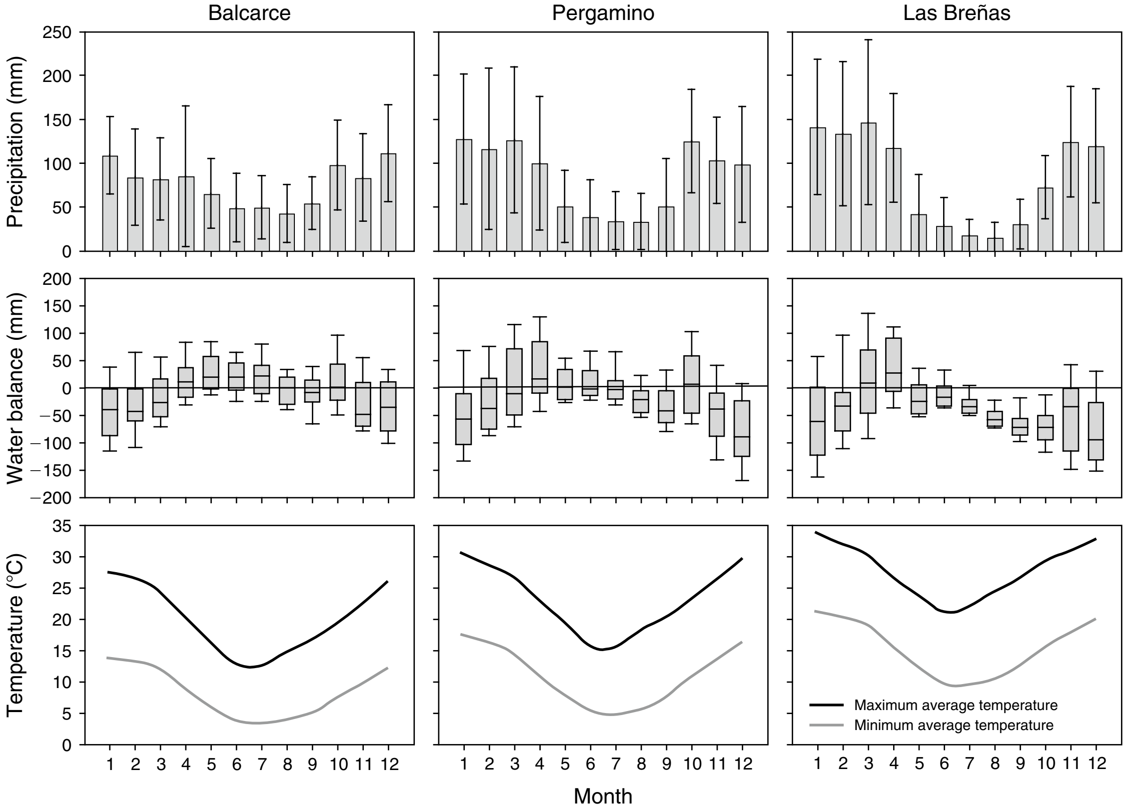

FIGURE 3

Climate (1971–2000) of three locations in a south–north transect in Argentina. Water balance is the difference between rainfall and reference evapotranspiration calculated with the method of Priestly and Taylor (1972). Error bars show standard deviation.

3. MAIN DRIVERS OF ATTAINABLE YIELD

The transect in this study allows for the interaction between soil and climate driving attainable yield, that is the best yield that can be achieved with current technology. Attainable yield was modelled for a common rotation at each soil by site combination (Table 2). The models included CERES-Wheat (Ritchie and Otter, 1985), CERES-Maize (Jones and Kiniry, 1985) and CROPGRO-Soybean (Boote et al., 1998), which have been locally tested and applied widely (Magrin and Rebella, 1991; Calderini et al., 1994; Savin et al., 1994, 1995; Travasso and Dellecole, 1995; Otegui et al., 1996; Ruiz et al., 1998; Bert et al., 2007; Monzon et al., 2007).

3.1. Wheat

Modelled wheat yield decreased northwards in our transect (Table 3). This is consistent with (a) the S-N decline in photothermal quotient and associated reduction in actual kernel set measured in field crops (Magrin et al., 1993) and (b) the S-N increase in water deficit and high temperatures that restrict grain filling (Figure 3).

Table 2 Three-Year Crop Rotations Modelled for Three Sites in a South–north Transect in the Pampas

Site	Crop			Variety	Sowing Date	Anthesis[a]	Maturity[a]
	Year 1	Year 2	Year 3				
Balcarce	Wheat			Baguette 10	10-June	06-November	17-December
	Soybean			DM 3100	30-December	17-February	17-April
		Maize		DK 682	10-October	13-January	15-March
			Soybean	DM 4800	01-November	08-January	28-March
Pergamino	Wheat			Baguette 10	01-June	13-October	20-November
	Soybean			DM 4800	30-November	14-January	25-March
		Maize		DK 682	20-September	13-December	05-February
			Soybean	DM 4800	20-October	05-December	01-March
Las Breñas	Wheat			K. Escorpión	01-May	16-August	04-September
	Soybean			A 8000	20-December	09-February	24-April
		Maize		DK 834	01-January	05-March	01-May
			Soybean	A 8000	10-December	03-February	04-April

Each rotation was evaluated for all the soils described in Table 1. We used DSSAT 3.5 models under sequence analysis option, with locally calibrated coefficients (Kantolic et al., 2007; Monzon et al., 2007; J. Mercau personal communication) and 1971–2000 climate records. Initial water for the first wheat crop was set at maximum water content, and simulations started on 1971, 1972 and 1973, to have each crop in every year. Simulations assumed no nitrogen deficiency.

[a]*Derived from long-term simulations.*

In Balcarce, modelled yield was over 4.9 $t\,ha^{-1}$ in deep soil and over 4.4 $t\,ha^{-1}$ in shallow soil during 80% of seasons (Table 3). In our transect, Balcarce has the mildest water deficit during the growing season and cooler temperatures during the critical window of grain yield determination (Figure 3). The key to maximise yield in this region is therefore manipulating sowing date and cultivar to achieve the earliest possible flowering compatible with frost risk. This allows for greater kernel set (associated with higher photothermal quotient) and less stressful temperature during grain filling. In this region, two variables collectively accounted for 65% of the variation in measured yield in well-managed fields: water availability in the critical period between 30 days before and 10 days after flowering, and mean temperature during grain filling (Calviño and Sadras, 2002).

The high and reliable wheat yield in Balcarce stimulates a high rate of technological innovation and rapid adoption of practices to capture the environmental benefits of the region. This dynamic process is often farmer driven, and farmers are keen to engage researchers in technological developments. The region features the highest rates of nitrogen and phosphorus fertiliser usage in the country, despite the natural N fertility of the soils (Table 1). Usage of fungicides is also widespread despite moderate disease pressure in comparison to other regions. The high rates of fertiliser and fungicide usage are partially associated with the introduction of new, high-yielding varieties. By 2006, around 40% of the wheat area around Balcarce was sown to high-yielding, French-type varieties (www.sagpya.mecon.gov.ar). The introduction of this kind of varieties shifted completely the way in which farmers managed the wheat crop. Traditional Argentinean wheat breeders used to focus on high resistance to diseases and good grain quality to the detriment of yield potential. With similar crop management, the French varieties outyield their local counterparts by ~1 $t\,ha^{-1}$ (Calviño and Sadras, 2002). These high-yielding varieties are responsive to fertiliser, and in this environment require fungicides to achieve around 7 $t\,ha^{-1}$.

Wheat is a minor crop in Pergamino, accounting for about 10% of arable land in this region. This is partially associated with the extended tradition of maize and soybean cropping, and with the less favourable

Table 3 Modelled Crop Yields Accounting for the Interaction between Climate and Soil

Site	Soil Type	Depth (cm)	Crop	Sowing Date	Yield ($kg\,ha^{-1}$)			Coefficient of Variation for Yield (%)
					Average	80% Percentile	20% Percentile	
Balcarce	Tandil	80	Wheat	10-June	5617	6977	4386	29
			Soybean	30-December	1767	2545	985	46
			Maize	10-October	7985	13203	1761	67
			Soybean	01-November	2298	3055	1490	38
		140	Wheat	10-June	6301	7368	4890	21
			Soybean	30-December	1995	2646	1492	38
			Maize	10-October	11862	15056	8753	37
			Soybean	01-November	3056	3868	2296	26
Pergamino	Rojas eroded	160	Wheat	01-June	5120	6265	4058	26
			Soybean	30-November	2766	3641	2236	34
			Maize	20-September	9458	11849	6243	34
			Soybean	20-October	3482	4165	2829	22
	Rojas	210	Wheat	01-June	5422	6412	4279	22
			Soybean	30-November	2971	3856	2296	32
			Maize	20-September	10279	12211	7076	26
			Soybean	20-October	3932	4878	3163	24
Las Breñas	Pampa	80	Wheat	01-May	518	960	0	103
			Soybean	20-December	1769	2635	904	49
			Maize	1-January	5043	8484	779	70
			Soybean	10-December	1795	2629	949	52
	Capdevila	180	Wheat	01-May	1180	1744	248	69
			Soybean	20-December	2807	3448	2234	24
			Maize	1-January	7959	9034	7087	20
			Soybean	10-December	2904	3594	2204	25

Rotations comprise wheat–soybean as a second crop after wheat–maize–soybean. Note the difference between late-sown soybean after wheat and timely sown soybean after maize (e.g. 30- December vs. 1-November at Balcarce). Results from 31 years of simulations using DSSAT 3.5 models.

environment for wheat in comparison to southern locations. Modelled wheat yields were above 4.1 $t\,ha^{-1}$ for eroded soils and above 4.3 $t\,ha^{-1}$ for good soil during 80% of the years (Table 3). A significant constraint for wheat yield in this region is the fungus *Fusarium graminearum*, causing a disease that occurs during 20% of the years (Moschini et al., 2001). This disease is not taken into account by CERES-Wheat, hence the over-estimation of wheat yields in our modelling exercise. Photothermal quotient during the critical period from 30 days before to 10 days after anthesis in Pergamino is 12% lower than that in Balcarce (Magrin et al., 1993). In addition to this relatively unfavourable condition for kernel set, maximum temperature during grain filling exceeds 30 °C during 90% of the years, and at least 10 days with temperatures higher than 30 °C occur during 50% of the years. Stressful conditions during kernel set and filling are compounded by foliar diseases, particularly leaf rust (*Puccinia recondita*). Bingham et al. (2007) highlighted the practical value of understanding source-sink constraints to crop yield to inform crop management decisions. The need to maintain active foliar tissue late in the season in Pergamino is therefore more pressing for French-type varieties (e.g. Baguette 10) not only because they are more susceptible to local pathogens, but also because they have greater sink demand driven by greater kernel number in comparison to local varieties.

Wheat in Las Breñas is seriously constrained by water deficits during the whole season, and in particular, at sowing and during the critical periods of flowering and grain filling (August–September, Figure 3). Common sowing dates vary from mid-March to early June depending on previous crop harvest. Early sowing implies a high risk of frost damage during flowering, whereas late sowing is associated with high temperatures during grain filling. Simulated yields were strongly dependent on soil type and depth (Table 3) and were positively correlated to water availability at sowing ($r^2 = 0.46$) that depends on previous crop consumption and autumn rainfall. Crop yield was weakly correlated to seasonal rainfall because most of the rainfall occurs at late crop stages when yield components are already determined. In this regard, the yield-rainfall relationships of this environment resemble more the Australian environments (Chapter 2) than the typical environments of the Humid Pampas.

Owing to the unfavourable conditions for wheat and the risk associated with uncertain rainfall, crop technology used in Las Breñas is low cost and conservative. Wheat cultivars are selected mainly for rust tolerance and stable seed weight. Sowing densities are low (100 pl m^{-2}). Nitrogen may limit wheat in high-yielding years (>2 t ha^{-1}), but usually no nitrogen fertiliser is used, and N requirements are attained by mineralisation. Yield targets and management of nitrogen for this environment are comparable to those of SE Australia (Sadras and Roget, 2004). The main role of wheat in the farming systems of the region is to generate stubble necessary for soil protection.

3.2. Soybean

Soybean acreage grew exponentially since the 1980s (Figure 1a). This involved the expansion of the crop in well-established grain producing regions in the Humid Pampas of which Balcarce and Pergamino are representative locations, and newer cropping areas in the north of the country, as represented by Las Breñas. The growth in soybean acreage resulted from its yield reliability, and compared with alternative crops, lower production cost and simpler management largely associated with glyphosate-resistant varieties. Three years after their first release, transgenic soybeans accounted for 99% of the total area devoted to the crop. This is a good example that refutes the cliché that farmers are conservative and reluctant to change; if the economic benefits of new technologies are clear, adoption is fast and widespread.

3.2.1. Soybean after maize

In Balcarce and Pergamino, yield of timely sown soybean, as in rotation after maize (Table 3) is directly linked to rainfall between developmental stages R3 and R6 (Calviño and Sadras, 1999). In both locations, water deficits are unlikely before R3 in deep soils (plant available water [PAW] > 250 mm); in this period, reference evapotranspiration for soybean maturity group III in Balcarce is below 200 mm (Della Maggiora et al., 2000). In shallow soils around Balcarce, season-to-season variability in yield is larger and early rainfall, from R1, also influences grain yield (Calviño and Sadras, 1999). The low temperatures of Balcarce, in comparison to Pergamino, constrain the yield of timely sown soybean. Night temperature at critical reproductive stages in Balcarce is often below 8 °C, and reduces pod set and grain growth (Thomas and Raper, 1981; Gibson and Mullen, 1996). Notwithstanding these constraints, potential yield is around 6 t ha^{-1} (Andrade, 1995); acclimation has been invoked that may partially account for these yields despite constraints in temperature.

Modelled variability of yield is very high for all crops in Las Breñas, but soybean has the lower interannual variability (Table 3). The sowing window for soybean is from September to January. In early sowings, water deficit usually reduces vegetative biomass, but the main problem is that grain filling takes place during December–January with a high probability of water deficit. Most common sowing date is December, when soil water recharge has occurred. The critical reproductive period occurs during March when weather conditions are more favourable.

3.2.2. Double-cropped soybean

Wheat–soybean double cropping substantially improved farm profitability and stability of cash flow in local farms (M. Redolatti, personal communication). The two key aspects of double cropping are an improved efficiency in the capture of radiation and water (Caviglia et al., 2004), and a dilution of farm's fixed costs. The improved efficiency in the capture of water has a beneficial environmental consequence in the form of reduced risk of runoff and deep-drainage (Caviglia, 2005). Improved capture of resources is a trademark of multiple cropping, as further illustrated in Figure 4 of Chapter 5.

Whereas Balcarce has cooler temperatures that favour wheat yield and constrain wheat–soybean double cropping, Pergamino warmer environment is detrimental for wheat but favours double cropping. Modelled yield of soybean after wheat in Balcarce is about 1 t ha^{-1} below their counterparts in Pergamino (Table 3). Constraints to double-cropped soybean in Balcarce include (i) short season, about 95–110 days, resulting from the combination of fast phenological development and early frosts (Calviño et al., 2002); (ii) dry soil profile at sowing after wheat crop (Egli, 1998); (iii) chronic water deficit during most of the growing season (Board and Harville, 1992; Board et al., 1992); (iv) low rate of grain filling associated with low temperature and radiation (Gibson and Mullen, 1996); and (v) shortening of grain filling period driven by photoperiod (Mayor et al., 1975). Water restrictions are obviously more severe in shallow soils common in the region. Sowing time of soybean is critical, with yield decline of 50–60 kg ha^{-1} per day delay from December 25 (Calviño et al., 2003b). Farmers seek, therefore, technologies for advancing flowering of wheat compatible with frost risk, at better temperature for grain setting **and grain filling allowing** early soybean sowing. Low-cost, low-risk practices to accelerate wheat harvest are being explored to allow for earlier and higher yielding soybean. These include early sowing of short-season wheat varieties accounting for topography and frost risk, sowing reduced-biomass wheat types to allow for easier soybean sowing on standing stubble and using herbicides for faster drying and anticipated harvest of wheat (Calviño et al., 2002; Monzon et al., 2007).

In Pergamino, modelled yield of double-cropped soybean averaged 0.71 t ha^{-1} less than their timely sown counterparts (Table 3). As in Balcarce, early harvest of wheat allowing for early sowing of soybean results in yield gains of 25 kg ha^{-1} per day (Menendez and Satorre, 2007).

In Las Breñas, double-cropped soybean is sown in late December, allowing for 50–60 days fallow after wheat harvest to ensure soil water recharge. This practice and the mild temperatures allowing for a wide sowing window are consistent with the small difference in modelled yield between double-cropped and timely sown soybean (Table 3). Yield in this cropping strategy is generally constrained by water availability from R3, or from R1 in dryer seasons. In this subtropical environment, diseases (e.g. soybean rust, *Phakopsora pachyrhizi*) and insects (mostly Lepidoptera) are more critical than in the temperate regions of the Pampas.

3.3. Maize

Maize is very sensitive to environmental stresses in the period bracketing flowering (see Section 3.2.2 in Chapter 15). In Balcarce, this period occurs around January (Table 2), when rainfall is usually below water requirements (Figure 3). Soil water storage is therefore critical to buffer periods between rains, and for this reason the yield of maize is much more variable in shallow soils than the yield of soybean, sunflower and wheat (Sadras and Calviño, 2001; Calviño et al., 2003a). Rainfall in the window between 30 days before and 20 days after anthesis accounts for much of the variation in maize yield in this region, and the importance of rainfall during vegetative growth increases with shallow soils (Calviño et al., 2003a).

Rainfall around flowering is also the critical driver of maize yield in Pergamino, although less reliable winter rainfall in comparison to Balcarce may extend the critical period to earlier developmental phases (Otegui et al., 1995). Two features of this environment that favour maize production include deep soils with large water-holding capacity (Table 1) and reasonable rainfalls in critical stages from late spring to early summer (November–January). Technological aspects of maize production include (i) stubble retention to improve infiltration and soil stability, (ii) sowing with at least 60% plant available water, (iii) early sowing (late August–early October), (iv) sowing density aiming at 90% of attainable yield in good seasons and (v) hybrids with high yield potential and no trade-offs with yield in poor season (Section 2 in Chapter 15 discusses this trade-off in detail). The aim of early sowing of a full season maize (850 °C from planting to anthesis, base temperature 8 °C) is that anthesis occurs in the first half of December, avoiding hotter summer conditions (Totis de Zeljkovich and Revella, 1980). Early sowing is constrained by soil temperature and trade-offs with frost risk (Andrade et al., 1996). Modelled variability of maize yield in Pergamino was comparable to that of soybean, but actual variability was larger for maize in farmers' fields. This relates to spatial variation in soils, which is not captured in our model and is often more relevant for maize, particularly as it relates to soil waterholding capacity, water infiltration and soil erosion (Sadras and Calviño, 2001; Calviño et al., 2003a). Beyond grain production, direct production cost of maize is twice that of soybean.

In Las Breñas, the main feature of grain production is the high interannual yield variation (Table 3). In this environment, crops like sorghum, maize and wheat are very important in the rotation to obtain good stubble cover. Besides the positive effects on soil organic matter and related soil properties, ground cover in subtropical places like Las Breñas, helps to reduce soil temperature and soil evaporation. Hence, stubble cover is very important for timely and successful sowing. Management aspects of maize in Las Breñas aim at reducing the risk of severe water deficit around flowering, including selection of deep soil with good stubble cover and managing the trade-off between sowing date and initial soil water content. Early sowing (August–September) aiming at earlier flowering compromises initial water content, which is constrained by typically dry autumn and winter, and previous crop water consumption. Even though rainfall around flowering (mid-November) is generally good, early-sown crops commonly experience water deficits during early stages, reducing canopy size, capture of radiation and crop yield. Sowing in the October–November period leads to flowering in December–early January; this is very risky because high temperatures (>35 °C) may reduce pollen viability. Late December to early January is the most appropriate sowing period; soil water recharge is good due to spring rainfall, and flowering occurs around early March when the risk of extreme high temperatures is lower (Table 3). Other technological aspects to achieve a target yield of 6 t ha^{-1} include sowing density ~5 pl m^{-2} and little or no fertiliser. Ideotypes for this environment combine traits from tropical germplasm, that is resistance to diseases and insects and tolerance to high temperature, and the yield potential of temperate hybrids.

In summary, for all the combinations of crops and environments analysed, the concept of a critical period for yield determination and avoidance of water deficit in this period is the keystone for devising cropping practices. Yield stability relies on practices aiming at storage of water between crops, reducing unproductive losses and avoiding the coincidence of critical periods with uncertain rainfall, high evaporative demand or both.

4. RISK MANAGEMENT

To illustrate the application of physiological principles to risk management, we develop a brief case study of a cropping company with activities in all three environments characterised in Sections 2 and 3. Briefly, El Tejar (www.eltejar.com.ar) is a company which crops ~650,000 ha (2008/2009 season); it primarily grows wheat, maize, barley, soybean and other regional crops such as cotton. 80% of the crop area is on rented land. The family-owned and managed company involves production units in five countries (Argentina, Bolivia, Brasil, Paraguay and Uruguay) supported by central units.

Table 4 Correlation Matrix for Simulated Crop Yield in a Wheat/Soybean–Soybean–Maize Rotation

Site	Crop	Balcarce				Pergamino			Las Breñas				
		Wheat	**Soybean 2[a]**	**Soybean**	**Maize**	**Wheat**	**Soybean 2**	**Soybean**	**Maize**	**Wheat**	**Soybean 2**	**Soybean**	**Maize**
Balcarce	Wheat	**1.00**	***0.14***	***0.10***	***0.03***	***0.21***	***0.11***	−0.02	−0.09	−0.15	−0.15	−0.20	−0.26
	Soybean 2	***0.14***	**1.00**	**0.83**	**0.73**	***0.09***	***0.14***	***0.12***	−0.11	***0.08***	−0.09	−0.15	−0.28
	Soybean	***0.10***	**0.83**	**1.00**	**0.74**	−0.03	***0.15***	***0.02***	−0.21	***0.21***	−0.04	−0.01	−0.13
	Maize	***0.03***	**0.73**	**0.74**	**1.00**	***0.09***	***0.05***	***0.06***	−0.07	***0.02***	***0.04***	−0.03	−0.13
Pergamino	Wheat	***0.21***	***0.09***	−0.03	***0.09***	**1.00**	***0.22***	***0.30***	***0.36***	−0.07	−0.09	−0.12	−0.29
	Soybean 2	***0.11***	***0.14***	***0.15***	***0.05***	***0.22***	**1.00**	**0.68**	**0.58**	−0.23	***0.03***	−0.18	−0.24
	Soybean	−0.02	***0.12***	***0.02***	***0.06***	***0.30***	**0.68**	**1.00**	**0.75**	−0.04	***0.00***	−0.24	−0.24
	Maize	−0.09	−0.11	−0.21	−0.07	***0.36***	**0.58**	**0.75**	**1.00**	−0.29	***0.02***	−0.24	−0.40
Las Breñas	Wheat	−0.15	***0.08***	***0.21***	***0.02***	−0.07	−0.23	−0.04	−0.29	**1.00**	***0.25***	***0.40***	***0.27***
	Soybean 2	−0.15	−0.09	−0.04	***0.04***	−0.09	***0.03***	***0.00***	***0.02***	***0.25***	**1.00**	**0.88**	***0.47***
	Soybean	−0.20	−0.15	−0.01	−0.03	−0.12	−0.18	−0.24	−0.24	***0.40***	**0.88**	**1.00**	**0.55**
	Maize	−0.26	−0.28	−0.13	−0.13	−0.29	−0.24	−0.24	−0.40	***0.27***	***0.47***	**0.55**	**1.00**

Roman values indicate negative correlations, values in italics are correlations between 0 and 0.5 and values in bold indicate correlations > 0.5.

[a] *Soybean 2 indicates soybean as a second crop after wheat harvest.*

Cropping systems in Argentina are under no-till, and more than half of agriculture in the Pampas relies on rented land (Section 1). There is also a well-established network of companies providing for sowing, pest and disease control, fertilisation and harvest. This means that companies with no land and no machinery can effectively concentrate on strategic aspects of crop production across regions. Using this approach, El Tejar combines climates, soils, crops and rotations to diversify its activities, to reduce the risk of financial losses and to capture the benefit of better seasons and environments.

Contrary to the notion that modelling is of limited value for practical decision-making (McCown, 2002; McCown et al., 2002), this company relies heavily on crop modelling for its decisions. The importance of modelling to generate probabilistic estimates of yields and yield projections for risk analysis is twofold. First, historical time-series of yields from public or private databases are often inappropriate for projections given the very fast development and adoption of new technologies. Second, vast new cropping areas are being developed for which there are no previous records.

Modelling yields for Las Breñas region (Table 3) were used to integrate this otherwise risky environment in the whole-of-the enterprise. In isolation, cropping in Las Breñas returns a net loss in one out of three years. However, owing to the lack of or slightly negative correlation between yields in this subtropical region and yields in the temperate parts of the Pampas (Table 4), allocating 10% of the total cropping activities to Las Breñas contributes to overall profit stability. The business strategy of El Tejar has broken the constraints of regionality, and manages risk by incorporating activities not only across regions but also across countries in South America. At the scale of rotations and management of individual crops, the constraints identified in Section 3 inform the decision of this company. Double cropping that allows for improved capture of resources and dilution of fixed costs, and horizontal growth in the form of better utilisation of indirect costs, technical skills and machinery are major elements of current production approaches in the region. Collectively, the improvements in profitability related to this approach have been much larger than those attributable to genetic improvement and standard agronomic practices such as fertilisation (Calviño, 2007). Central to this approach is the shift envisaged by Evans and outlined in Chapter 1 (Box 1); this shift involves thinking in terms of whole-of-system production, rather than yield per crop. Chapter 19 (Section 4) provides another example of whole-of-farm integration using a combination of risk management tools.

5. NOVEL CROPPING SYSTEMS

Although intercropping has traditionally been a feature of subsistence farming, mostly in the tropics (Chapter 5), intercropping in the temperate Pampas represents the cutting edge of agricultural technology. This section outlines novel systems being developed by leading farmers and researchers.

5.1. Sunflower/soybean intercropping

The structure of this system involves wide-row spacing sunflower (1.5 m) sown at its optimum date, and two internal rows of soybean sown either simultaneously or up to 50 days after sunflower. Sunflower is harvested, for example in the southern region, late in February and soybean in mid-April. The idea of large-scale, fully mechanised sunflower/soybean intercropping relies on two physiological principles and enabling agronomy, including:

(i) The relative maintenance of sunflower yield in wide-row spacing (1.5 m) in comparison with conventional single crop (0.7 m). This is accounted for by photomorphogenetic responses that allow for spreading of foliage and relatively high capture of radiation (Lopez Pereira et al., 2008).

(ii) The possibility of displacing the most critical period for yield determination of soybean in relation to that of sunflower (Figure 4).

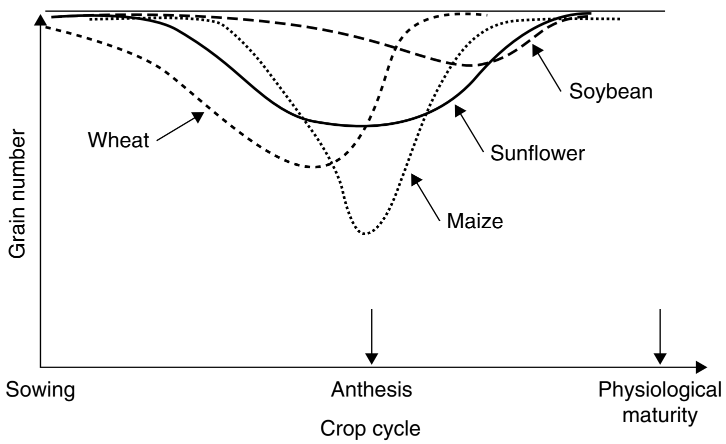

FIGURE 4

Comparison of critical periods for grain number determination, the main yield component of grain crops. Grain number is presented in an arbitrary scale where the horizontal line represents 100%, or the grain number in unstressed controls. Deviations from this line show reductions due to stress in different periods of the crop cycle. Source: Andrade and Sadras (2002) and Fischer (1985).

(iii) Established no-till technology, and weed control based on glyphosate-resistant soybean and imidazolinone herbicide-resistant sunflower. Interfield® herbicide has been specifically tailored for this system. Difference in height of harvestable organs allows for mechanical harvest of sunflower over standing soybeans.

The expectation, based on preliminary estimates, is that intercropped sunflower will reduce its yield by about 75% with respect to pure crops, and soybean will reduce its yield by 50%, hence a net profit benefit for the intercrop. Active research programs are aiming at improving this technology, where the bottleneck is the establishment and early growth of soybean in the low-radiation environment under the established sunflower canopy (Cerrudo personal communication). Intra-specific differences in photomorphogenetic responses of soybean have been identified (Cerrudo et al., 2006), and combinations of sunflower hybrids (short season, dwarf types, wide-row adapted) by soybean (shade-tolerant) cultivars are being explored. Close engagement between a new generation of skilled farm managers and scientists is vital to the success of this approach.

5.2. Canola/soybean double crop

Driven by economics and technology, canola acreage increased from 14,000 ha in 2007 to about 100,000 in 2008. A typical rotation including double-cropped wheat/soybean-soybean leaves a five to seven month gap between soybeans. In this period, a canola crop would fit in the rotation allowing for a high-yielding double-cropped soybean (Figure 5), effectively increasing cropping intensity from 1.5 to 2 crops per year. The main constraints for the inclusion of canola in this rotation are related to the establishment of this small-seed crop in no-till system with large amounts of stubble ($7\,\mathrm{t\,ha^{-1}}$ or more), and frost risk during this phase. In addition to machinery-based solutions to this problem, research is underway for intersowing canola on standing soybean (R7); this would significantly reduce early frost risk.

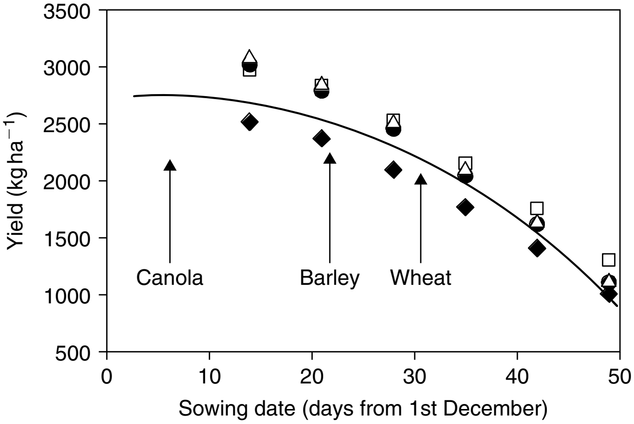

FIGURE 5

Expected yield of double-cropped soybean sown after canola, barley or wheat in Balcarce. Measured (curve) and modelled (symbols) yield responses to sowing date for soybean. Rhombuses correspond to cultivar DM2000, squares to AW2886, circles to A3901 and triangles to DM4800. Source: Monzon et al. (2007).

6. CONCLUSION: THE CHALLENGE AHEAD

Increasing land allocated to continuous cropping and the exponential growth in the soybean-sown area (Figure 1a) generate environmental problems. These are particularly serious in recently cleared tropical and subtropical areas with fragile soils. Maize contribution of carbon to maintain soil organic matter is critical to the preservation of soil resources. Where maize is economically risky, high-yielding wheat or barley allow for both carbon input and profitability. Physiological principles applied to design more profitable systems, where the time dimension of production and profit is made explicit (Evans, 1993, 2003), are the core of a cropping intensification process (from 1.2 to 1.7 crops per year). This is largely based on variations of wheat/soybean double cropping; new promising variants have also emerged such as maize/soybean and sunflower/soybean intercropping and canola/soybean double crop.

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CHAPTER 4

Improving Farming Systems in Northern European Conditions

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1. SPECIAL FEATURES OF NORTHERN EUROPEAN CONDITIONS FOR CROP PRODUCTION

Northern European growing conditions have particular features that differ markedly from those typically associated with the rest of Europe. These features are critical for crop development, growth and yield determination per se, as well as for the mechanisms and approaches needed and used in adapting to and managing such northern agricultural systems. Finland is the northernmost agricultural country (Figure 1), having all of its arable land of some 2 million hectares above 60°N. Agriculture is possible at such northern latitudes due to the Gulf Stream. The Gulf Stream, together with its northern extension towards Europe, the North Atlantic Drift, is a powerful, warm and swift Atlantic Ocean current that originates in the Gulf of Mexico and influences the climate of the west coast of Europe. Hence, due to the Gulf Stream, the northern European temperature regimes during the growing season differ from those elsewhere at comparable latitudes and from those in the more southern regions.

Finland represents the uppermost extreme for field crop production and is an interesting case with respect to how crop physiology needs to be taken into account when targeting improved, sustainable agricultural systems under exceptional conditions. In Finland, over 60% of the arable land is allocated to small-grain cereals and rapeseed. The second most important group is grass crops, occupying 30% of the total arable land. Other crops are grown on much smaller areas. This article addresses small-grain cereals and rapeseed, as these are the crops that can be successfully grown under such northern conditions – not only considering Europe but also in a global context.

The most typical features of northern growing conditions are harsh winters; intensive, exceptionally rapid rates of development due to exposure of very early growth stages to long days and relatively rapidly increasing mean temperatures, generally cool mean temperatures during the growing season; and risk of night frosts, early summer drought and risk of abundant precipitation close to harvest and later at the time of sowing of winter cereals. Successful crop production under these conditions requires specific adaptation mechanisms. However, it is not only the degree of difficulty that such basic conditions represent but also, particularly, the substantial fluctuations in conditions that occur within and among years and seasons that determine the requirements of plant breeding and development of adaptive crop management practices. As our examples will indicate, such specific adaptation strategies are very vulnerable to changes in political and

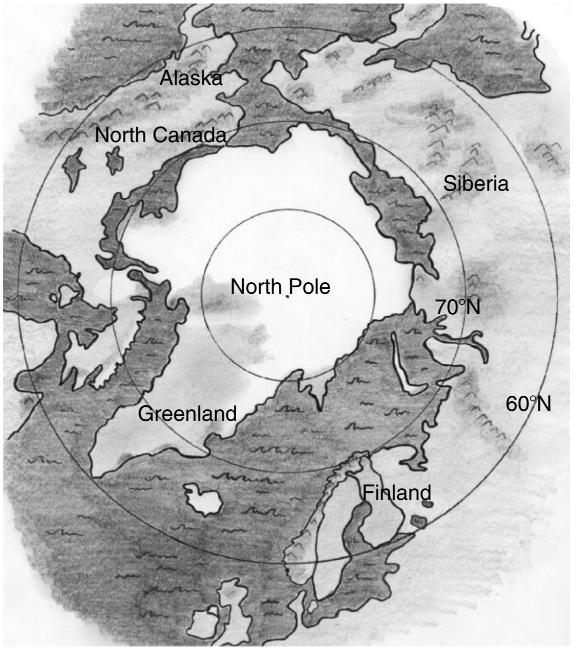

FIGURE 1

Europe has the northernmost conditions for active field crop production with the largest areas of arable land. The Nordic countries have a total of 9.1 Mha of arable land (FAO Statistics, 2008; in http://faostat.fao.org). While all of the arable land and seed cropping in Finland is above 60°N, in Sweden 90% of seed cropping is at lower latitudes, in Norway 50% and in Denmark 100%. Evidently, in such northern extremes, differences in growing conditions and production risks change markedly according to latitude. (Drawing: Jaana Nissi.)

economic environments (Peltonen-Sainio et al., 2009b), as these are invariably dynamic and unpredictable, and their impacts are difficult to quantify (Richards, 2002).

1.1. Harsh winters

Winters in the north are harsh in many ways (Mukula and Rantanen, 1989a, b; Hömmö, 1994; Mela, 1996; Lindén et al., 1999; Hofgaard et al., 2003; Serenius et al., 2005). When over-wintering conditions have been too harsh and resulted in problems of winter survival, or even total crop failure, it is typically due to a combination of unfavourable, critical conditions and stresses that are, when occurring together or when succeeding each other, lethal for the crop.

Under northern conditions, winter survival of crops is typically dependent on latitude, species and winter-hardiness of the cultivar. Low temperatures rarely cause crop death, as hardened over-wintering crops in the north usually tolerate freezing temperatures during winter (Hömmö, 1994; Antikainen, 1996). In addition, where the temperatures are the lowest, there is usually a protective snow cover on the fields. On the other hand, abundant snow cover often maintains the temperature at the plant stand level close to zero, favouring infection by low-temperature parasitic fungi such as *Microdochium nivale*, *Sclerotinia* spp. and *Typhula* spp. that can cause serious economic damage to cereals, grasses and legumes (Ylimäki, 1969; Hömmö and Pulli, 1993; Hömmö, 1994; Nissinen, 1996; Serenius et al., 2005). The typical period for permanent snow cover in southern Finland (Jokioinen) in the last three decades was from 16th December to 10th April and in central Finland (Jyväskylä) from 26th November till 22nd April. Melting of snow can result in formation of hermetic ice cover, which impedes oxygen flow needed for crop maintenance respiration (Hofgaard et al., 2003). Moreover, too moist soils that result from melted snow and heavy rains reduce soil aeration. Cycles of melting during the day and freezing at night of the uppermost soil layers can also cause frost heaving and damage such as root breakage, especially in spring. Furthermore, insufficient carbohydrate reserves for maintenance respiration are a problem when winters are long and plants are covered with snow or when winters are exceptionally warm and temperatures are above zero for long periods and enhance crop metabolism (Niemeläinen 1990; Antikainen, 1996; Gaudet et al., 1999; Hakala and Pahkala, 2003). Last but not least, different combinations of these and other stresses represent a challenge for winter survival when they occur once or several times during winter (Hömmö, 1994).

1.2. Short and intensive growing seasons

The thermal growing season, the period when daily mean temperatures are permanently above a base temperature of +5 °C, is short in the north. Typically in the last three decades, it lasted from 27th April till 15th October in southern Finland (Jokioinen) and from 2nd May till 6th October in central Finland (Jyväskylä). The proportion of the agronomically relevant and physiologically advantageous part of the season is likely to be less relative to that in central Europe. This is because, under northern growing conditions, there is a period during the beginning of the thermal growing season that cannot be utilised for crop growth for various reasons, including too moist soils (melted snow that is directed from the fields with sub-soil drainage systems) that need to dry before sowing is possible with heavy machinery, and low temperatures that slow down germination, seedling establishment and early growth. Also risks of night frost are higher the earlier the sowing. In addition to losing part of the thermal growing season prior to sowing, an additional period for growth is lost post-sowing when the canopy is closing. This is proportional to light interception at emergence and initial maximum relative growth rate (Goudriaan and Monteith, 1990; Monteith, 1993) and is therefore likely to be relatively short under northern conditions with long days and rapidly increasing temperatures following sowing. Nevertheless, the length of this lost, early part of the growing season, is not only dependent on local conditions but also on crop species. For example, rapeseed is far more susceptible than cereals to low temperatures at germination and night frosts during the early seedling stage; therefore it is sown later and has a longer lost thermal period early in the growing season (Peltonen-Sainio et al., 2006).

Under northern growing conditions, there is also time lost for growth at the end of the thermal growing season that is characterised by decreasing mean temperatures and increased risks of night frost (Peltonen-Sainio et al., 2009c). Heavy rainfall also causes problems with maturation and harvesting (Rajala and Peltonen-Sainio, 2000). Furthermore, at the end of the summer, day length shortens rapidly and low light intensities reduce photosynthetic activity. For example, in Jokioinen, southern Finland, day length is 12 h at the autumnal equinox in late September, shortens to 8 h at the end of October and reaches a minimum of 5.5 h around 21st December (e.g. www.gaisma.com, 24.1.2008).

Typically, conditions during the northern European growing season are cool, but are favourable for growth of cereals, rapeseed and many other temperate crops that are adapted to the short growing season. On the other hand, temperatures are even relatively high at crop establishment because it takes some time for the field to dry prior to sowing, and during late spring, mean daily temperatures increase quite quickly as days lengthen. The question of temperatures sustaining early growth is, however, dependent on crop species. For cereals adapted to northern growing conditions, the temperature regime in early summer is always sufficient for good establishment in regions where they are commonly grown. However, because germination and early seedling establishment of rapeseed are favoured by higher temperature after sowing (Peltonen-Sainio et al., 2006), rapeseed benefits from delayed sowing in comparison with cereals. Such differences between cereals and rapeseed in response to temperature in northern conditions differ from those described by Angus et al. (1981) for temperate cultivars grown in a Mediterranean climate.

The growing season in northern Europe does not end in increasingly high, stressful temperatures and terminal drought typical of Mediterranean (Acevedo et al., 1999) and continental climates of vast regions of

North America and Asia (Johnson et al., 2004; Sadras and Angus, 2006). In Nordic countries, temperatures and potential evapotranspiration typically fall and precipitation increases towards the end of the growing season (Mukula and Rantanen, 1987). However, it was recently reported that turnip rape (*Brassica rapa* L.) is very sensitive to elevated temperatures at seed set and fill (Peltonen-Sainio et al., 2007a). An increase in mean daily temperature during the seed-filling phase of 2–3 °C, when compared with long-term average temperatures (13.8 °C for 1970–1989, 15.3 °C for 1990–1999 and 16.9 °C for 2000–2005), reduced yield by up to 450 $\mathrm{kg\,ha^{-1}}$, depending on the cultivar (Peltonen-Sainio et al., 2007a). In contrast, the yield of oilseed rape (*Brassica napus* L.) was even slightly enhanced by such increases in mean temperature at seed filling. It is therefore more likely that oilseed rape, which suffers from high temperature stress in other regions (Morrison and Steward, 2002), is less sensitive than turnip rape, and temperatures that would reduce oilseed rape yields are not yet experienced in northern regions.

The risk of night frost can hold farmers back from sowing very early in years when a warm spring begins earlier than usual. In the event of severe night frosts, below −5 °C, occurring after seedling emergence, cereal stands are rarely completely destroyed as the developing apex is close to the soil surface and is well protected and insulated by the expanding leaves. However, rapeseed is sensitive to night frosts, and at −5 to −7 °C, most seedlings are lost (Pahkala and Sovero, 1988; Pahkala et al., 1991). Hence, early sowing of rapeseed might necessitate re-sowing later in the season, and this can expose the plant stand to unfavourable conditions at maturation if done too late. Night frosts occur typically in spring and early summer. Midsummer is the only period when crop-damaging frost does not occur. For example, in Jokioinen, such a frost-free period is between 20th June and 10th August (Solantie, 1987).

At the end of the growing season, not only do temperatures become lower, but there is also an increased risk of night frosts (Peltonen-Sainio et al., 2009c). In general, the only likely economic risk related to late-season night frost concerns rapeseed, for which the seed-ripening processes are interrupted (Bonham-Smith et al., 2006), resulting in high chlorophyll content in the seed and reduced quality. Heavy rain rather than late-season frost is the major driver for harvesting well before the end of the thermal growing season (Rajala and Peltonen-Sainio, 2000).

1.3. Early summer drought and uneven distribution of precipitation

Fluctuations in the amount and timing of precipitation are substantial within and between the seasons in northern Europe, but there are some typical features. One of these is early summer drought resulting from low precipitation and rapid drying of soils in late spring. As this occurs during the reproductive pre-anthesis phase, it is the most critical stress in terms of reducing the yield potential of grain crops (Rajala et al., 2009). It further emphasises the limitations of floret viability already caused by long-day-induced enhancement of developmental rate (Peltonen-Sainio and Rajala, 2007); Box 2 in Chapter 12 presents new insights on the genetic and physiological regulation of floret survival in wheat, and its response to photoperiod.

We compared the availability of water with that needed by a cereal crop at its most critical phase of yield determination (from 200 to 450 °C d from sowing under Finnish conditions) using the model reported by Peltonen-Sainio et al. (2005). The model, designed on the basis of long-term datasets, predicted grain yield and protein content at the regional and national levels in Finland. Such a window for yield determination of two-row malting barley (*Hordeum vulgare* L.) is generally comparable and in agreement with findings from regions at lower latitudes (Garcia del Moral et al., 2002). When calculating probabilities for precipitation at the regional level for this critical window of yield determination, according to 30-year climate datasets from the Finnish Meteorological Institute, our studies indicated that only 30–60% of the rainfall needed for undisturbed and non-limited formation of yield was achieved on a long-term average basis, and this depended on the region (Peltonen-Sainio, unpublished data).

In contrast with the Mediterranean climate (Acevedo et al., 1999), in northern Europe rains are more common later in the growing season. Sufficient rains at grain filling can somewhat compensate for the reduced number of grains resulting from early summer drought (Peltonen-Sainio et al., 2007b; Peltonen-Sainio and Jauhiainen, 2008). Such compensation occurs in environments that particularly favour seed growth (Egli, 2006). Compensation is, however, limited for many reasons, for example, lower total sink capacity of reduced number of grains in the ear and/or lower potential grain size. Early, high temperature before flowering, when carpels develop and their size is determined, could impose an upper limit on grain size (Scott et al., 1983; Wardlaw, 1994; Calderini et al., 1999a, b; Calderini and Reynolds, 2000), as could the events soon after pollination through endosperm cell division (Rajala and Peltonen-Sainio, 2004; Egli, 2006). Due to only limited compensation ability, more abundant rains at the end of the cereal and rapeseed growth cycles represent a risk for crop production, especially when heavy rains cause lodging, heavy disease infestations, yield losses, quality deterioration and problems with the moist soils unable to support heavy machinery (Rajala and Peltonen-Sainio, 2000).

2. ADAPTATION: A MATTER OF CROP RESPONSES WHEN COPING WITH NORTHERN CONDITIONS

As described above, northern European growing conditions have many special features that are exceptional and challenging. This means that adaptation measures developed to cope with such special conditions are partly unique or at least tailored to meet the demands set by the northern climate. Success in northern field crop production requires interplay between breeding of cultivars adapted to grow and yield in such an exceptionally short and intensive growing season and development of farming systems sustaining yield potential.

2.1. Development and growth: The need to hurry

2.1.1. Phenophases

The life cycles of the cultivars adapted to northern European conditions must match the requirements of the short and intensive growing season. Both long days and relatively rapidly increasing mean temperatures enhance ear development rate (Peltonen-Sainio and Pekkala, 1993; Peltonen-Sainio and Rajala, 2007), which is maintained at a steady, high pace throughout the period when spikelet, floret and floret organ primordia viability is determined, until pollination at 400–600 °C d, depending on the cereal species. In Jokioinen, southern Finland, the day lengthens from 12 h at the vernal equinox in March to 16 h at the end of April, reaching a maximum of 19 h around midsummer (e.g. www.gaisma.com, 24.1.2008).

Evidently, such rapid development during the pre-anthesis generative phase, which is a vital adaptation to the short, northern growing season (Peltonen-Sainio and Rajala, 2007), reduces yield through fewer viable florets. Hence, adaptation to high latitudes through enhanced development rate is a costly but vital element for cereal production under short-season conditions. Nevertheless, even though development is enhanced by long days, early cultivars, particularly bred for northern conditions, are necessary to sustain stable production in the short growing season. This is the most important adaptation strategy. Because the environment is so restrictive, growers have a reduced opportunity to compensate for poor management, and none at all through having several sowing windows during the season. Therefore, farmers in northern Europe have to have not only well-adapted cultivars but also a fine-tuned management strategy to sustain their yield formation.

Despite early developmental phases being hastened by long days in the north (Peltonen-Sainio and Rajala, 2007) and cereal stands heading earlier than at lower latitudes, the grain-filling phase is not markedly shortened when measured in days (Kivi, 1967). Hence, the balance between pre- and post-heading phases is critical for obtaining high yields with sufficient duration for both pre- and post-anthesis phases. This is further emphasised by differences in how favourable the climatic conditions are. Often yield is favoured by precipitation at grain fill, in contrast to typical early summer drought, which induces reductions in viability of florets. The earliest maturing cultivars are likely to suffer most from this due to lower capacity for compensation. On the other hand, even though days at grain fill get shorter, crops are harvested before being subjected to short days and low light intensities. Hence, under northern growing conditions, grain-filling rates remain high throughout the grain-filling period (Peltonen-Sainio, 1990, 1991). Also according to Saarikko and Carter (1996), under Finnish conditions, development of cereals is dependent only on temperature as the day length during the growing season generally exceeds the optimal requirement (Section 3 in Chapter 12).

2.1.2. Yield components and their compensation

A rapidly proceeding pre-anthesis generative phase – the vital adaptation mechanism for a short growing season – results in a lower number of viable grain-producing florets and therefore reduced grain number and yield (Peltonen-Sainio and Rajala, 2007). Despite this, also under long days, there seems to be excess production of florets at pre-anthesis (Chapter 12), particularly under non-water-limiting and non-nutrient-limiting conditions (Peltonen-Sainio and Peltonen, 1995) when compared with set of grains (Peltonen-Sainio et al., 2007b). However, high numbers of immature florets that cease their development without producing fertile florets are likely to further limit yield formation under long-day conditions. Early summer drought limits viability of florets, and then grain number, more than photothermal quotient (Fischer, 1985) under northern conditions (Table 1). Therefore, photothermal quotient does not explain any differences in grain number of wheat (*Triticum aestivum* L) and barley when analysed on the basis of daily mean values of degree days and radiation over the last 35 years at two locations (data not shown). As grain number predominates in yield determination over grain weight (Garcia del Moral et al., 2003; Gonzalez et al., 2003; Borras et al., 2004; Sadras, 2007), grain yields at high latitudes are modest compared with those of central Europe (Peltonen-Sainio et al., 2007b; Rajala et al., 2007). Cereals have some capacity to compensate for the reduced grain number through higher grain weight, but only to a limited extent (Peltonen-Sainio et al., 2007b). Furthermore, small-seeded turnip rape has less such compensation capacity compared with oilseed rape (Peltonen-Sainio and Jauhiainen, 2008).

When considering the effects of early summer drought at the critical window for yield determination, the responsiveness or vulnerability of this particular pre-anthesis phase occurs when the number of major

Table 1 Growing Season Climate of Two Locations in Finland

Month	Mean			Precipitation			
	Temp (°C)	Radiation (MJ m^{-2})	PTQ (MJ m^{-2} °C^{-1})	Mean (mm)	Min (mm)	Max (mm)	S.D.
Jokioinen, Southern Finland							
May	9.6	18.2	1.5	36.6	0.9	87.2	21.6
June	14.1	19.9	0.6	59.3	11.2	131.1	34.8
July	16.3	18.5	0.4	83.1	0.8	164.3	38.9
August	14.6	14.2	0.5	76.7	12.8	158.6	32.6
September	9.4	8.3	1.7	61.3	11.5	135.9	32.9
Jyväskylä, Central Finland							
May	8.7	17.7	5.3	39.5	5.4	113.5	22.4
June	13.9	18.7	2.5	60.9	8.3	156.7	30.9
July	16.2	17.9	1.7	82.0	17.8	145.8	35.9
August	13.8	12.9	1.7	81.7	23.3	181.8	44.6
September	8.4	7.4	3.0	61.6	14.3	101.3	27.8

Values are monthly means. PTQ, photothermal quotient, S.D., standard deviation.

yield components is set. Furthermore, at that particular time, there is also increasingly strict competition for resources between generative, developing organs: elongating stems and tillers. Floret numbers per spike no longer increase but start to decline during the pre-anthesis phase, several apical developmental stages before pollination (Peltonen-Sainio and Peltonen, 1995). As cereal stands cannot sufficiently compensate, for example, through tillering for stresses at pre-anthesis, a short growing season results in low numbers of grains per unit area (Peltonen-Sainio et al., 2007b), emphasising the negative effects of early summer drought.

2.1.3. Dynamics of tillering

Although tillering is species and cultivar dependent, the environment plays a major role in modifying tiller performance (Simmons et al., 1982; Lafarge, 2000; Prystupa et al., 2003). During long days, tiller initiation, tiller development and growth, heading capacity of tillers and contribution of tiller spikes to grain yield have special features. In contrast with many other regions in the world, tillers generally play only a modest role in grain yield of spring cereals at high latitudes (Peltonen-Sainio and Järvinen, 1995), as long days greatly suppress tillering (Lafarge, 2000). Vegetative tillers sustain early canopy closure and are produced despite the high seeding rates used to enhance the uniculm habit induced by long days (Peltonen-Sainio, 1997). Long days typical of high latitudes contribute to low tillering directly by enhancing apical dominance (Michael and Beringer, 1980) and indirectly by rapid stem elongation that leads to shading and changes in the red:far red ratio within the canopy (Evers et al., 2007). Such changes in light conditions signal increasing competition (Franklin and Whitelam, 2005) and thereby imminent shortage of resources. In contrast to branching in spring cereals, branching of spring-sown turnip rape and oilseed rape is an important characteristic for the crop under northern growing conditions, for optimising the formation of yield components in relation to the resources available. In these crops, branching successfully compensates for reduced plant numbers per unit land area as indicated by a narrow range of variation in yield despite large variations in seeding rate, number of emerged seedlings or seedling survival after early summer frost (Pahkala and Sovero, 1988). When the number of harvested plants per square metre ranged from some 50 up to more than 500, the number of branches per plant and the number of pods per branch changed, but their compensation ability was largely dependent on the availability of resources (Pahkala et al., 1994). The complexity of compensation and the interplay between yield-determining components in oilseed rape were comprehensively described by Berry and Spink (2006).

Early summer drought stops tillering and thereby markedly decreases tiller contribution to total growth (Lauer and Simmons, 1988; Lafarge, 2000). Lauer and Simmons (1988) indicated that short-lived tillers are expensive for the crop energy balance. Early summer drought, typical of northern Europe, depresses tiller growth; hence tillers are unlikely to reach their genetic yield potential. Furthermore, suppressed tillering increases the risk of tillering at late grain filling. Such a risk increases with more frequent and heavier late-season rainfall and over-supply of nutrients that remain in the soil, especially when plant stands have been thinned from early summer drought. Such late tillering is disadvantageous, as it maintains moisture in mature plant stands and hampers harvest.

Cereal species differ in their tillering performance as well as tiller contribution to grain yield (Mela and Paatela, 1974; Peltonen-Sainio and Järvinen, 1995; Peltonen-Sainio et al., 2008d). Spring barley, particularly two-rowed cultivars, tiller most, and oat (*Avena sativa* L.) tillers are less productive with respect to their ability to produce grains in tiller panicles. On the other hand, tiller number for spring wheat is negligible. According to Peltonen-Sainio et al. (2008d), every fourth oat plant and every third wheat plant and six-row barley plant had a single tiller spike, while every two-row barley plant had almost one tiller spike on each main shoot.

In contrast to spring cereals, for autumn-sown winter cereals, short days and low temperatures with high precipitation typical of northern autumns favour tillering, particularly in winter rye (*Secale cereale* L.), which unlike winter wheat tillers mostly in autumn. For example, in winter rye, 53–58% of total grain yield was produced by lateral shoots, depending on the cultivar and the growing conditions (Hakala and Pahkala, 2003). The numbers of lateral shoot spikes and the weights of spikes in both main and lateral shoots were higher when plant density was lower, resulting in about the same yield at lower and higher seeding rates. The compensation strategy varied from higher tiller number to higher spike weight, depending on the cultivar (Hakala and Pahkala, 2003). For winter cereals, autumn weather favours not only tillering but also the establishment of the root system prior to spring drought. Hence, their cultivation could be considered an interesting adaptation mechanism to avoid problems caused by early summer drought. Despite this, grain yields fluctuate far more in winter than in spring cereals (Peltonen-Sainio et al., 2009b). This mainly results from large variation in over-wintering capacity (Mukula and Rantanen, 1989a, b; Hömmö and Pulli, 1993).

As indicated above, tillering is strongly associated with species, cultivars and environmental conditions. However, the uniculm growth habit – sustained by strong apical dominance controlled by endogenous hormonal balance (Michael and Beringer, 1980) – seems to be hard to manipulate, for example, through exogenous application of plant growth regulators (Peltonen-Sainio et al., 2003; Rajala and Peltonen-Sainio, 2001) or by using crop management practices to break it (Peltonen and Peltonen-Sainio, 1997; Peltonen-Sainio and Peltonen, 1997). On the other hand, restricted-tillering cultivars such as those of wheat with a major *tin* gene (Richards, 1988; Motzo et al., 2004; Palta et al., 2007) may offer a way of avoiding harmful late tillering at grain filling, especially when drought inhibits tillering during early phases. The growth and yield of uniculm barley lines with the uc_2 gene were studied in northern American extremes, in Alaska (Dofing and Karlsson, 1993; Dofing and Knight, 1994; Dofing, 1996). Those experiments showed that reduced grain yields in uniculm lines compared to conventional tillering lines were primarily due to lower grain number per spike. Nevertheless, they considered that the uniculm phenotype results in several favourable modifications of phenological development that may be of particular value in northern environments, with the need to avoid too late ripening of plant stands that late-developed tillers prolong. On the other hand, in wheat the *tin* gene has pleiotropic effects, including *gigas* features (Richards, 1988; Motzo et al., 2004).

2.1.4. Adaptation to over-wintering

Winter conditions and their impacts cannot be reliably forecasted (Hollins et al., 2004) to allow decisions to be taken well in advance as to whether to sow winter cereals in a particular year. Development of other adaptation strategies for harsh winters is also challenging. There are two major ways to adapt to northern winters: using spring types and completely avoiding the challenges of over-wintering or using a complex combination of adaptation mechanisms for the various risks that might result in crop failure. The first is realised by the limited number of winter cereal types grown at above 60°N. Winter rye and wheat are the only winter cereals adapted to such northern conditions, while winter barley, oat and rapeseed are of no economic importance. There are also regional differences in cultivation of the two winter cereals. As winter rye is clearly more winter-hardy, it is recommended for cultivation up to 63°N, while winter wheat is recommended only in the most favourable areas up to 61°N (inland) or 62°N (coastal) in Finland (Kangas and Teräväinen, 2006). Nevertheless, the total area of winter cereals at present in Finland is only about 5% of the total cereal cultivation area (www.mmmtike.fi, 7.2.2008), with even smaller areas being cultivated when autumn conditions are not favourable for sowing.

Risks and uncertainties associated with growing winter crops are reflected not only in small areas of cultivation but also in the large differences in sown and harvested areas over years. Abundant autumn rainfall can increase problems by preventing sowing, as fields are not able to support the machinery. Nevertheless, an example of one adaptation strategy is that winter cereals are often sown on sloping fields to aid surface water run-off from the fields and thereby reduce risks of formation of hermetic ice cover. Late sowing to avoid dense canopies before winter and use of cultivars resistant to pathogens are important to avoid winter damage (Serenius et al., 2005). For susceptible winter cereals, especially in the northernmost areas with thick snow cover, plant protection measures against snow mould infections are also strongly recommended (Serenius et al., 2005).

3. GAPS BETWEEN POTENTIAL AND ACTUAL YIELDS

Yield can be defined and measured in many ways (Box 1 in Chapter 1). Here we use the definitions of *potential yield*, that is, 'the maximum yield that could be reached by a crop in given environments' as determined from physiological principles, and *yield potential*, that is, the 'yield of a cultivar when grown in environments to which it is adapted, with nutrients and water non-limiting and with pests, diseases, weeds, lodging and other stresses effectively controlled' (Evans and Fischer, 1999). Actual yield is the realised part of the existing yield potential under prevailing conditions.

National, regional and global yields have increased not only due to genetic improvement and better crop management but also due to their interaction, that is, the interplay between breeding innovations and agronomy (Evans, 2005; Box 1 in Chapter 2). However, achievements per se and the roles of both of these components and the interplay affecting yield trends vary markedly from one country to another and with time, being dependent not only on prevailing growing conditions but also on market and policy environments. Challenges arising from the climatic environment are emphasised in the northern agricultural production areas (Slafer and Peltonen-Sainio, 2001; Peltonen-Sainio et al., 2009b).

3.1. Changes in yield trends in northern growing areas

Levelling off of crop yields, reduced rates of improvement in crop yields or even decline in yield trends are recently experienced features of agricultural production in many farming systems of the world (Bell et al., 1995; Calderini and Slafer, 1998; Slafer and Peltonen-Sainio, 2001; Peltonen-Sainio et al., 2007a, 2009b). Both timings of and reasons for such turning points differ according to the region. Evans (1993) reported examples of potential reasons for yield plateaus and declines – including extension of increasing cultivation areas to less favourable regions and changes in socio-economic policies, markets, costs and input use – and ways to analyse and interpret the changes in annual yields. In addition to these, in some production systems, one of the reasons for declining yield is general intensification of farming. For instance, when farmers try to grow more crops per year, they sacrifice yield of individual crops (Egli, 2008). Because the proportion of double cropping is greater, the better environments show less yield progress per harvest. Multiple cropping is not practised in Finland due to rigid climatic restrictions. Hence, it can be excluded when searching for potential contributors to the recently recorded lowering or levelling off in yield trends.

3.1.1. Steady increases in genetic gains

Keeping pace with genetic improvements requires continuous updating of breeding methods (Chapter 14) and trait identification (Foulkes et al., 2007; Table 2 in Chapter 15). Hence, it is possible that levelling off in genetic yield potential in certain regions is a result of fully exploited traits such as shortening of stem length and associated increase in harvest index (HI) and grain number (Austin et al., 1980; Siddique et al., 1989; Foulkes et al., 2007; Peltonen-Sainio et al., 2007b; Mäkelä et al., 2009; Table 1 in Chapter 15). However, Peltonen-Sainio et al. (2008d) indicated that under northern conditions, the HI of modern wheat cultivars, as opposed to barley and oat cultivars, was lower than those for other temperate spring cereals and also when compared with the HI in many of the important wheat production regions. This example might indicate that such traits are not yet thoroughly exploited in breeding for yield enhancement under northern conditions.

In Finland, genetic gains were evident for cereal grain yields during the entire study period from 1961 till 2006 (Peltonen-Sainio et al., 2007a, 2009b). This was the case for all spring cereals (barley, oat and wheat), winter rye and winter wheat, as well as for rapeseed. The mean genetic yield increases were 28 $\mathrm{kg\,ha^{-1}\,year^{-1}}$ for barley and winter rye, 21 $\mathrm{kg\,ha^{-1}\,year^{-1}}$ for oat, 36 $\mathrm{kg\,ha^{-1}\,year^{-1}}$ for spring wheat, 29 $\mathrm{kg\,ha^{-1}\,year^{-1}}$ for winter wheat and 17 $\mathrm{kg\,ha^{-1}\,year^{-1}}$ for rapeseed (Peltonen-Sainio et al., 2007a, 2009b). Quality traits have also been continuously improved. One example is rapeseed, for which oil content has increased with higher yields, and seed chlorophyll content, which reduces yield quality, has decreased. This indicates the importance of plant breeding for better-adapted cultivars to the northern climatic conditions (Peltonen-Sainio et al., 2009c; Peltonen-Sainio and Jauhiainen, 2008).

Not only have there been no signs of slowed pace of increase in yield potential in recent years for any of the temperate crops, but achievements in genetic yield potential have also been higher during the last 10 years than earlier. This was true especially for barley, oat and winter wheat and also where the pace of genetic improvement was comparable with that of earlier periods for spring wheat and rapeseed (Peltonen-Sainio et al., 2007a, 2009b). Thus, in northern areas, breeding has been successful in increasing yield potential (Figure 2), particularly when focused on better yield stability (e.g. reduced standard deviation to mean ratio).

Breeding cultivars specifically to northern conditions is a major challenge. Before discussing the traits that contribute to genetic yield increases, it is important to underline that earliness as an adaptation strategy has always been the principal trait in breeding programmes for improving adaptation to northern conditions (Kivi, 1963; Aikasalo, 1988; Rekunen, 1988; Peltonen-Sainio, 1990). Comparison of historical and present-day oat cultivars revealed that modern oat cultivars had a slightly shorter grain-filling period than their predecessors (Peltonen-Sainio and Rajala, 2007). This was also reflected in the growth period from sowing to maturity. This means that no trade-off between the durations of pre- and post-anthesis main phases occurred. However, despite the shorter growing time, grain yields were improved. Earlier maturity in cereals – and even without any yield penalty – evidently indicates improved adaptation to the short northern growing season and thereby enhanced yield stability.

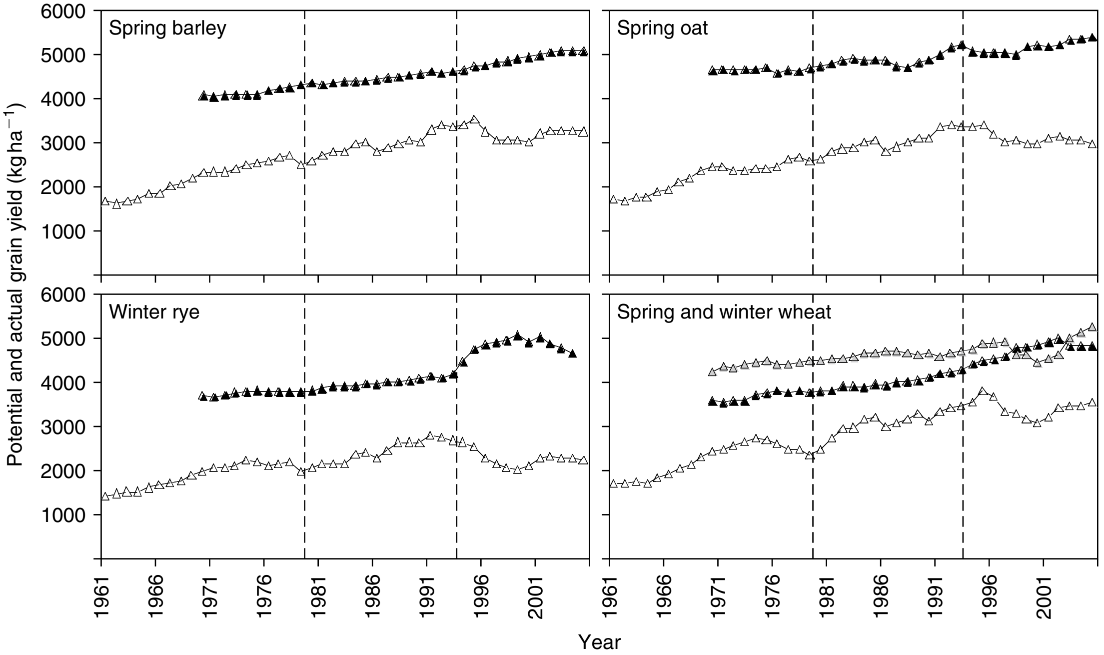

FIGURE 2

Genetic gains in grain yields of spring and winter cereals according to long-term multi-location experiments carried out in Finland since 1970 and national yield trends in Finland since 1961. Genetic gains (increase in potential yields) are measured according to the year of introduction of a new line/cultivar to the MTT testing programme. The solid triangles are potential yields and open triangles actual yields; both as five-year moving averages. Potential yield of winter wheat is indicated with a grey triangle and that of spring wheat with a closed triangle. Vertical broken lines differentiate three agronomical sub-periods: pre-modern and the first and the latter parts of modern periods. (Source: Peltonen-Sainio et al., 2009b.)

As reported for other regions, in northern regions also, increased yield potential of modern cultivars resulted from reduced plant height and increased HI and number of grains per spike (Peltonen-Sainio, 1990). However, improved yields of oat were not merely a consequence of increased HI, but also a consequence of higher total phytomass (Peltonen-Sainio, 1991).

3.1.2. The challenge of reaching yield potential

The successful use of management practices for controlling crop growth under prevailing conditions determines the extent to which increases in yield potential are achieved. There have been major changes of crop stand management in Finland during the period 1961–2006. Between 1961 and 1980 (later termed the pre-modern period), widespread agricultural mechanisation occurred, farmers adopted improved agricultural practices and commercial inputs were introduced and applied. In the 1981–1994 period (the first part of the modern period), crop management was further intensified, while in 1994 Finland became a member of the European Union, and especially since then (the latter part of the modern period) Finnish field crop production has been driven towards greater sustainability, often supported by policy and economic incentives. Furthermore, changes in cereal pricing on global and regional markets have impacted on input use for cereal and rapeseed production. Peltonen-Sainio et al. (2009b) reported the changes in major components that affect the achievement of yield potential.

Production was intensified in the first part of the modern period, and the equation governing the process was

$$\begin{aligned}\text{Actual yield} = f[&(\text{growing conditions} \times \text{genetic gains})\\ &\times (\text{growing conditions} \times \text{crop management gains})\\ &\times (\text{genetic gains} \times \text{crop management gains})]\end{aligned}$$

while in the latter part of the modern agricultural period, the equation gradually broadened to become

$$\begin{aligned}\text{Actual yield} = f[&(\text{growing conditions} \times \text{genetic gains})\\ &\times (\text{genetic gains} \times \text{crop management gains})\\ &\times (\text{growing conditions} \times \text{crop management gains}\\ &\times \text{market effects} \times \text{environmental motives})]\end{aligned}$$

All these major elements, influencing rate and direction of changes in yield trends, comprise numerous subcomponents. Fitting trend lines to data is relatively easy, but the complexity of components and changes in them over time makes interpretation of the causal effects on changes in yield trends challenging (Chapter 2).

Peltonen-Sainio et al. (2007a) reported periodic fluctuation in rapeseed yield trends: During early stages of adaptation of rapeseed to northern conditions, yields increased by up to 50 $\text{kg}\,\text{ha}^{-1}\,\text{year}^{-1}$; thereafter, they levelled off for about 20 years, increased again for a short period in the early 1990s by about 65 $\text{kg}\,\text{ha}^{-1}\,\text{year}^{-1}$ and markedly declined by 27 $\text{kg}\,\text{ha}^{-1}\,\text{year}^{-1}$ over the last 15 years, despite steady and marked improvements in genetic yield potential. The decline in national rapeseed yields was so dramatic in the 2000s that the yields approached those associated with the very early stages of rapeseed adaptation to Finland (Peltonen-Sainio et al., 2007a). That study indicated that the national yield trend for rapeseed was not consistent with genetic gains in yield potential, thereby emphasising the importance of crop management and the prevailing growing conditions to actual yields.

Also some fluctuations were noted in national cereal yield trends in Finland, which share some of the features discussed for rapeseed. Realisation of yield potential varied according to the time period. Furthermore, for all cereal species except wheat, despite the evident success of plant breeding, yields declined during the last 10 years (Figure 2) (Peltonen-Sainio et al., 2009b). Such recent decline in yield contrasted with periods prior to 1995, when national grain yields increased between 32 and 76 $\text{kg}\,\text{ha}^{-1}\,\text{year}^{-1}$ depending on species. In the pre-modern period, national yields of all cereals increased on average by 42 $\text{kg}\,\text{ha}^{-1}\,\text{year}^{-1}$

(Peltonen-Sainio et al., 2009b). In the first part of the modern period, the mean rate of yield increase was even slightly higher, 53 kg ha^{-1} $year^{-1}$. At that time, higher rates of fertiliser, plant growth regulator and pesticide input were used to sustain improved yield potential of less-lodging-prone cultivars. Hence, both plant breeding and management practices were successful and interplayed in increasing national yields more than that solely due to plant breeding, which increased 1.7–5.4-fold (depending on species) in 1970–1980 and 1.7–2.8-fold in 1981–1994 (Peltonen-Sainio et al., 2009b). In 1970–1980, national oat and winter rye yields were more enhanced by crop management than by breeding, in contrast to barley, while in 1981–1994 national yield increases were higher than genetic gains for all cereals other than winter rye. For all cereals except wheat, national yields declined since the mid-1990s. The decline was greatest in oat (−37 kg ha^{-1} $year^{-1}$) and winter rye (−36 kg ha^{-1} $year^{-1}$) and least in barley (−12 kg ha^{-1} $year^{-1}$) (Peltonen-Sainio et al., 2009b). Wheat yields might have even continued to increase also during the latter part of the modern period if cultivation had not extended into less favourable, northern regions. In rapeseed, the decline in yield trend is attributable to changes in production risks, most of all increased sensitivity of modern cultivars to elevated temperatures during the seed-filling phase and large yield losses caused by increasingly serious pathogen infections, but also due to sub-soil compaction causing serious problems with growth of the rapeseed taproot (Peltonen-Sainio et al., 2007a; Hannukkala, personal communication). Kirkegaard et al. (2006) and Lisson et al. (2007) reported similar evidence for declined oilseed rape yields in high-rainfall areas of southern New South Wales in Australia and concluded that sub-soil constraints, late-season water stress and diseases were the most common factors associated with underperformance of oilseed rape. After identifying the main contributors to reduced rapeseed yield under northernmost European conditions, principles of crop physiology need to be applied to reverse the yield trends. In contrast to rapeseed, decline in cereal yields likely resulted from changes in markets and policy following the incorporation of Finland into the European Union (Peltonen-Sainio et al., 2009b).

The EU environmental programme for agriculture, introduced in Finland in 1995, seeks increased sustainability and a reduced environmental footprint. Rates of fertiliser for arable crops were restricted, and economic incentives to produce efficiently decreased dramatically as producer prices for cereals fell by two-thirds while the prices of inputs remained the same (Peltonen-Sainio et al., 2009b). Consequently, there was a reduction in intensive cereal production, and the use of inputs slightly decreased in the absence of incentives to be efficient. Since 1995, the average annual change in productivity (the relationship between production volume and the inputs used) has been negative for cereal farms (Niemi and Ahlstedt, 2007).

Even though Peltonen-Sainio et al. (2009b) concluded that the likely key reason for the recent decline in Finnish cereal yield trends was the simultaneous changes in various management practices and input use (e.g. use of fertilisers and agrochemicals and timing of practices), they also noted that growing conditions fluctuated more in recent decades than during the first agronomic period of 1970–1980, and yield stability of the modern cultivars declined. Öfversten et al. (2002) compared the yield stability of 10 spring wheat cultivars accepted to the national list of recommended plant varieties during 1987–2001 and noted that 2 of 3 cultivars accepted in 2001 were among the more unstable cultivars.

Understandably, if yield potential is increased but is not achieved due to changes in markets and policy, solutions based on understanding of crop physiology are unlikely to be useful. Nevertheless, in such situations and also when considering the improvements needed for increasing sustainability of field crop production in the future, it is important to exploit the genetic component in yield trends. However, increasing and sustaining yield via improved resource use efficiency, and developing cultivars better adapted to low-input conditions, might also be useful in high-productivity environments, as Raven et al. (2005) stated in their exhaustive review. Improved resource use efficiency is further discussed in Part 2 of this book.

Considering future prospects for cereal trends in northern areas, it is likely that changes will occur again, but for different reasons. Substantial global changes will affect agriculture also in the northernmost European regions, particularly when it comes from improved living standards in many highly populated areas of the world. There will be increased demand for cereals to feed the expanding human population, and competing land uses will have substantial effects on global markets and pricing (Chapter 1). In addition to this, climate change (Chapter 20) will influence global changes and alter the trends for and balances among many field crops in northern Europe (Olesen and Bindi, 2002; Ewert et al., 2005).

4. ATTEMPTS TO IMPROVE SUSTAINABILITY

Chapter 1 (Section 2) defined agricultural sustainability in general, with emphasis on economic, social and environmental outcomes, and increasingly important matters of food security and quality. Sustainability in northern Europe is mainly concerned with reduced leaching of nitrogen and phosphorus and trade-offs with maintenance of soil fertility. Alternative tillage systems, cover crops, arrangement of crops in rotations, multiple cropping and improved resource use efficiency are increasingly important in this context. In recent years, increased concern over climate change has also led to assessing gas emissions from agriculture, including field crop production and the effects of tillage. Improved sustainability also includes elements of floral and faunal diversity.

4.1. Nutrient leaching

In northern Europe in general, but especially in Finland, with its more than 100,000 lakes, 14,000 km of Baltic coastline and substantial annual precipitation, the risks of nutrient leaching to natural water systems are high. Grasslands ensure continuous ground cover mainly in the central and northern parts of Finland, whereas partial ground cover from annual crops in southern areas determines the potential for nutrient leaching, particularly in autumn. Leaching can also occur during mild winter periods when large volumes of water run from the fields and in spring when the snow melts. Nutrients, especially nitrogen and phosphorus, leach in run-off water and soil particles in uncovered soils are prone to erosion. Therefore, it is essential that most of the nutrients are available for crop growth and are also utilised for biomass production, instead of remaining in the soil after harvest. This is ecologically and economically desirable.

One major challenge is to match the available nutrient supply to crop needs (see Chapter 8 for principles and Section 2.2 in Chapter 19 for applications). Typically, in the short growing season characterised by intensive and early crop development and growth, nutrients are applied only at sowing and are expected to sustain growth for the entire period from sowing to maturity. However, the major constraint is early summer drought, which can constraint nutrient uptake early in the season. Due to only modest capacity of crop stands to compensate for the losses occurring during early growth stages, as discussed in the earlier sections, early summer drought heightens the risk of nutrient leaching.

The EU environmental programme for agriculture included a special scheme aimed at increasing agricultural sustainability by reducing the associated environmental load. For example, fertiliser application levels for arable crops were restricted. At the same time, economic incentives to produce efficiently decreased dramatically as producer prices for cereals dropped by two-thirds while the prices of inputs remained the same (Niemi and Ahlstedt, 2007) and national cereal yields declined (Peltonen-Sainio et al., 2009b). However, when fertiliser input use and national yields declined, the effectiveness of this scheme depended on the changes in nitrogen and phosphorus load in the natural waterways. This indicated that reduction of nutrient load in the environment includes interesting crop physiology dimensions and challenges. Owing to the spatial variation in soils and yield (Rajala et al., 2007), precision farming methods can help to reduce nutrient leaching (Blackmore et al., 2003).

4.2. Maintenance of soil fertility and production

Leaching of nutrients is primarily reduced by cutting down on excessive fertiliser use with the associated consequences of large fluctuations in yield. Over 90% of arable land in Finland is included in the EU environmental programme, in which use of nitrogen and phosphorus is restricted according to the nutrient and productivity (mean yield) of each field. If soil phosphorus is high, no additional fertilisation is allowed. The most essential elements for greater nutrient use are crop species and cultivars adapted to the conditions of the particular fields, successful crop establishment and plant protection according to the needs of the crop.

Changes in nutrient use have resulted in not only declining yields in cereals but also changes in main yield components. According to analyses of Finnish cereal yields from 1990 to 2005, reduced nitrogen application rates were associated with lower test weight, grain weight and also grain protein concentration, while reduced rates of phosphorus application were associated with reduced grain weight and protein concentration in some cases (Salo et al., 2007). However, during that period, many other changes to crop management occurred that probably affected yield and yield-related traits, as economic incentives to produce efficiently decreased dramatically (Niemi and Ahlstedt, 2007). Examples of such changes include inadequate investment in drainage and liming, and increases in areas of reduced tillage and direct drilling.

4.3. Reductions in soil tillage

Traditionally, most fields sown to annual crops were autumn ploughed, but this practice has declined recently. Reducing soil tillage is a means of decreasing erosion and thereby nutrient leaching. It is therefore favoured in the EU environmental programme. Conservation tillage systems have been attractive because of the high cost of fossil fuels and labour. In northern Europe, the mouldboard plough is usually replaced by chisel or disc implements. Both represent potential conservation tillage methods for spring cereals on clay and silty clay soils typical of these humid climates (Rydberg, 1987; Aura, 1999; Heinonen et al., 2002). Effects of no till on greenhouse gas emissions are uncertain, particularly when considering the expected reduction in carbon emissions (Reicosky, 2003) against the putative increase in NOx emissions (Regina et al., 2007). According to Baker et al. (2007), the net effect of reduced tillage would be an increase in greenhouse gas emissions.

No till has been practised on increasing areas in Finland. In 2007, 30, 10 and 17% of the winter cereal, spring cereal and oilseed rape area, respectively, were direct drilled. The success of reduced tillage and direct drilling depends not only on weather conditions but also on soil quality. According to Rasmussen (1999), this method proved to be most advantageous in Scandinavia on the heaviest clay soils, which are the most difficult soils to prepare using conventional soil tillage methods. Direct drilling has been studied under the northernmost European conditions by MTT Agrifood Research Finland since the 1980s, long before it was adapted for use at the commercial farm scale.

Differences in the amount and quality of yield from ploughed and no-till soils vary between years, fields and crop species. Timing and implementation of drilling in no-till soil is especially challenging. When early summer drought occurs after drilling, which is typical of the northern areas, it may interfere with crop establishment. On the other hand, if plant stands establish well, prospects are good for successful growth during pre-anthesis, when yield is determined (Chapter 12), even if there is inadequate early summer precipitation because of the relatively high water content in no-till soil. Typically, yields are higher in rainy summers when soils are ploughed, while under dry conditions, direct-drilled crops may yield more than those sown in ploughed fields. In rainy summers, the yield decrease can be quite marked when the crop is direct drilled, and especially so with spring barley, which is sensitive to wet soils. Direct-drilled crops are also more sensitive to dry and warm periods during the grain-filling phase, leading to early maturity and smaller grains. Section 4.3 in Chapter 13 analyses the role of root vigour in reducing negative biotic and physical effects of reduced tillage in wheat.

Oat grows and yields more reliably than other spring cereals when direct drilled. Spring wheat often yields less when direct drilled, but in dry summers, it can out-yield crops from tilled fields. Direct drilling also works for winter cereals. Establishment is better than on ploughed soil, especially in dry autumns, but is poorer in wet autumns that are more typical of northern conditions. Establishment of direct-drilled spring turnip rape is problematic, mainly because the fertiliser is placed too close to the seed, and in turnip rape, it reduces germination markedly. This problem is avoided by increasing the amount of seed, but this is not necessarily economically sound and may increase the risk of volunteer turnip rape in the subsequent crop in the rotation.

The protein content of spring cereal grains has been low in direct drilling, which is positive for malting barley but negative for other cereals, especially for bread wheat. This is obviously a consequence of low mineralisation of nitrogen in no-till soil (Kristensen et al., 2000). Protein content could be improved by increasing nitrogen fertiliser application rates, but this is conflictive with general environmental aims. Variation in grain size of malting barley increases with direct drilling, and the share of small grains increases, especially in years when reaching the optimal grain size is otherwise difficult. Alakukku (2006) found no decrease in grain nitrogen concentration from crops grown on clay soil. However, no till in clay-loam soils reduced both nitrogen and phosphorus content more than grain yield. This indicates the need for evaluation of long-term effects of no till.

Special attention has to be paid to crop rotation in no-till fields. The amount and quality of crop residues affects drilling performance, and yield is threatened by diseases spreading from straw. Snails have caused some damage to winter cereals, especially when direct drilled. Growing the same species in successive years is therefore even more risky than when the soil is ploughed. Winter and spring cereals as well as crops with various amounts of crop residue require rotation. On the other hand, direct drilling of small-seeded oil crops is difficult after a crop with a high straw yield if the straw is not removed. Section 5 in Chapter 17 analyses the interactions between diseases and cropping practices, including tillage and residue management, and Section 6.1 in Chapter 2 discusses aspects of wheat-on-wheat cropping.

The degree of sustainability of these methods adopted in northern regions depends on how successful reduced or no till is, compared with conventional methods with respect to plant stand establishment, determination of yield potential and yield realisation during the post-anthesis phase. As described earlier, under northern European conditions, fields are often highly heterogeneous with respect to plant growth conditions and yield production capacity (Rajala et al., 2007). No till in heterogeneous fields increases the risk of uneven growth and ripening. Furthermore, sowing normally occurs later in untilled than in tilled soil. Although less fossil fuel is needed if a field is not ploughed, the advantage is partly lost as late harvest often results in higher grain moisture content and increased energy use in drying the grain, which is generally required to secure high quality in northern areas.

Contrary to what was expected with the EU environmental programme, Muukkonen et al. (2007) reported that no till increased the loss of dissolved phosphorus in surface run-off. They found that even short-term no till can increase the labile phosphorus in clay soil but pointed out that future soil management studies should focus on the long-term effects. An additional drawback is the often increased need for pesticides, which can be reduced to some extent through sound crop rotation and use of resistant cultivars.

4.4. Crops for nutrient uptake and soil coverage

Cover or uptaking crops are used for reducing nutrient leaching, transferring nitrogen to the next main crop, increasing biodiversity and maintaining or improving soil structure. The mode of action of the cover crop largely depends on climatic conditions (Schröder, 2001). In the short growing season of northern latitudes, the time after cereal harvest is too short for sowing the cover crop; hence inter-sowing in standing cereals is the only method for establishing a cover crop stand (Alvenäs and Marstorp, 1993; Jensen, 1991). Inter-sowing enables immediate uptake of residual nitrogen by the cover crop after harvest of the main crop (Breland, 1996). Undersown crops can grow until late autumn or even the next spring before being either incorporated into the soil or eliminated with glyphosate.

Undersown grass crops uptake available nitrogen from the soil, thus reducing nitrogen leaching. Italian ryegrass (*Lolium multiflorum* Lam.) uptakes nitrogen effectively in autumn and timothy (*Phleum pratense* L.) mainly in the following spring (Känkänen and Eriksson, 2007). Clovers fix atmospheric nitrogen and transfer it to the next crop. Undersown crops compete with the main crop for water, nutrients and space. However, these effects on main crop yield are relatively low if the undersown crop species are chosen carefully, taking competition into account and using moderate seeding rates. Delayed inter-sowing does not benefit the yield formation of the main crop and greatly decreases the biomass production of the uptaking crop (Kvist, 1992; Ohlander et al., 1996). Thus, inter-sowing is used. The yield decrease and seed costs are, however, the main reasons for limited inter-sowing in Finland, despite its positive effects on soil, biodiversity and environment.

Buffer zones are uncultivated areas between fields and watercourses that have been established to slow run-off water from agriculture, enhance infiltration and absorb phosphorus in soil and vegetation, thereby trapping sediment and nutrients. Their extensive use in Finnish farms is a measure of the success of the environmental programme. Buffer zones and constructed wetlands are good at reducing soil and particulate phosphorus losses via surface run-off, but the effect on dissolved reactive phosphorus remains uncertain (Uusi-Kämppä et al., 2000).

4.5. Multiple and versatile cropping

Relay inter-cropping, which normally is carried out by sowing winter cereal under spring cereal in northern Europe, could improve nutrient usage and reduce negative effects of tillage in conventional autumn sowing. Relay cropping of spring barley and winter wheat has been studied in Finland and Sweden, and different conclusions were reached. In Finland the system was uncertain and resulted in yield decreases of both crops (Känkänen et al., 2004), while in Sweden Roslon (2003) concluded that relay inter-cropping of spring barley and winter wheat was possible, although further studies were needed.

Crop rotation is a basic operation in sustainable agriculture; however, this has been neglected when short-term economic goals have been pursued in recent years. Appropriate crop rotations increase the diversity of farming systems, reduce crop diseases and maintain and improve soil structure. The companion chapters in this part of the book present contrasting rotations common in Australia, the pampas of Argentina and temperate-to-tropical regions of Asia.

The need for taking care of soil and other aspects of the environment will increase as climate change proceeds (Chapter 20). Clay soils, common in Sweden and especially in southern Finland, are particularly vulnerable. A change from cold winters with soil frost and snow cover to wet and mild winters represents a risk of deteriorating soil structure. The importance of methods to improve and maintain soil structure and conditions, such as reduced tillage, versatile crop rotations and use of cover crops, will increase as the climate changes. Furthermore, many of these examples from northern regions not only describe how changes in farming systems and crop management practices can improve sustainability, but also highlight the marginal nature of the environmental advantages in the case of the crop management being challenged by variability in climate and growing conditions and when economic incentives to produce efficiently decrease dramatically.

4.6. Improving resource use efficiency

In addition to developing crop management systems as indicated, it is important to search for the potential solutions that plant breeding could offer through cultivar development. Improved resource use efficiency is especially important today and will increase in importance in the future as fertiliser prices rise with increasing energy costs. Capture and efficiency in the use of major resources, namely, radiation, water and nitrogen, are the subject of Part 2 of this book.

Nitrogen use efficiency (NUE) is defined as grain yield produced per unit of nitrogen available in the soil (Moll et al., 1982). Like grain yield itself, NUE is a complex trait determined by many physiological processes during the life span of the crop (Chapter 8). In intensive and short growing seasons typical of high latitudes, capacity to uptake nitrogen according to crop growth requirements is essential to avoid both partial achievements of yield potential and higher risks of nutrient leaching (Løes, 2003). Furthermore, according to Ortiz-Monasterio et al. (1997), nitrogen uptake is an important element of NUE, especially when nitrogen is in short supply. Therefore, with reduced use of fertiliser, improved ability of the crop to uptake nitrogen and phosphorus should be an aim of plant breeding.

Under northern conditions, nutrient uptake and nutrient use efficiency have not been a central aim of plant-breeding programs. Despite this, our recent results indicated significant improvements of NUE of wheat and oat in Finland between 1909 and 2002 (Muurinen et al., 2006). Furthermore, most of the improvement in NUE originated from improved nitrogen uptake. However, there was no comparable, clear trend of NUE and year of release in two-row barley (Muurinen et al., 2006). It is, however, possible that two-row barley differed from other crops and the general trend because breeding for malting barley, contrary to other crops, involves consistent selection for low grain protein concentration (Muurinen et al., 2006). This was, however, not the case in the study of Abeledo et al. (2008) with old and modern malting barley cultivars. Nevertheless, breeding for improved nitrogen uptake and NUE represents a new, under-utilised way to improve the cost efficiency of input use in agriculture, reduce nutrient losses to the environment and sustain the formation and achievement of yield potential. It requires a source of variation in breeding programmes and cost-efficient tools for selecting the desired combination of NUE traits in the future (Elen, 2003; Jalli et al., 2006). Section 4 in Chapter 8 analyses in detail the components, physiological bases and potential for improvement of NUE.

5. THE FUTURE AND CLIMATE CHANGE

The global mean temperature has risen by 0.76°C (IPCC, 2007a) during the last century. In Finland, the average increase has been about the same, with the largest statistically significant increase in spring (Tuomenvirta, 2004). Chapter 20 deals with climate change in general, including global trends and modelling approaches to evaluate the agricultural impact in a range of scenarios. Here we present a perspective from high-latitude cropping systems.

A warmer climate will mitigate some of the climatic constraints that currently limit agriculture at high latitudes. One of the main constraints is the short growing season. Increases in average temperatures during the last century have already extended the growing season in Finland, especially in spring (Carter, 1998; Kaukoranta and Hakala, 2008). In 1965–2007, the advancement of the start of growing season was 2.0–2.8 days per decade, and the corresponding advancement in the start of sowing was from 0.6–1.7 days per decade for cereals (depending on the region in Finland) to 2.5 days per decade for sugar beet and 3.4 days per decade for potato (Kaukoranta and Hakala, 2008). The same trend is projected to continue in the future even in the case of considerable reductions in greenhouse gas emissions, but especially if these reductions are not completely realised (IPCC, 2007a; Peltonen-Sainio et al., 2009a).

In the future, however, the lengthening of thermal growing season will occur more at the end than at the beginning of the growing season (Table 2), with a considerable fraction of the increased temperature sum accumulating late in autumn. Because of the rapid reduction in sunlight hours and light intensity in autumn, an increase in the length of the thermal growing season in autumn would benefit crop production only partially. Most of the increase in thermal growing season in spring could be used for crop growth, at least when fields are dry enough to carry heavy machinery and spring frosts not too severe for crop growth, allowing sowing of spring cereals earlier in the season. Because of technological problems in spring, cultivation of winter cereals and perennials will become increasingly crucial in the future, as they can start growing once the conditions become favourable and can also make use of the wintertime moisture in the field. The intrinsically lower productivity of perennials is analysed in Section 3 of Chapter 9.

Warmer and shorter winters in the future will probably result in diminished risk of freezing damage and better over-wintering conditions for autumn-sown crops and perennials. However, the benefits of milder autumns and winters may be compromised by several factors. For example, warmer autumns provide shorter periods for cold hardening of over-wintering plants, leading to higher vulnerability to winter injury by severe frosts, which will continue to occur regularly, despite the general warming of climate (Bélanger et al., 2002). Reduced snow cover may also cause increased risk of winter injury when periods of severe frosts coincide with periods of reduced or no snow cover, leaving the over-wintering plants unprotected. On the other hand, the

Table 2 Current Growing Season and Climatic Variables for Jokioinen, Finland (60°48′N, 23°30′E – average of 1971–2000, year 1986), and Scenarios for the Future [periods 2010–2039 (year 2025), 2040–2069 (year 2055) and 2070–2099 (year 2085)] according to the A2 Scenario of IPCC (2000), and Calculated as a Consensus of 19 Climate Models (Peltonen-Sainio et al., 2009a)

	Growing Season			Winter Days (d)	Temp Sum (°C d)	Precipitation			
	Start	End	Length (d)			MAM (mm)	JJA (mm)	SON (mm)	DJF (mm)
Jokioinen 60°48′N 23°30′E									
1986	Apr 27	Oct 12	169	139	1193	106	209	195	139
2025	Apr 22	Oct 18	181	121	1371	108	215	201	145
2055	Apr 16	Oct 28	196	93	1577	112	221	210	155
2085	Apr 05	Nov 09	219	27	1859	119	228	224	170
Denmark 54–56°N, 8–12°E									
	Apr 1–15	Nov 1–15	>225	0–25	1400–1600	125–150	175–225	150–300	150–200

MAM, spring (March, April, May); JJA, summer (June, July, August); SON, autumn (September, October, November); DJF, winter (December, January, February). Danish (54–58°N, 8–12°E) temperatures derived from Tveito et al. (2001) and precipitation from Frich et al. (1997) are the average for 1961–1990. Temperature Sum (Temp Sum) and growing season length are calculated at >5°C, and the number of winter days is calculated at <0°C. Precipitation in mm per season.

projected increase in wintertime precipitation (Table 2) may also result in deeper snow cover, which under relatively mild winter conditions may melt and again freeze, resulting in soil heaving and injuries, especially to root tissue, and ice encasement leading to anoxia problems (Bélanger et al., 2002). According to the latest scenarios, the conditions for freezing and melting of snow during winter will become more frequent in the future as winter days with daily maximum temperatures passing 0 °C are predicted to increase, although the number of days with average temperatures below 0 °C will decrease (Jylhä et al., 2008).

Trends in precipitation during the last century are not as clear as trends in temperature (Tuomenvirta, 2004; IPCC, 2007a). However, according to the IPCC, annual precipitation has increased in northern Europe during the last century and the increase is 'very likely' (IPCC, 2007a) to continue in the future. This increase is projected to take place more during winter than during the growing season. Whether the wintertime precipitation will increase as much as in the present scenarios is of course not certain, considering the difficulties in predicting rain in general and the great variation in precipitation on average. The scenarios show increases in precipitation in Jokioinen, Finland, of 2 mm in spring (MAM) and 6 mm in the other seasons (JJA, SON and DJF) by 2025 (Table 2), while the standard deviation for the same periods in Jokioinen at present (averages from 1984 to 2005) is 8, 2, 11 and 3 mm (Klein Tank et al., 2002). By the end of the next century, according to emission scenario A2 (greenhouse gas emissions are not efficiently restricted, IPCC, 2000), the increase in precipitation would be 13, 19, 29 and 31 mm for MAM, JJA, SON and DJF, respectively (Table 2), which would exceed the natural variation observed at present. In any case, even though the precipitation will increase in the North, the increase is likely to benefit agricultural production only little, as it will mainly take place outside the growing season. Early season drought will thus remain a problem in the future. The projected slight increases in growing season precipitation will probably not compensate for the increased evapotranspiration caused by higher growing season temperatures and higher canopy biomasses in the field. Moreover, a trend showing increase in heavy precipitation events has been detected for the past century, and this trend is 'very likely' to strengthen during the twenty-first century (IPCC, 2007a). Heavy rain events tend to lead to surface flow of water, benefiting the crop water economy less than rain falling over a longer time period.

Autumn-sown crops and perennials that can make use of winter moisture in spring would help to adapt agriculture to the conditions of early season drought. However, over-wintering problems may reduce the yields of autumn-sown crops during the next few decades and cause substantial variation within and between years. In addition, not all crops can be sown in autumn, although the range of suitable varieties will probably increase in the future. Another practical tool to minimise the effects of drought is irrigation. Irrigation is little used at present in the north, but if the occurrence of early season drought increases and especially if the prices of the agricultural products increase, irrigation could become an increasingly attractive method to reduce annual yield fluctuations, as there are large water reservoirs available for irrigation in northern Europe. Irrigation during the early growing season would favour grain set and thereby improve the effective nutrient utilisation for crop growth and thus also reduce the risk of nutrient leaching.

The future climatic conditions of southern Finland have often been compared with the current conditions in Denmark (Figure 1). When climatic variables only are considered, the conditions in southern Finland (e.g. Jokioinen) for the period 2070–2099 (year 2085 in Table 2), according to scenario A2, resemble those currently pertaining to Denmark. The modelled temperature sum in Jokioinen would reach the values of present-day Denmark much earlier, in the period 2010–2039 (year 2025 in Table 2). Even if the actual growing season (the period from sowing to harvesting) would not extend as much as the thermal growing season, it is evident that the growing season will become considerably longer and temperature sums higher in the near future. However, the most striking differences between the climates of Denmark and Finland are the number of winter days and springtime precipitation, which seem to be more favourable in Denmark even if the effects of climate change are severe.

Currently, crop yields in Denmark are from 50 to 100% higher than those in Finland, depending on the crop (FAO Statistics, 2008; in http://faostat.fao.org). One reason for this is the longer growing season and milder winters in Denmark. With a longer growing season, crops with a longer growth period and thus higher yield potential can be cultivated. Also autumn-sown crops and perennials commonly cultivated in areas with mild winters usually produce better yields because they can start growing early in the season and benefit from the winter moisture in the fields.

In Finnish open-top chamber experiments, meadow fescue (*Festuca pratensis* Hudson 'Kalevi') benefited from increases in growing season temperatures, length of growing season and ambient CO_2 (Hakala and Mela, 1996). In the same experiment, the yield of the variety of spring wheat 'Polkka' decreased in elevated growing season temperatures due to hastened development. Elevated CO_2 concentration did compensate for the yield loss, but only to the extent of bringing the yield to the same level as at ambient temperatures (Hakala, 1998). In a warmer climate, yield increases of cereals in Finland require new, more productive cultivars adapted to the longer growing season. The present forage grass cultivars, again, seem to adapt better to the improved growth conditions. With more suitable crop varieties, the increase in the concentration of CO_2 should also bring about real yield benefits, at least as suggested by the considerable increase in photosynthetic efficiency of both wheat and meadow fescue at higher CO_2 concentrations (Hakala et al., 1999).

While crop yields are likely to increase in the future in Finland, reaching the current yield levels of Denmark will require several types of adaptive measures. Firstly, in addition to warmer temperatures, the long-day conditions during the Finnish growing season also hasten the development of determinate crops such as cereals, leading to a shorter growth period and lower yield. Moreover, long days strengthen apical dominance, which may interfere with tillering and thus full realisation of yield potential (Rajala and Peltonen-Sainio, 2000). Even though breeding has succeeded in increasing HI, nutrient use efficiency and yields of crops worldwide, long-day conditions may hamper full exploitation of the longer growing season in the future. Secondly, the actual future growing season will also have to end earlier than the thermal one because of rapidly diminishing light levels late in the season from September onwards (e.g. www.gaisma.com, 24.1.2008). To take full advantage of a longer growing season, new improved varieties of autumn-sown crops should be taken into cultivation in order to promote crop growth early in the season. Investment in field drainage should also be promoted by the government and the European Union in order to avoid extreme soil moisture and subsequent difficulties during spring cultivation, and also to reduce nutrient leaching and erosion. Thirdly, besides climate, Finland and Denmark differ in many other aspects, including soil and geography, as well as distances and logistics both within the country and between possible markets for agricultural products. Therefore, it is probable that farmers in Finland will continue to cultivate their fields more extensively and invest less in production inputs than farmers in Denmark. However, if the demand for agricultural products increases, for example, due to decreased production capacity in areas suffering from serious drought (IPCC, 2007b), the situation may change. Given better income prospects, farmers would probably be willing to invest more in inputs such as machinery, plant protection measures, seed quality and accurate fertilisation. Higher inputs by the farmers would lead to higher yields and better exploitation of the improved climatic conditions. Development in the direction of more efficient agriculture depends, however, not only on farmers but also on political preferences and decisions within Finland and the European Union.

As suggested by the observed adjustment of sowing time according to earlier growing season start (Kaukoranta and Hakala, 2008), Finnish farmers adapt readily to new conditions. They are also eager to experiment in growing new varieties of the commonly cultivated crops, and also completely new crops such as forage maize (*Zea mays* L.) and oilseed rape, whenever possible. Oilseed rape has already given reasonable yields and is forecasted to replace the less productive turnip rape during the first scenario period 2010–2039 if plant breeding can produce suitable varieties for the long-day conditions of Finland (Peltonen-Sainio et al., 2009a).

Until recently, Finland has been relatively free of many pests and diseases that are common in central Europe. With longer growing seasons and milder winters, the pathogen and pest problems will probably increase (Carter et al., 1996; Kaukoranta, 1996; Hannukkala et al., 2007). Even though most problems with pests, pathogens and weeds will be manageable under the new climatic conditions in Finland, just as they are in warmer areas at present, the required protection measures will decrease the profit that climate change would otherwise bring to Finnish agriculture. Higher fertilisation rates to match the increasing yield potential will also increase the input costs of farming. More importantly, higher inputs of pesticide and fertiliser will lead to new environmental and production challenges. Under conditions of higher precipitation, especially heavy rains, and longer warmer winters, there will be an increased risk of leaching of both plant protection chemicals and fertiliser nutrients and of soil erosion.

6. CONCLUDING REMARKS

Both breeding cultivars adapted to northern growing conditions and developing crop management to sustain yield potential have represented exceptional challenges for northern Europe, compared with the global, large-scale challenges that crop production typically faces. During earlier decades, development was largely based on testing management practices and application of methods for large-scale comparative trials, in which yield response per se, economic outcome and general applicability of the method were often sufficient for adopting a novel method or systems; crop physiology did not contribute much to these early developments. However, crop physiology will evidently play a far more important role in the future in plant breeding and developing crop management practices as climate and cropping systems change in line with the extended growing season.

Substantial challenges will be faced when northern agriculture has to cope with climate change-induced opportunities and risks, especially when more environment-friendly, truly sustainable production systems have to be developed in the typically variable conditions of northern Europe. This will take place against a background of increasing demand for food and reduced global production capacity, driven by population growth, the drive for an increased standard of living and climate change.

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CHAPTER 5

Cereal-Based Cropping Systems in Asia: Nutrition and Disease Management

Ram C. Sharma

1. INTRODUCTION

Cereals are the most important staple crops worldwide including Asia. This group of crops has the oldest record of cultivation by mankind, and has followed a very complex and interrelated course of evolution (Harlan et al., 1973). Human civilisation has been, and still is, closely linked with cereals and has moved across the globe carrying cereal culture during mankind migrations. This is reflected through the journey of wheat, rice, barley and millets from the old to the new world and of maize in the opposite direction. Many other crops are grown with, before or after the cereals, to satisfy the taste and meet the need of humans as well as their requirement for clothing, shelter and animal feed. It is in this light that, influenced by the prevalent eco-physical conditions, the cereal-based cropping systems (CBCS) of Asia evolved over time (Table 1, Figure 1). Thus, the present day CBCS in Asia and their management falls within an evolutionary framework influenced by eco-physical (mainly radiation, precipitation and soil conditions) and socio-economic factors and government policy (Cramb, 2005).

Rice, wheat and maize provide 60% of the human food globally (Tilman et al., 2002). These three crops account for more than 90% of Asia's cereal production over 284 million ha of prime agricultural land (FAO, 2008). The minor cereals include barley, sorghum and different types of millets. Figure 2 shows time-trends in area, production and yield of major cereals in Asia. Overall production of cereals has been constantly increasing in Asia despite declining in total area compared to 1980s (FAO, 2008). The decline is primarily due to decrease in wheat and millets areas. On the other hand, all the other major cereals have been recording increases in yield. In Asia, the population is expected to grow by 40% in 2050 compared to 2000. Thus, this continent is facing a tremendous challenge for meeting food production at the pace of people demand as well as the sustainability of its natural resource base (Rosegrant et al., 2006). This is becoming even more challenging due to the threat of global warming (Hodson and White, 2007; Section 5 in Chapter 20) and deterioration in soil health.

Even though the CBCS in Asia are highly diverse due to contrasting eco-physical conditions in different regions, there are a few mega-systems that account for a greater share of food production in the continent. These include cropping systems such as rice-rice in the tropical climate of East and Southeast Asia, rice-wheat in the intensive agro-ecosystems of China and South Asia, cereals-legumes in South Asia and wheat-fallow and wheat-cotton in the drylands of China, India and West and Central Asia. This chapter will discuss the eco-physical background and management of some of these systems, with emphasis on nutrition and diseases.

Table 1 Geographical Distribution and Water Regime of Major Cereal-Based Cropping Systems in Asia

Region	Water Regime	Cropping Sequence
East and Southeast Asia	Dryland/rainfed	Rice–wheat, rice-fallow. Wheat-fallow, maize-fallow
	Irrigated	Rice–rice, rice–wheat[a], rice–maize
South Asia	Dryland/rainfed	Rice–wheat, rice–legumes, rice-fallow, wheat–maize, wheat–cotton
	Irrigated	Rice–wheat, rice–maize, rice–wheat–maize, rice-vegetables
Central Asia	Dryland/rainfed	Wheat-fallow
	Irrigated	Wheat–cotton
West Asia	Dryland/rainfed	Barley-barley, barley-fallow, barley–forage legume
	Irrigated	Wheat-fallow, wheat–barley, wheat–faba bean, wheat–chickpea, wheat–lentil, wheat–melon, wheat–sunflower, wheat–sesame

[a] *The most widely adopted system in Asia.*

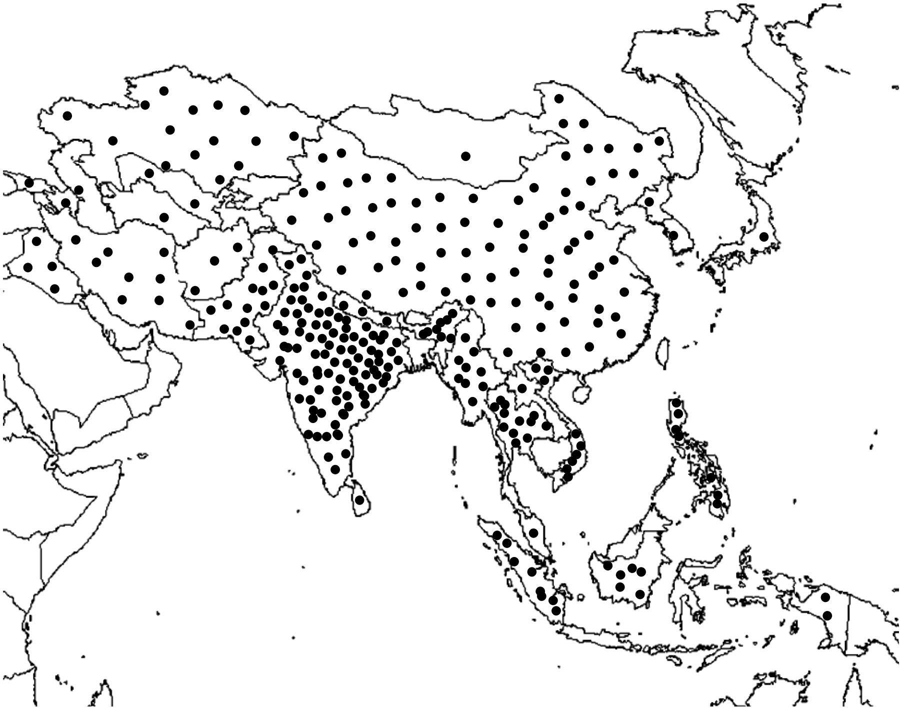

FIGURE 1

Area harvested under cereal crops in Asia in 2006. One dot represents 1 million ha. The country borders are purely a graphical representation and are only intended to be indicative. These boundaries do not necessarily reflect the official border. (Data Source: FAO, 2008.)

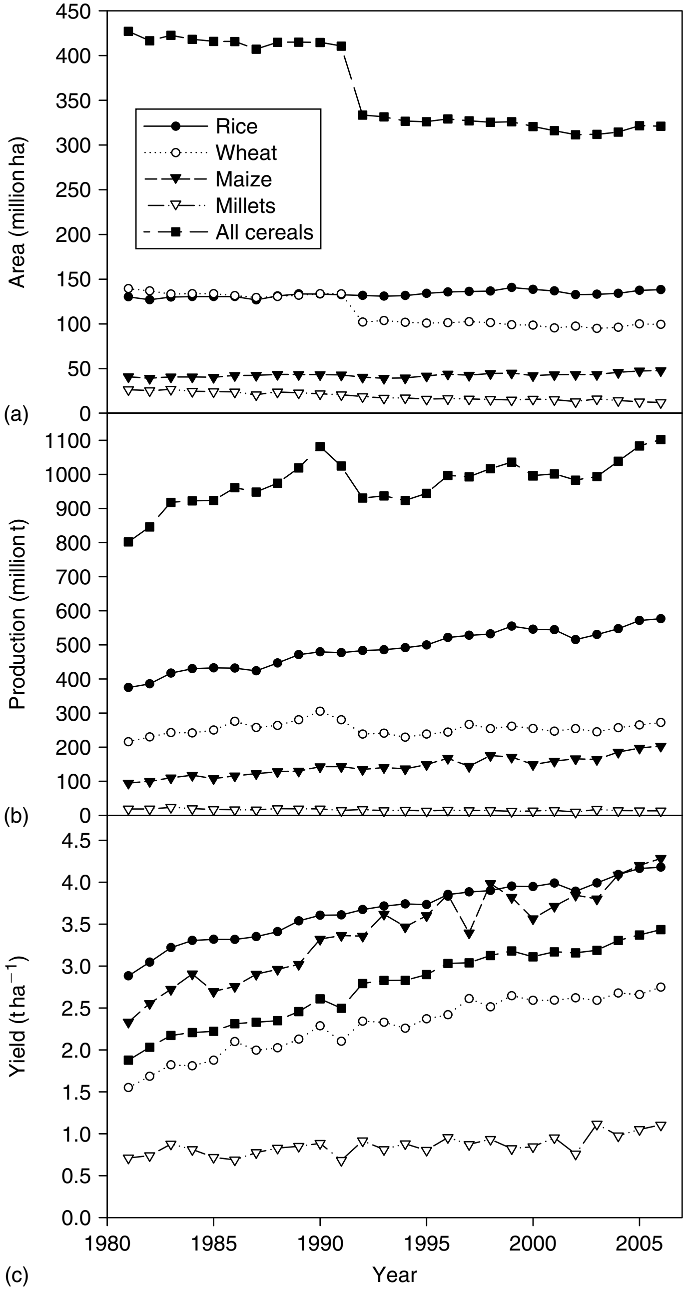

FIGURE 2

Trend in area, production and yield of major cereals in Asia. (Source: FAO, 2008.)

2. ECO-PHYSICAL BACKGROUND OF CEREAL-BASED CROPPING SYSTEMS IN ASIA

There are several eco-physical, social and economic factors that have played important roles in the development of the present CBCS of Asia (Table 1, Figure 1). The monsoon rains in a large part of south and southeast determine the traditional rice-based cropping system. Similarly, low spring precipitations in West and Central Asia have been the major determinant of the cereal (wheat and barley)-fallow cropping system in these regions. Maize-based cropping is primarily important in temperate hilly regions of South Asia where crops on hill slopes fully utilise pre-monsoon rain. High precipitations and high radiation have particularly helped in the development of widely adopted cereal-based intensive cropping systems (rice-wheat, rice-legumes) over the vast Gangetic Plains of South Asia and a large part of China.

Precipitation patterns in South Asia could be erratic posing a threat to crop harvests and livelihood. However, farmers have developed strategies to counter the unpredictability of precipitation. Farmers would often plant a mix of two or more crops of contrasting drought tolerance nature, for example maize with millets, upland rice with millet or pigeon pea and so on. This ensures crop harvests irrespective of a wet or dry season. This approach to risk is even utilised in the more favourable, intensive agro-ecosystem of South Asia.

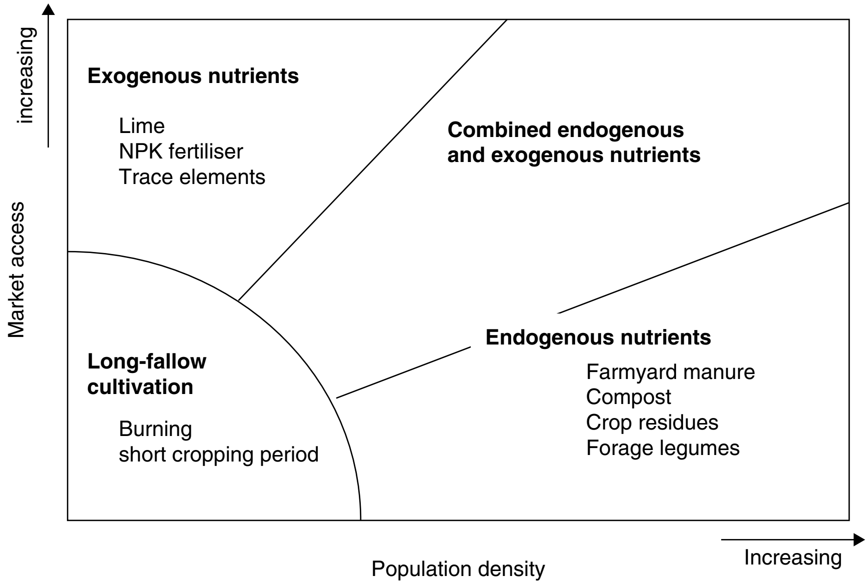

FIGURE 3

Hypothetical management of fertility in acid upland soils in relation to population density and market access. At low population density and reduced market access, farmers typically rely on shifting cultivation; slash-and-burn reduces acidity, provides nutrients for one to two years and is consistent with low labour:land ratios, limited cash flow and high input cost. The combination of high population density and poor market access hypothetically favours incorporation of livestock to the system and other sources of endogenous nutrients, and is consistent with high labour:land ratios. At low population density and good market access, commercial crops and livestock became viable, providing a source of cash that in turn allows for the purchase of exogenous nutrients. (Source: Cramb's (2005) case studies: long-fallow system in Sarawak (Malaysia), short-fallow system in South Kalimantan (Indonesia), continuous cropping system in Bukidnon (Philippines), an agro-forestry intercropping system in southern Thailand and a livestock grazing system in Daclac [Vietnam].)

For example, rice-wheat-maize and rice-legumes (chickpea or lentil) systems are used on heavy clay soil, whereas wheat/maize-groundnut/potato is grown on medium-to-light soil. Cramb (2005) provides a good example of cropping systems and practices accounting for specific soil conditions, population density and market access (Figure 3).

3. MAJOR CEREAL-BASED CROPPING SYSTEMS IN ASIA

Diverse cropping systems in Asia have developed around a few mega cereal-based systems (Table 1). Rice-wheat and rice-legumes in South and Southeast Asia and wheat-fallow and barley-fallow in Central and West Asia are most widely grown cropping systems in Asia. A full account of all the CBCS in Asia is beyond the scope of this chapter, but the most significant ones are briefly described below. Further reference to rice-wheat system, the more widespread in Asia, can be found in Hobbs and Morris (1996) and Timsina and Connor (2001).

3.1. Rice based

Rice is the most widely grown cereal in East, Southeast and South Asia. Depending on the supply of water, rice ecosystems are classified into upland, rainfed lowland, irrigated and flood prone (Fischer, 1998). Within each of these ecosystems, further diversity arises from differences in temperature, soil type and season (Garrity et al., 1996; Ramasamy et al., 1996; Widawsky and O'Toole, 1996). In terms of cropping intensity, rice-based systems range from single crop of rice under dry upland and flood-prone conditions to three crops under intensive irrigated conditions in the tropical and subtropical environments. Of the many rice-based systems (Table 1), rice–wheat is the most widely grown; it covers more than 24 Mha in South Asia alone (Ladha et al., 2000). The rice-wheat system has been dominant in China, accounting for 13 Mha at one time; however, the area has been declining in the past decade (Dawe et al., 2004). In part, the decline in wheat-rice acreage is related to more favourable outcomes from maize-rice (Section 3.3).

Photoperiod sensitivity was a common trait of old rice varieties when a single crop of rice was grown in many parts of South Asia. However, the release of photoperiod insensitive varieties allows multiple rice crops under tropical environments of East, Southeast and South Asia. This has also allowed growing summer rice in large parts of South and Southeast Asia where rice cultivation was traditionally done with the onset of monsoon in July. With one or two supplemental irrigations, rice is planted at the end of the spring season. Such rice crops take advantage of pre-monsoon rain in May and June and mature towards the end of the monsoon season in August-September. The summer rice crop utilises long hours of sunshine, which allows higher biomass production and higher grain yield than the monsoon rice that completes half of the growing period under short day hours. Early maturing, photoperiod insensitive varieties have permitted rice cultivation in areas where long day and short night summer season was traditionally not suitable to grow photoperiod sensitive varieties (Okumoto et al., 1996). Thus, photoperiod insensitive rice varieties have helped in extending rice-based cropping systems in Asia. Chapter 12 deals with the genetic and environmental control of phenological development from the perspective of crop adaptation and yield of individual crops, and Box 1 in Chapter 1 outlines Evans' concept of yield per unit area and time as the next step in the evolution of grain yield where the yield of individual crops may be reduced (e.g. by shorter season) to allow for improved annual yield of the whole system.

3.2. Wheat based

The wheat-based cropping systems are mostly annual, and include wheat–rice, wheat–maize, wheat–cotton, wheat–grain legumes–rice, wheat–potato–rice and wheat–millet–maize. However, a great diversity in wheat-based cropping systems exists in different countries depending on temperature, type of wheat grown (spring, facultative, winter) and water availability. For example, on the dryland of Central and West Asia, a single crop of wheat is grown under rainfed or supplemental irrigation (Ilbeyi et al., 2006). On the other hand, three crops are grown under intensive wheat-based cropping systems in South Asia. In many parts of the continent, two crops are grown in the wheat-based annual cropping system. However, rice-wheat cropping system in the non-traditional warm wheat growing environments on the Gangetic Plains allows only 90–120 days of crop cycle. Often, late harvest of traditional rice varieties compels the farmers to delay sowing of wheat until late December and early January instead of the optimum sowing date during the second half of November. Late-sown wheat completes the vegetative period under optimum temperature conditions; however, grain filling can be reduced by up to 50% (average 60 days reduced to 30 days) causing severe reductions in grain yield primarily due to reductions in biomass production (Sharma, 1992; Sharma and Duveiller, 2004). On average, yield declines at 37 kg ha^{-1} per delayed day in sowings later than 25 November (Mushtaq et al., 2007). High temperatures during grain filling hasten senescence and crop ripening, curtailing potential assimilate production that reduces grain weight (Sharma et al., 2008); the length of grain-filling period is positively correlated with wheat grain yield (Sharma, 1992, 1994). Research efforts are underway to deal with this problem using a combination of breeding and agronomic solutions. Most effort is directed at developing (a) early maturing rice using photoperiod insensitive varieties and (b) low-till wheat seeders that allow sowing wheat two to three weeks earlier than the traditional tillage practices. Such a system would allow for cool nights and warm spring days for wheat grain filling. The breeding × agronomy synergy sought to improve rice-wheat systems in Asia is the main theme of Chapter 2. Interestingly, many of the problems and opportunities for improvement in Asia cropping systems are comparable with those in developing novel, multiple cropping systems in the Pampas (Section 5 in Chapter 3).

Wheat-cotton is another widely grown system in drylands of South Asia. The timely harvest of the cotton crop is critical for optimum seeding and maximum yield of wheat. A different wheat-cotton relay intercropping is practiced over a large area in northern China. In this system, the time and pattern of cotton seeding in maturing wheat crop could be critical for attaining the highest productivity of the system (Zhang et al., 2007, 2008b). The aggregate yield of the cotton–wheat system is greater than that of the monocultures, with land equivalent ratios around 1.39–1.28; this is largely accounted for enhanced capture of radiation (Figure 4). On marginal lands unsuitable for wheat-based cropping, barely-based systems have been adopted (Table 1).

3.3. Maize based

Maize is widely grown on uplands, where multiple year cropping systems also include fodder legumes and sugarcane. Recently, there has been increasing interest in expanding maize-based cropping systems in Asia. The traditional rice–wheat mega cropping system is losing a part of its area to the expansion of rice–maize. Summer rice followed by winter maize is becoming important both in South (Waddington et al., 2006; Zaidi and Singh, 2006) and Southeast Asia (Doberman, 2006). This system is becoming more important due to higher yield of winter maize over wheat and other alternative winter crops, and the increasing demand of maize for animal feed and biofuel (see Box 3 in Chapter 1). Even though maize has been traditionally a summer crop, the mild temperatures during winter allow for a maize crop cycle, with the advantage of increased water use efficiency associated with lower vapour pressure deficit in comparison to typical summer crops. Section 2.4.2 in Chapter 6 explains the influence of environmental factors, including vapour pressure deficit, on water use efficiency.

3.4. Cereal-based intercropping

Intercropping has been a feature of traditional, intensive farming systems in South and Southeast Asia. Alleys and bunds in rice field for sowing black gram and pigeon pea is a common practice in South Asia. This system of intercropping improves the capture of radiation and the borders of non-cereal species could also slow down the spread of insects and pathogens (Section 5.2 in Chapter 17) between fields. Sowing oilseed *Brassica* spp. in wheat field is still a widely adopted practice in the Indian subcontinent. Sowing rice, millets or maize with pigeon pea or black gram on the uplands is a common practice to safe guard against unpredictable monsoon in South Asia; both grain and fodder are harvested from this intercropping.

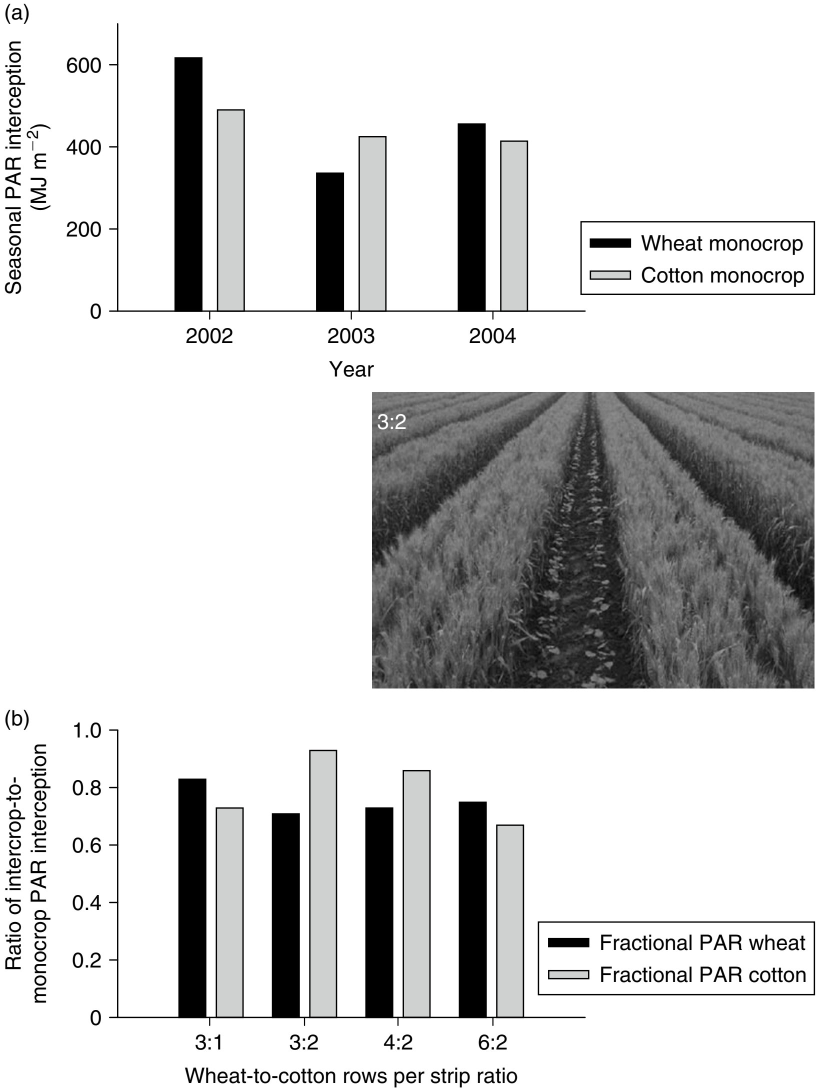

FIGURE 4

Relay cotton-wheat intercropping in northern China. (a) Approximate seasonal interception of photosynthetically active radiation (PAR) in monocrops. (b) Ratio of PAR interception between intercrop components and their respective monocrops. Inset illustrates the 3:2 arrangement in June, shortly before wheat harvest. Land equivalent ratios were 1.39 for all arrangements except 6:2 which had a ratio = 1.28. Capture of radiation (a, b) accounted for these improvements in production, with no effect of radiation-use efficiency. (Source: Zhang et al., 2007, 2008a.)

A number of cereal-based intercropping options including different legumes and hedgerow crops are regularly practiced in Thailand and Indonesia (Whitmore et al., 2000; Hoang Fagerström et al., 2001). Other important contribution of intercropping involving cereals and legumes is a lower requirement of nitrogen fertilisation (e.g. Fujita et al., 1992; Li et al., 2001; see also Section 4.1).

4. MANAGEMENT OF ABIOTIC AND BIOTIC CONSTRAINTS FOR CEREAL PRODUCTION

This section briefly describes the main constraints for cereal production and their management, and discusses in more detail nutrition and diseases to further illustrate the diversity of CBCS and management practices in Asia.

Major constraints in cropping systems of Asia include drought, high temperature, soil restrictions (e.g. acid and saline), nutrient deficiencies and diseases. Drought is a major problem in upland and rainfed lowland rice across Asia, and is often the most important abiotic stress for wheat in Central and West Asia. Heat shock is a major constraint to late-sown wheat in South, Central and West Asia, and high temperatures account for a significant proportion of wheat yield decrease under delayed sowing (1–1.5% per day after November 30) in South Asia (Hobbs et al., 1997). There is general concern about global warming and its specific detrimental effect on wheat production (Black, 2006; Hodson and White, 2007; Ortiz et al., 2008; Section 5.2 in Chapter 20). The observed and forecasted impact of climate change on cereal-growing areas of Asia, mainly for wheat and rice, has been documented (Wassmann and Doberman, 2006; Hodson and White, 2007). Increasing temperatures, however, are already showing an impact on wheat production in South Asia (Rane et al., 2000; Nagarajan, 2005; Black, 2006; Sharma et al., 2007b). High temperature directly affects yield by hastened physiological maturity and reduced grain filling duration, and indirectly by increasing disease severity (Sharma et al., 2007a). Garrett et al. (2006) have underlined the intricate interrelationships between plant disease and climate. Climatic change could in turn modify pathogen virulence in some regions prompting less important cereal diseases to become potential new threats (Duveiller et al., 2007). There is a trend towards slight decrease in radiation due to prolonged cloudy and foggy days over a large part of South Asia (Debi, 2003), which also favours diseases on temperate cereals. Another phenomenon resulting from human activities and known as the 'Asian Brown Cloud' may also have a direct impact on agriculture through reduction in total solar radiation due to air pollution (UNEP and C^4, 2002). Sections 2.1 and 3.4 in Chapter 20 discuss further the putative causes and direct consequences on crops of the reduced amount of radiation and increasing diffuse component of radiation.

A large part of agricultural upland soil in Southeast Asia (Vietnam, Thailand, Malaysia, Indonesia and China) and Indian subcontinent has soil acidity problems. One of the main constraints for crop production in these soils is aluminium toxicity (Kinraide, 1991), which has detrimental effects on root systems of cereals affecting nutrient and water uptake from the soil. In addition, negative effects of acid soils and Al toxicity on grain yield has been associated with lower grain number and aboveground biomass production (Valle et al., 2009). Surface application of lime is a common technique to increase soil pH and reduce Al toxicity. Diverse crop management practices are traditionally adopted by the farmers on the upland acidic soils in different parts of Southeast Asia (Figure 3). However, the most economically feasible and environmental safe management practice is to sow Al and acid tolerant cultivars (Delhaize et al., 1993; Tang et al., 2001). Figure 5 compares the yield of Al-sensitive and Al-tolerant wheat against a wide range of soil pH (4.9–6.2) and soil Al content ($0–0.74\,\text{cmol}(+)\,\text{kg}^{-1}$). Genotype tolerance to Al toxicity has been mainly ascribed to exudation of organic acids by roots, which chelate Al in the rhizosphere (Pellet et al., 1996; Delhaize et al., 1993).

Soil salinity, caused by high levels of salt in the soil or movement of salt with the water, is a major issue all over Asia. Evidence of soil degradation has been found in semi-arid parts of South Asia where paddy-wheat systems are irrigated with alkaline water (Minhas et al., 2007). Many salinity-prone areas have taken task of reclaiming soil water and drainage management by leaching harmful salts out of plant root zone.

Management of CBCS in Asia is complex and diverse because of agro-ecological, social, economic and cultural diversity across the continent (see Figure 3). Management ranges from traditional, as in many parts of Nepal, to fully mechanised, as in Japan, South Korea and several parts of China and India. Tillage management includes preparing grounds with hand hoes to automated tractors. Water management varies from managing rainwater as in rainfed to fully irrigate automated systems. Crop varieties include landraces and old and new

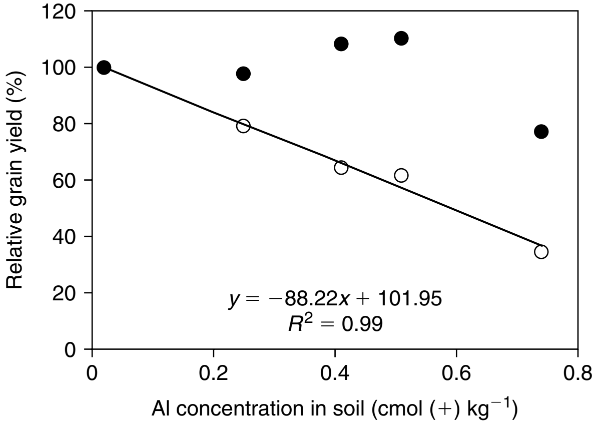

FIGURE 5

Relationship between relative grain yield and aluminium concentration in soil of Al-sensitive (open circles) and Al-tolerant (closed circles) wheat cultivars under field conditions where exchangeable Al concentrations in the soil were increased by applying Al sulphate. Values of each cultivar are relative to the Al control treatment (0.02 cmol(+) kg^{-1}). The line shows the regression analysis for the Al-sensitive cultivar. (Source: Valle et al., 2009.)

improved genotypes. Cropping sequences varies from cereal-fallow in dryland to three crop sequences under intensive farming; both mixed and sole crops of cereals are grown in different regions of Asia (Table 1). This diversity in cropping intensity leads to a range in productivity from less than 1 t ha^{-1} year^{-1} as for sole dryland crop to 15 t ha^{-1} year^{-1} under two or three crops per year in the irrigated, intensive agro-ecosystems. With proper management there could be a potential of up to 30 t ha^{-1} of productivity in rice–wheat–maize system (Dobermann, 2006). Resource conservation technologies include combinations of practices such as surface seeding, bed sowing, laser levelling and water and residue management (Suleimenov et al., 2006; Akhtar, 2006). These technologies are increasing in importance against the backdrop of shrinking supply of water for farm irrigation due to competition with urban development (Hossain and Fischer, 1995; Rosegrant et al., 2006; Chapter 6), and higher doses of external inputs needed to sustain the yield in both traditional (Regmi and Ladha, 2005) and more intensive irrigated systems (Mussgnug et al., 2006).

4.1. Nutrition

Nutrient deficiency associated with low input and imbalanced doses of nutrients is widespread in CBCS of the continent. In South Asia, suboptimal nutrient application could cause 25–46% reductions in wheat yield (Ortiz-Ferrara et al., 2007). Traditional rice-wheat systems have depleted soil nutrients and weakened soil health (Regmi et al., 2002; Bhandari et al., 2002), reduced productivity (Tirol-Padre and Ladha, 2006) and increased the vulnerability of the crop to diseases (Regmi et al., 2002; Sharma and Duveiller, 2004). Nutrient management in cereals primarily involves application of inorganic fertilisers and organic manures; however, other practices like crop rotation, intercropping and residue management also supplement crop nutritional requirements (Figure 3).

The most widely applied mineral nutrient to cereal production in Asia has been N followed by P; this is consistent with estimates that these two elements could account for more than 70% of the total resource limitation in crop production (Kho, 2000). Commonly, the nutrients are applied to the individual crops based on general recommendation for a given region, soil test and crop response in the field. On the other hand, nutrient application requires considerations of the entire cropping systems that include different crops and prevalent climatic conditions at different times of the year. Several studies have analysed productivity of the rice-wheat systems in South Asia using long-term fertility experiments (Bhandari et al., 2002; Regmi et al., 2002) and trend analysis (Aggarwal et al., 2000; Tirol-Padre and Ladha, 2006; Sharma et al., 2007b). The conventional use of N and P fertilisers with little K and no micronutrients caused decline in productivity of rice and wheat primarily through lower biomass production.

Inorganic fertilisers have been dominant sources of nutrients, despite their high cost and unavailability in developing countries of Asia, and their negative effect on soils and groundwater when improperly used. Organic manures are becoming increasingly important on its own or in combination with inorganic fertilisers (Figure 3). The primary sources of organic manures include farmyard manure, green manure and crop residues. While the farmyard and green manures have been used since time unknown, recent studies have shown promising results from crop residue management in wheat-, rice- and maize-based cropping systems in many Asian countries. Significant yield improvement has been recorded through crop residue management (Bahrani et al., 2007). Further, there is progressively more emphasis on system-wide (Timsina and Connor, 2001) and site-specific nutrition management in cereals (Dobermann et al., 1998; Buresh et al., 2005). Site-specific nutrient management has substantially increased productivity of rice (Fan et al., 2005; Haque et al., 2005; Witt et al., 2005; Khurana et al., 2007; Pampolino et al., 2007; Wang et al., 2007; Yadav et al., 2007), wheat (Gill and Rothore, 2004) and maize (Kumar et al., 2006; Witt et al., 2006) in many countries in Asia. Often a guideline technique, such as the leaf colour chart for application of nitrogen, is used. Chapter 8 (Section 2.3) details the physiological principles used in diagnostic of crop nitrogen requirements and Chapter 19 (Section 2.2) illustrates the application of these principles for site-specific nutrient management.

Crop rotation and mixed and relay cropping with food, forage and green manure legumes are traditional methods to complement cereal crop nutrient requirements in many parts of Asia, as reviewed by Lauren et al. (2001) for South Asia. The benefit of such systems is well documented and recent studies continue to enrich the topic in many parts of Asia (Dwivedi et al., 2003; Ghosh et al., 2006a, b). However, to harness the maximum benefits from intercropping, comparative crop physiology must be considered so that the critical growth stages with high nutrient requirements of the cropping components do not coincide (Ghosh et al., 2006b). Critical growth stages of major crops are considered in other parts of this book, from the perspective of integrating crops in rotations (Figure 4 in Chapter 3), in relation to phenological development (Section 5 in Chapter 12) and from the viewpoint of improving potential yield (Section 3.2.2 in Chapter 15).

The intercropping of legumes with cereals increases dry matter production and grain yield in relation to sole crops. Biological N-fixation and its relocation from legume to cereal increases the productivity and nitrogen-use efficiency of the system (Fujita et al., 1992). The relative distribution of root systems of the two species is important for N transfer. Often the taller cereal species would shade the legume and hence reduce N-fixation. Light interception by the legumes can be improved by proper selection of the plant types of the two species (Section 5 in Chapter 3). A different proportion of mixtures may be needed for different cereal-legume combinations; Fujita et al (1992) recommended a semi-additive mixture. Cereal-legume crop rotations may also improve nutrient-use efficiency to the cereal component (Dwivedi et al., 2003). The physiological perspective of Chapter 8 (Section 2.4) illuminates important aspects of nitrogen nutrition in grass-legume mixtures.

Integrated nutrient management (INM) refers to the technologies that can help improve fertiliser use efficiency, minimise their losses and reduce undesirable environmental effects (Pasuquin et al., 2006; Singh et al., 2006a). Benbi and Beri (2007) showed that the use of INM not only helped in saving nutrients (by 20–30 kg N ha^{-1}) but also improved soil health and crop production in rice–wheat system. Pillai et al. (2007) reported that the use of INM in four cropping systems improved productivity, soil organic carbon and nitrogen balance. Behera et al. (2007) concluded that the application of organic manures along with recommended dose of N, P and K fertilisers to wheat was vital for improving productivity, grain quality, profitability, soil health and sustainability of wheat–soybean system. Often, in the INM system, certain nutrients applied to one crop also benefit the second crop in the sequence (Gupta et al., 2006). Additionally, INM helps build up N, P and K in soil (Singh et al., 2006b), and help sustain soil fertility in the cereal–cereal systems (Si and Datta, 2005; Gupta et al., 2006). Such a build-up of nutrient could help improve their use efficiency from the applied sources as fertilisers (Dwivedi et al., 2003).

4.2. Diseases

Diseases are serious constraints in cropping systems all over the world (Chapter 17 and Table 1 in Chapter 18), and are widespread in cereal crops in Asia. There are several physiological mechanisms by which diseases impair growth and yield (Johnson, 1987; Boote et al., 1983). According to these mechanisms, Boote et al. (1983) classified pests and diseases into seven categories: tissue consumer, leaf senescence accelerator, stand reducer, light stealer, photosynthetic rate reducer, assimilate sapper and turgor reducer. This classification aimed at coupling crop simulation models and pests. Likewise, Johnson (1987) considered two categories, that is reducers of radiation capture and reducers of radiation-use efficiency, which allows linking pests and the crop growth framework outlined in Chapter 7. Simulation models developed to estimate yield losses are based on crop growth stages critical for pest damage whereby crop biomass and the components of yield are affected (Willocquet et al., 2000).

Using the classification of Boote et al. (1983), major diseases of cereals in Asia fall within a narrow range of physiological categories and many could be included in multiple groups, for example rusts are both photosynthetic rate reducers and leaf senescence accelerators (Table 2). Cereal diseases often reduce grain yield through reductions in dry matter production either by reducing leaf area index (Aggarwal et al., 2006) or by depressing leaf chlorophyll content (Rosyara et al., 2007). Ibeagha et al. (2005) demonstrated that entire leaf tissue structure could be invaded by pathogens, leading to reduction in CO_2 concentration in the cells around stomata and ultimately depressing photosynthesis (Zuckerman et al., 1997).

Leaf and neck blast, bacterial leaf blight and viruses are most widely distributed rice diseases in Asia. Losses caused by blast disease of rice depend on climatic elements with temperature playing an important role. Using simulation models, it was predicted that increase in ambient temperature could result in a greater economic loss due to blast in cool subtropical zones, whereas lower temperatures led to a higher risk of yield loss in warm humid subtropics and humid tropics of Asia (Luo et al., 1998). Wheat stripe, leaf rust and foliar blight affect millions of hectares in Asia. Other diseases affect cropping systems in specific pockets where they can be very important. For example foliar blights are important diseases in the non-traditional warm wheat growing regions of South and Southeast Asia (Sharma et al., 2007a). Similarly, rice viruses are prevalent in specific regions where they cause substantial yield reductions.

Often, there are several pathogens that could attack a given cereal crop in the same crop-cycle in the same ecosystem, producing an injury profile (Savary et al., 2000b, 2006b). The impact of individual diseases on crop productivity has been widely investigated; however, there is a research gap on pathogen injury profile (Savary et al., 2006a). Moreover, information on yield loss caused by different groups of pathogens (fungi, bacteria, viruses) is available from studies not widely replicated in time and space (Savary et al., 1998). A simulation model based on injury profile in rice predicted a mean yield loss of 37% (Savary et al., 2000a).

The methods for controlling cereal diseases in Asia are diverse depending on many factors such as nature of crop, group of pathogen, socio-economic considerations, agricultural development and environmental concerns. Basically there are three broad approaches of managing diseases in crops: chemical, cultural and genetic. These methods circle around three principles of control: avoidance, tolerance and resistance, which are often incorporated in disease management systems applied with some degree of success to control wheat rust (Wan et al., 2007) and foliar blight (Iram and Ahmad, 2005).

Resistant varieties are by far the most common approach to deal with diseases in cereals. However, adoption of resistant varieties varies from country to country, and they are more often used for commercial farming in more developed countries. Chemical control is particular important in the advent of new races of the pathogens for which development of resistant varieties may take many years. The most commonly used chemicals for seed dressing in cereals are systemic fungicides. Many diseases of rice (blast, bacterial leaf blight), wheat (rusts, foliar blight, powdery mildew), maize (Turcicum leaf blight, grey leaf spot, powdery mildew) and millets are regularly controlled with pesticides. However, the use of pesticides is often limited by their unavailability and higher costs in many developing countries of Asia. For example,

Table 2 Important Cereal Diseases and Management Practices in Asia

Crop	Disease	Management[a]	Importance	Pathogen Group[b]
Rice (*Oryza sativa* L.)	Leaf and neck blasts (*Magnaporthe oryzae*)	CC-FS, GR, BC	High	2, 4
	Brown spot (*Cochliobolus miyabeanus*)	CC-ST, GR	High	2, 4
	Stem rot (*Leptosphaeria salvinii*)	CP, GR	Medium	1, 2
	Foot rot (*Fusarium moniliforme*)	CC-ST, GR	Low	1, 2
	False smut (*Claviceps oryzae-sativae*)	CC-ST	Low	5
	Sheath blight (*Corticium sasakii*)	CC-Soil, CC-FS, BC	High	2
	Bacterial leaf blight (*Xanthomonas oryzae pv. oryzae*)	CC-ST, GR	High	2, 4
	Bacterial leaf streak (*Xanthomonas sp.*),	CC-ST, CC-FS, GR	Medium	2, 4
	Viral diseases: tungro, yellow dwarf, grassy stunt and orange leaf	CP, GR, CV	High	1, 2, 5
Wheat (*Triticum aestivum* L.)	Stem (black) rust (*Puccinia graminis tritici*)	CP, CC-FS, GR	High	2, 3
	Stripe (yellow) rust (*Puccinia striiformis*)	CP, CC-FS, GR	High	2, 3
	Leaf (brown) rust (*Puccinia triticina*)	CP, CC-FS, GR	High	2, 3
	Loose smut (*Ustilago nuda*)	CC-ST, GR	Low	1, 5
	Flag smut (*Urocystis agropyri*)	CC-ST, GR	Low	1, 5
	Karnal bunt (*Neovossia indica*)	CP, CC-ST, GR	High	1, 5
	Alternaria leaf blight (*Alternaria triticina*)	CC-ST, CC-FS, GR	Low	2, 3
	Spot blotch (*Cochliobilus sativus*)	CC-ST, CC-FS, GR	Medium	2, 3
	Tan spot (*Pyrenophora tritici-repentis*)	CC-ST, CC-FS, GR	Medium	2, 3
	Scab (*Fusarium graminearum*)	CC-ST, CC-FS, GR	Low	2, 3
	Sptoria leaf blotch (*Septoria tritici*)	CC-ST, CC-FS, GR	Low	2, 3
	Powdery mildew (*Erysiphe graminis*)	CP, CC-FS, GR	Medium	2, 3, 4
Maize (*Zea mays* L.)	Turcicum leaf blight (*Drechslera turcicum*)	CC-FS, GR	High	2, 3
	Common smut (*Ustilago maydis*)	CC-ST, GR	Low	5
	Head smut (*Sphacelotheca reiliana*)	CC-ST, GR	Low	5
	Brown spot (*Physoderma zeae-maydis*)	CP	Low	2, 3
	Rust (*Puccinia sorghi*)	GR	Low	2, 3
	Downy mildew (*Sclerospora philippinensis*, *Sclerophthora rayssiae*)	CC-FS	Medium	2

	Stalk rot (*Pythium aphanidermatum*)	CC-FS	Medium	1, 2
	Bacterial stack rot (*Erwinia carotovora*)	CP, CC-FS	Medium	1, 2
	Seedling blight (*Fusarium moniliforme)*	CC-ST	Low	1, 2
Barley (*Hordeum vulgare* L.)	Stem (black) rust (*Puccinia graminis tritici*)	CP, CC-FS, GR	Medium	2, 3
	Yellow rust (*Puccinia glumarum*)	CP, CC-FS, GR	Medium	2, 3
	Brown rust (*Puccinia hordei*)	CP, CC-FS, GR	Medium	2, 3
	Covered smut (*Ustilago hordei*)	CP, CC-ST	Low	1, 5
	Loose smut (*Ustilago nuda*)	CP, CC-ST	Low	1, 5
	Neck blotch (*Drechslera teres*)	CC-ST, CC-FS	Low	2, 3
	Powdery mildew (*Erysiphe graminis*)	CC-FS, GR	Low	2, 3, 4
	Root rot (*Cochliobolus sativus*)	CP, CC-ST	Low	1, 2
	Leaf stripe (*Drechslera graminea*)	CC-ST	Low	2, 3
	Barely mosaic, barley dwarf	CP, CV	Low	1, 2, 5
Sorghum (*Sorghum bicolor* L. Moench)	Kernel smut (*Sphacelotheca sorghi*)	CP, CC-ST, GR	Medium	1, 5
	Loose smut (*Sphacelotheca cruenta*)	CP, CC-ST, GR	Low	1, 5
	Long smut (*Tolyposporium ehrenbergii*)	CP, CC-ST	Low	1, 5
	Head smut (*Sphacelotheca reiliana*)	CP, CC-ST	Low	1, 5
	Rust (*Puccinia purpurea*)	CP, CC-FS, GR	Low	2, 3
	Downy mildew (*Sclerospora sorhi*)	CC-Soil, GR	Low	2, 5
	Cercospora leaf spot (*Cercospora sorghi*)	CC-FS	Low	2, 3
	Anthracnose (*Colletotrichum graminicolum*)	CC-ST, CC-FS, GR	Low	2, 3
	Leaf blight (*Drechslera sativum*)	CC-ST, CC-FS, GR	Medium	2, 3
	Leaf spot (*Drechslera halodes*),	CC-ST, CC-FS	Medium	2, 3
Pearl millet (*Pennisetum typhoides* L.)	Downy mildew (green ear) (*Sclerospora graminicola*)	CP, CC-ST, GR	Medium	5
	Rust (*Puccinia penniseti*)	CC-FS	Low	2, 3
	Smut (*Tolyposporium penicillariae*)	CP, CC-ST, CC-FS	Low	1, 5
	Ergot (*Claviceps microcephala*)	CP, CC-ST, CC-FS	Medium	5
	Leaf blast (*Pyricularia setariae*)	CC-FS	Low	2, 3
Finger millet (*Eleusine coracana* Gaertn)	Blast (*Pyricularia setariae*)	CC-ST, GR	Low	2, 3

(Continued)

Table 2 Continued

Crop	Disease	Management[a]	Importance	Pathogen Group[b]
	Seedling blight (*Drechslera nodulosus*)	CC-ST, CC-FS	Low	1, 2
	Downy mildew (*Sclerophthora macrospore*)	CP, CC-FS	Low	2
	Wilt (*Sclerotium rolfsii*)	CP	Low	1, 2
	Smut (*Melanopsichium eleusinis*)	CP. CC-ST	Low	1, 5
Proso millet (*Panicum miliaceum* L.)	Head smut (*Sphacelotheca destruens)*	CC-ST,	Low	1, 5
Barnyard millet (*Echinocloa frumentacea* L.)	Downy mildew	CP, CC-FS	Low	2
	Smut	CP, CC-ST	Low	1, 5
	Rust	CC-FS	Low	2, 3
Foxtail millet (*Setaria italica* L.)	Smut (*Ustilago crameri*)	CC-ST, GR	Low	1, 5
	Rust (*Uromyces setariae-italicae*)	CC-FS, GR	Low	2, 3

[a] *BC = biological control, CC-FS = chemical control through foliar spray, CC-ST = chemical control through seed treatment, CC-Soil = chemical control through soil treatment, CP = control through cultural practices, CV = control of viral disease through the control of the insect vector, GR = genetic resistance, IDM = integrated disease management.*

[b] *Pathogen classification based on type of damage as described by Boote et al. (1983): 1 = stand reducers, 2 = photosynthetic rate reducers, 3 = leaf senescence accelerators, 4 = light stealers, 5 = assimilate sappers, 6 = tissue consumers and 7 = turgor reducers.*

wheat farmers in the eastern Gangetic Plains often have to live with about 15% yield losses caused by foliar blights (Sharma et al., 2007b) because suitable chemicals are either costly or unavailable (Sharma-Poudyal et al., 2005).

Mixtures of cultivars with different responses to pathogens can be useful, as illustrated for wheat in Nepal (Figure 6). Chapter 17 (Section 6) comments on the benefits of crop genetic diversity for the control of *Magnaporthe grisea* in rice, as measured in large-scale studies in China. Destruction of alternate hosts could be effective for important diseases like wheat rusts and rice blast; however, it does not seem to feature in cereal disease control in Asia. Crop rotations could help containing soil-borne diseases like rots in cereals; however, this method is also uncommon in Asia. The farmers in Asia seem to have a conviction about following certain CBCS that they are unwilling to change. Many seed-borne diseases of cereals could be reduced by heat treatment through soaking in hot water. This is particularly recommended for smuts; however, there is little evidence that the Asian cereal farmers are doing this on any significant scale. Nevertheless, seed treatment with chemicals is practiced on a large scale to eliminate seed-borne inoculums. This has been shown as a practice to control many cereal diseases including smuts, rusts and foliar blights of cereals. Field sanitation is a common practice adopted by cereal growers in most Asian countries where plant debris in the field are collected and destroyed before sowing crops. This practice often applied to suppress weeds and clean cereal fields before sowing also destroys many plant pathogens surviving in the plant debris. This method is helpful in particular for foot rots and powdery mildews. Cleaning of fields also destroys pathogens surviving in weeds that serve as alternated host during the off-season. Breaking the green bridge through field sanitation is an important strategy in managing disease in the CBCS in Asia. Chapter 17 (Section 5) expands on the concept of green bridge from the perspective of integrated genetic and agronomic control of diseases.

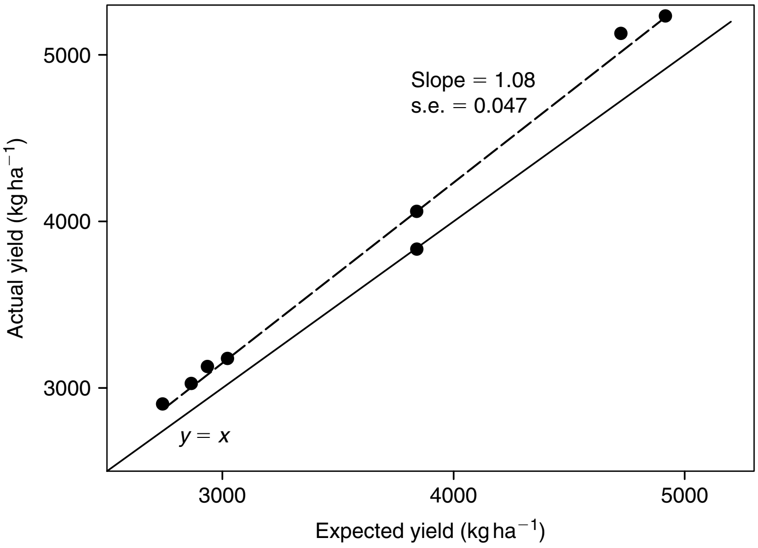

FIGURE 6

Mixtures of wheat varieties outyield pure crops in small-plot (1.5 m × 5 m) experiments in Nepal. Experiment 1 sowed equal-weight seed mixtures of cultivars RR21, UP262 and Nepal 251, and Experiment 2 sowed equal-weight seed mixtures of cultivars RR21, UP262 and Nepal 297. Cultivars differ in maturity, vegetative traits, yield potential and resistance to spot blotch (Bipolaris sorokiniana) and rusts (Puccinia recondita). (Source: Sharma and Dubin, 1996.) Chapter 17 (Section 5.2.1) discusses the bias in small-plot experiments of crop mixtures in relation to disease dispersal.

Biological control has so far not been a widespread feature of disease control in CBCS in Asia because of a lack of facilities to multiply biological agents; however, this method bears potential for advanced agriculture. *Trichoderma viridae* is one such pathogen being used as seed coat to control fungal diseases in wheat in some parts of the eastern Gangetic Plains. Detailed strategy of using biological control for managing disease in the CBCS in Asia has been outlined by Prasad (2005).

Managing disease through environmental modification includes manipulation of moisture, nutrient and temperature regimes. For example, well-irrigated and fertilised wheat crops showed lesser loss in grain yield due to foliar blight compared to the control (Sharma and Duveiller, 2004). Similarly, early-sown wheat reached maturity during cool temperatures and suffered less disease-induced yield losses than the late-sown counterparts (Sharma and Duveiller, 2004; Duveiller et al., 2005).

5. CONCLUSIONS: FUTURE PROSPECTS IN CEREAL-BASED CROPPING SYSTEMS IN ASIA

CBCS would continue to be important to meet increasing food demands in Asia. Even though rice-wheat system would remain the most important sequence in South and Southeast Asia, the rice-maize system would expand in the future. In Central and West Asia, wheat and barley-based cropping system would be predominant. These cereal-cereal cropping systems would have a sustainability challenge; hence, it would be important to include grain legumes into these cereal-based systems.

Cropping intensification will increase in Asia to meet the growing food needs (Box 1 in Chapter 1). If managed improperly, this intensification may have undesirable consequences in terms of increased salinity and waterlogging, groundwater depletion, decline in soil nutrients, soil toxicity, impaired soil structure and a greater loss due to pests. However, new technologies with the dual purpose of improved production and resource conservation are feasible as outlined by Gregory et al. (2002) and further illustrated in Chapter 3. New cropping approaches will also be needed to account for warming that could shrink the area under cereals, wheat in South Asia in particular.

Blast, bacterial blight and certain viruses would remain dominant diseases of rice. While leaf and yellow rust would remain the most dominant wheat diseases, the Ug-99 race of stem rust is a serious threat in near future. Turcicum leaf blight, grey spot and powdery mildew would continue to be disease constraints in maize. Research on disease management of cereal-based systems indicates that despite availability of many pesticides, resistant varieties of cereals in combination with certain cultural practices would dominate in most Asian countries (Chapter 17).

The future of CBCS in sustaining food production in Asia lies in scientific advancements that could alleviate a string of problems including shrinking fertile land, marginal land under cereal cultivation, soil degradation, dwindling water availability for irrigation, biotic and abiotic stresses, yield gaps, genetic yield stagnation, localised labour shortages and unsupportive cereal-related policy. The threat of pathogens, such as wheat rusts and rice blast that cut across the agro-ecosystems in Asia, needs to be tackled. There are considerable opportunities for sustainable increase in the productivity of CBCS in Asia. These include:

- Advances in management practices – integrated and site-specific nutrient management, integrated pest management and integrated crop management collectively aiming at enhancing productivity, resource-use efficiency and conservation of the resource base.
- Genetic improvement in cereals – new plant types in rice and wheat (Chapter 15), expansion of maize hybrids, hybrid rice, improved diseases tolerance (Chapter 17) and drought- and heat-resistant cereals (Chapters 14–16).
- The development of more diverse cropping systems where new crop cultivars and management techniques are integrated (Stancich, 2008; Chapter 19).

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2

PART

Capture and Efficiency in the Use of Resources: Quantitative Frameworks

CHAPTER 6

Improving Productivity to Face Water Scarcity in Irrigated Agriculture

Elias Fereres and Victoria González-Dugo

1. INTRODUCTION AND BACKGROUND

Agriculture consumes about 85% of the total water used worldwide in various human activities (Jury and Vaux, 2007). Most of agricultural consumptive use is from rainfall (80%), while the rest originates from water withdrawals that are diverted for irrigation. Although the water used by rainfed crops represents the major component of agricultural water use, irrigation is perceived by society as the primary user of water and is the subject of increased criticism. The surface area under rainfed agriculture largely exceeds the area devoted to irrigation; in fact, only 18% of the cultivated lands in the world are irrigated. However, the value of irrigated production is over 45% of total, indicating the importance that irrigated agriculture has for feeding the world now and in the future (Molden, 2007). Population growth, economic development and environmental concerns have increased water demand from several sectors outside agriculture, notably from the environment, and this has intensified the competition for scarce water resources in many world regions. Such competition focuses on the dominant water user, and it is therefore normal that, despite its pivotal role in food production, irrigation attracts significant criticism (Postel, 1999), with some even questioning its sustainability (see review by Hillel and Vlek, 2005). It is essential that a productive and sustainable irrigated agriculture is firmly established on scientific principles, and on sound engineering and management. This chapter provides an overview of how irrigated agriculture is facing increased competition for water, focusing on the role of crop physiology and its interactions with farm irrigation management in coping with water scarcity. Principles of dryland agronomy and crop physiology inform this chapter, and reciprocally we illustrate how understanding of irrigated systems may shed light on water management in dryland cropping.

Many of the challenges that irrigated agriculture faces are related to water economics, policies and institutions, and are outside the scope of this book; the interested reader is directed to the pertinent chapters in the book by Molden (2007) and to the studies by Jury and Vaux (2005, 2007). Looking at the future, by far the most important challenge would be the limitations in water supply against a continuous increase in demand. The second half of the twentieth century experienced the fastest rate of irrigation expansion in the world, increasing from 94 to 263 million ha between 1950 and 1996 (Howell, 2001). At present, the irrigated lands may well exceed 300 million ha (Thenkabail et al., 2006). Because of the increasing demands for food production caused by population growth and by the recent diet changes of emerging countries (von Braun, 2007), it is anticipated that irrigation water demand will continue to increase in the foreseeable future, albeit at a slower rate than that experienced in past decades (Jury and Vaux, 2007). Two recent developments may contribute to further irrigation expansion, adding more pressure to the fixed water supplies. The recent sharp increase in food prices against a declining trend for decades (Figure 1) and the production of biofuels on agricultural lands are two developments that deserve attention. Although less than 10 years ago most predictions

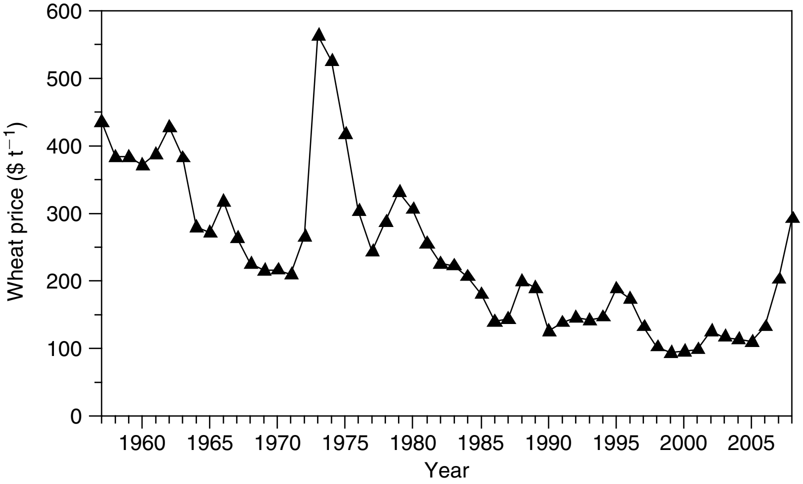

FIGURE 1

Evolution of wheat prices in the USA from 1957 to 2008 expressed in constant US dollars (year 2000). (Source: http://www.nass.usda.gov [last update: 01/03/2008].)

indicated stable or declining cereal prices until 2020 (e.g. IMPACT model, Rosegrant et al., 2002), prices started to increase after 2000 (Figure 1), and the same model (presumably under different assumptions) now predicts price increases until 2016 (von Braun, 2007). Current prices constitute an incentive for the expansion of irrigation and for increased water use in this sector. The evolution of biofuels is even more uncertain, but several different scenarios suggest an increase in demand of land-based agricultural products from this sector (von Braun, 2007; Section 4 in Chapter 1) that can also promote additional irrigation development.

What are the options of meeting future demands by increasing water supply? Additional supplies may be generated with new storage facilities, desalination, wastewater reuse and with inter-basin transfers. Construction of dams and reservoirs is largely responsible for the large irrigation expansion of the twentieth century (World Commission on Dams Report, 2000). Development of significant additional storage will be limited in the future, though, for economic and environmental reasons. The best locations in economic terms have already been exploited, and new dams and diversions are a threat to many ecosystems that society wants to preserve. Improvements in desalination technologies have been significant but the basic processes are energy dependent, and that makes the price of desalted seawater (Karagiannis and Soldatos, 2008) too high for most irrigated agricultural systems. Wastewater may be used in irrigation after appropriate treatment, with the advantage of the constancy and reliability of supply of this source of water. All health concerns related to wastewater may be eliminated by purifying it to any desired standard (Asano et al., 2007). The contribution from this source to increased demand is modest, given the relatively small volumes used by the urban and industrial sectors. Finally, large-scale water transfers have been successful in providing new irrigation supplies in the past, where political and economic constraints were overcome (Jury and Vaux, 2007). Nowadays, such transfers may be feasible for urban water supply, but they are increasingly difficult to justify in economic, environmental and political terms just for irrigation purposes.

The difficulties in developing additional irrigation water supplies to meet the anticipated demand increase will lead to a scenario of increased water scarcity in the foreseeable future. Therefore, most efforts should concentrate on how to increase the efficiency of water use in irrigation, or, in other words, on how to increase the water productivity (WP; € m^{-3}) beyond present values. However, making the most efficient use of the water available would not be sufficient; such goal has to be compatible with making irrigated agriculture more sustainable, as discussed below. The challenge ahead is how to improve productivity while minimising waste and, at the same time, achieve a high level of sustainability. Action is needed in different disciplines and at different scales, from the modernisation of irrigation networks and their management (Playan and Mateos, 2006) to a much more precise on-farm irrigation that includes strategies for managing crop water stress, thus saving irrigation water. For the latter, advances in irrigation engineering and in the understanding of crop responses offer now a real opportunity to change what has been the traditional approach to irrigation. Faced with uncertainty about their water needs, farmers always tend to avoid risk by staying on the safe side and applying excessive irrigation water. This approach is not only becoming unacceptable, but it is not even feasible in water-scarce areas. Farmers will have to produce more with less irrigation water, a path that has already been taken in recent years (Seckler, 1996), but that has to be more vigorously pursued worldwide.

There are many avenues to increase the efficiency of water use in irrigated agriculture, both in situations where water supplies are adequate and where they are insufficient to meet the full crop demand. In this chapter, we first describe the concept of water use efficiency (WUE), and then explore the limitations and delineate the options to achieve efficient use of water in irrigated agriculture. The increased attention that deficit irrigation is receiving (Fereres and Soriano, 2007) requires a better understanding of how yield-determining processes respond to water stress, in particular those that could lead to the maintenance of harvest index (HI) under water deficits. Finally, moving from the crop to the field scale, we discuss aspects of the interface between on-farm irrigation management and the crop responses to water supply, which are essential for effective management in water-scarce situations.

2. EFFICIENT USE OF WATER IN IRRIGATED AGRICULTURE

There is an urgent need to evaluate how efficient is water being used in irrigated agriculture. In this section, we describe the parameters used for assessing efficiency and their usual values, and the equations defined to quantify these parameters. A systematic approach for the assessment of WUE is outlined and finally, the avenues to improve WUE are delineated.

2.1. Water use efficiency and water productivity

Since the discovery of the association between plant growth and water use centuries ago, there has been an interest in determining the volume of water required for crop production. De Wit (1958) was among the first that associated crop yields with the consumptive use of water, in relation to the evaporative demand of the environment. His seminal work led to a number of analyses carried out subsequently on the relations between transpiration (T) and biomass production, as new knowledge about the CO_2 assimilation and evaporation processes developed (Arckley, 1963; Tanner and Sinclair, 1983; Steduto et al., 2007). Agronomists used the term transpiration efficiency to denote the biomass-transpiration ratio, but the term water use efficiency (WUE) has also been used for the same purpose (Fischer and Turner, 1978; Sinclair et al., 1984; Steduto et al., 2007).

As it happens frequently in irrigation, soon after the first efforts by agronomists on quantifying crop water use were published (Briggs and Shantz, 1913, 1919 as cited by Tanner and Sinclair, 1983), engineers were assessing in parallel the performance of irrigation schemes from an efficiency standpoint. Jensen (2007) has described the early efforts by Israelsen and others in the 1930s and 1940s, when the term irrigation efficiency (IE) was first coined to define the ratio of consumptive use or evapotranspiration (ET) to applied irrigation water, at the field or farm scale. Subsequently, the IE concept was scaled up to scheme and to hydrologic basin levels as the ratio of ET to the water diverted for irrigation (Israelsen, 1950). Agronomists and engineers have since used the term WUE to describe many ratios derived from the water used for beneficial purposes relative to the total water diverted, applied or used (Burt et al., 1997; Howell, 2001). The introduction of the term 'efficiency' (as an output–input ratio frequently used in engineering) has had implications for societal perception of irrigated agriculture. In many world areas, the low efficiency of irrigation has generated a perception that it is a wasteful practice, an important criticism in an era of water scarcity (Postel, 1999). In part to eliminate such perception, the concept of water productivity (WP) was introduced more recently (Kijne et al., 2003). Water productivity is defined as the ratio between crop yield (expressed in mass or monetary terms) and ET. Contrary to the case of WUE, there has been less confusion with the WP term, because, until now, it has used ET as the denominator. The only other term used is the irrigation WP defined as the ratio of the yield increase from rainfed to irrigated conditions to the irrigation water applied (Bos, 1997; Lorite et al., 2004a). More recently, a range of WP definitions have been proposed where both the numerator and denominator vary, as in the various WUE definitions (Molden, 2007).

Until now, WP has been mostly used for comparative studies among crops and/or regions, and has particular value when used in economic terms. Molden et al. (1998) was among the first that compared the WP of a range of irrigation schemes around the world and found wide WP variations among schemes. Lorite et al. (2004b) showed how WP can vary widely among crops (about 100%) within an irrigation scheme. The range of WP for a given crop may go up to 2–300% for the same yield, and varies more than an order of magnitude for different yield levels (Zwart and Bastiaanssen, 2004). As shown in Figure 7 of Sadras and Angus (2006), yield of rainfed wheat ranged from 1 to 6 t ha^{-1} for an ET about 300 mm. Wide ranges in yields for similar ET are also found in irrigated crops, even within the same geographical area. González-Dugo and Mateos (2008) found variations in sugar beet and cotton farm yields of over 40% for the same ET in an area in southern Spain. Consumptive water use in irrigated areas also vary, but not nearly as much as yields (Sarwar and Perry, 2002; Lorite et al., 2004b, González-Dugo and Mateos, 2008). The examples of WP values described above would suggest that WP improvements should focus more on increasing the numerator (yield) than on decreasing the denominator (ET).

2.2. Quantifying water use efficiency in irrigated agriculture

When faced with the need to improve efficiency, quantification of WUE and of WP is of paramount importance, but it should be based on clear definitions, and on an understanding of the different forms of water disposition in irrigation. The objective of irrigation is to avoid yield-reducing water deficits by applying water to crops. The water application process introduces a change in the hydrology of the land unit considered, and its correct management is essential for achieving the desired objectives of improved productivity and sustainability (Fereres and Connor, 2004). Water inputs that constitute the crop water supply are rainfall, irrigation and the stored soil water in the potential crop root zone at planting. Water is lost by evaporation from soil (E) or plant surfaces (T), surface runoff and deep percolation. All water diverted for irrigation is *used* in the process, but not all is *consumed*. Surface runoff and deep percolation losses may be recovered downstream within the hydrologic unit, albeit at an energy cost and with some quality deterioration. By contrast, the water used in ET cannot be recovered and is considered consumed. When the losses from runoff or percolation flow to saline sinks beyond recovery, they are considered equally consumed. More details about the hydrology of irrigation may be found in Fereres and Connor (2004). The definitions of WUE depend on whether the water used or consumed is used as input. Burt et al. (1997) made an effort to standardise the definitions of IE. Figure 2 depicts the partitioning of irrigation water into consumptive and non-consumptive use, and into beneficial and non-beneficial use. When the changes in the volume of stored soil water are relevant relative to the volume of irrigation, they should also be included in the efficiency calculation (Burt et al., 1997). From this figure, it is possible to choose and define the appropriate measure of efficiency based on the objective pursued. Other useful WUE definitions that are applicable to irrigated agriculture are given in Table 1.

Some feel that the use of WUE in the irrigation literature has been misleading, and cite many examples where confusion abounds (Perry, 2007), while others prefer now the use of WP that does not have the connotations of the word efficiency (Kijne et al., 2003). Because both terms have been used so widely, at so

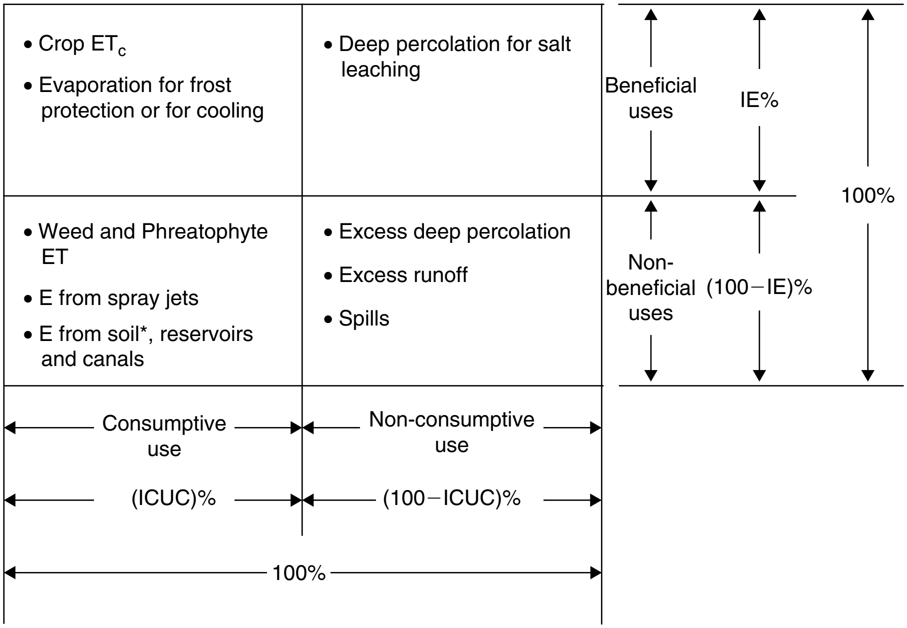

FIGURE 2

Disposition of irrigation water with a division between consumptive and non-consumptive uses, and between beneficial and non-beneficial uses. IE is the irrigation efficiency and ICUC is the irrigation consumptive use coefficient. (Source: Fereres and Connor, 2004; used by permission.)

many scales, and for so many purposes, there is no need to argue about which one to use, whether WUE or WP as indicator of irrigation performance. What is required is that a precise definition is attached to each specific case describing the attribute chosen to characterise irrigation performance.

2.3. A systematic approach for assessing the efficiency of water use

Traditionally, collective irrigation schemes were developed from a single source of water, being it a diversion from a river or from a dam. From there, a main canal carried the water to the irrigated area where it was distributed along secondary and tertiary canals to farms. Every farm had one or more intake points from where it was distributed and applied to the different fields. Hsiao et al. (2007) reviewed the underlying physical and biological processes that determine the efficiency of water use in agriculture, and developed a systematic approach to quantify WUE. Viewed from a given field, the irrigation process occurs in a sequence of steps: water storage, diversion, conveyance, distribution and application. The effectiveness of each of these steps may be quantified by calculating its efficiency in terms of the ratio of the water volumes that are outputs and inputs of each particular step. It has been shown that the overall efficiency for a chain of sequential steps may be calculated as the product of the efficiencies of each step (Hsiao et al., 2007); thus, it is possible to compute the efficiency from storage to field application as the product of the sequential efficiencies along the chain. Hsiao et al. (2007) provide an analysis in irrigated agriculture where the overall efficiency assessment starting with reservoir water may be broken down into two segments: one mostly physical and the other biological.

Table 1 Definitions of WUE Used in Irrigated Agriculture

Definition		Application	Comments	Author
$\mathrm{WUE} = \dfrac{Y_\mathrm{i} - Y_\mathrm{d}}{\mathrm{ET_i} - \mathrm{ET_d}}$	(1)	Engineering: for assessing the impact of irrigation	Not easy to use because Y_d and $\mathrm{ET_d}$ are difficult to estimate	Bos (1980, 1985)
$\mathrm{WUE} = \dfrac{B/T}{1 + (E/T)}$	(2)	Functional: for assessing factors affecting WUE	Indicates what terms of the water balance govern WUE	Cooper et al. (1987)
$\mathrm{WUE} = \dfrac{\mathrm{HI} \times B}{T(1 - \mathrm{WC})[1 + (E/(P + I + \mathrm{SW} - D - Q - E))]}$	(3)	Functional: for assessing factors affecting WUE	More comprehensive than Eq. 2	Howell et al. (1990)

Y_i (g m^{-2}) and ET$_i$ (mm): yield and evapotranspiration under irrigation, Y_d (g m^{-2}) and ET$_d$ (mm): yield and evapotranspiration under dry conditions, B: dry matter (g m^{-2}), WC: standard water content used to express the economic yield (as a fraction), E: soil evaporation (mm), P: precipitation (mm), I: irrigation (mm), SW: soil water depletion from the root zone (mm), D: deep percolation (mm) and Q: surface runoff (mm).

The physical component (E_P) may be considered as the ratio of the water volume used in transpiration (W_{tr}) to the volume that left the reservoir for irrigation of that particular field (W_{re}):

$$E_P = \frac{W_{tr}}{W_{re}} = \frac{W_{fg}}{W_{re}} \times \frac{W_{fe}}{W_{fg}} \times \frac{W_{rz}}{W_{fe}} \times \frac{W_{et}}{W_{rz}} \times \frac{W_{tr}}{W_{et}} \quad (4)$$

where W_{fg} is the water supplied at the farm gate, W_{fe} the water at the field edge, W_{rz} the water retained in the root zone and W_{et} the evapotranspired water.

The biological component of the overall efficiency (E_B) would be the ratio of the yield mass (M_{yd}) to the volume of water consumed in transpiration (W_{tr}):

$$E_B = \frac{M_{yd}}{W_{tr}} = \frac{M_{as}}{W_{tr}} \times \frac{M_{bm}}{M_{as}} \times \frac{M_{yd}}{M_{bm}} \quad (5)$$

where M_{as} is the mass of carbon dioxide assimilated by photosynthesis and M_{bm} the biomass produced.

The estimation of all of these ratios forms the basis for any assessment of the efficiency of water use in irrigated agriculture. This is a challenge that must be tackled before any improvements are sought, but which is often overlooked or is conducted without sufficient accuracy. Hsiao et al. (2007) compiled ranges for all of the ratios under two irrigated agriculture scenarios: good and poor practices and circumstances. Both scenarios were based on average and not on extreme values. The overall theoretical efficiency ratios, estimated as the product of the mid-values of the range of all the ratios, were 1.22 and 0.024, respectively, about 50 times difference! Such vast range is one measure of the many opportunities that exist for improving the efficiency of water use in irrigated agriculture.

2.4. Avenues for improvement: the role of genotype, environment and management

The improvement of WUE by manipulating a single factor has proven challenging for any single discipline in agricultural sciences. Plant breeding, physiology and agronomy have all contributed to yield improvement and therefore to increase WUE (Passioura, 2006). Section 2 in Chapter 2 outlines the factors underlying long-term improvement in WUE of rainfed wheat in Australia. Improving WUE by increasing yield or decreasing ET may be achieved by one or more of the following three options: changing the genotype, modifying the environment or by changes in management. It is difficult to isolate the impact of one measure from the overall response to change, because many modifications need to be introduced in the management of an agricultural system every time there is a change (see Box 1 in Chapter 2 for examples of breeding by agronomy synergies). Nevertheless, it is instructive to evaluate the role of the different options in improving WUE.

2.4.1. Genetic improvement of WUE

There is general agreement that the significant improvements in yield potential (Evans and Fischer, 1999) of the main crops generated in past decades by breeding efforts have slowed down more recently (Chapter 9, but see Section 3 in Chapter 1 for an alternative view point). The search for genetic variation in features related to water use that would contribute to yield and WUE improvement has been elusive. The vast number of physiological mechanisms involved in determining the relation between transpiration and yield contrasts with the simplicity and robustness of that relationship under field conditions. Because of the attractiveness of this subject, many notable efforts have been conducted in the investigation of physiological responses to water deficits and in exploring the opportunities that breeding has in improving WUE (Ludlow and Muchow, 1990; and see www.plantstress.com for a comprehensive coverage). While there has been much progress in improving water-limited yields, the improvement of the M_{as}/W_{tr} ratio has proven very difficult. Tanner and Sinclair concluded in 1983 that there were many avenues for improving the efficiency of water use in crop production, but that, outside changes in photosynthetic pathways (C_3 vs. C_4) or differences in biomass composition, the variation in M_{as}/W_{tr} was very small. However, at about the same time, an exciting new avenue to improve M_{as}/W_{tr} was discovered based on selecting for carbon isotope discrimination in C_3 plants (Farquhar and Richards, 1984). The initial excitement led to an in-depth exploration of genetic variation in isotope discrimination in the major crops (Ehleringer et al., 1986; Korner et al., 1988; Garten and Taylor, 1992). While variation in carbon isotope discrimination and in M_{as}/W_{tr} was found in many important C_3 crop species (Condon et al., 2002), the relation of that variation with yield was complex, depending on the environment and on whether a high M_{as}/W_{tr} was due primarily to a reduction in transpiration caused by a low stomatal conductance (Condon et al., 2002). These authors concluded that in the major cereals a high M_{as}/W_{tr} was often associated with slow growth rate that partially offsets the benefits of high M_{as}/W_{tr}, particularly in the favourable, irrigated environments (Condon et al., 2002). Richards (2006) has pointed out that, despite extensive efforts in improving water-limited yields, there are only a few examples where genetic improvement combined with physiological trait identification has been successful. Those traits were not related to plant water relationships, but were quantitative traits, often acting throughout most of the crop life cycle (Richards, 2006). To achieve further progress along these lines, Sinclair et al. (2004) emphasised multidisciplinary work and a long-term commitment, two ingredients which are rare in today's agricultural research.

2.4.2. Relationships between WUE and the environment

Environmental manipulation can help increasing M_{as}/W_{tr} quite significantly. The evaporative demand dictates the value of that ratio and, in temperate climates, evaporative demand varies quite dramatically among seasons. In tropical and subtropical areas, the variation in vapour pressure deficit (VPD) within the year may also be significant. In Mediterranean climates, such as that of Cordoba, Spain, the M_{as}/W_{tr} ratio for alfalfa in spring or autumn is almost double that of summer (Fereres and Soriano, 2007). Measurements and simulations in sunflower at Cordoba showed M_{as}/W_{tr} of winter-sown crops was 20–25% higher than that of the spring-sown counterparts (Soriano et al., 2004). In temperate climates, the highest M_{as}/W_{tr} is obtained in protected cultivation during winter, where crop ET is a small fraction (1/5 to 1/3) of that outdoors in the summer (Orgaz et al., 2005). Tanner and Sinclair (1983) had suggested earlier that irrigated agriculture should move from the arid zones to the more humid zones, where VPD is much lower. Under water scarcity, irrigation needs may be reduced if the season is displaced, where the temperature regime allows, to times of low evaporative demand. For a given environment, crop choice is the most important determinant of water use. The contrast between the ET of a perennial crop as alfalfa (over 1000 mm in Cordoba) and that of barley (350 mm) gives an indication of the expected ET range in one location. Within a given crop, short-season cultivars have lower ET than long-season ones (Fereres, 1987), although there may be trade-offs in terms of yield potential.

2.4.3. Optimising management to improve WUE: the role of evaporation

While breeding options to improve WUE are limited, and it is not easy to manipulate the physical environment, management opportunities abound to improve the efficiency of water use (Loomis, 1983; Cooper et al., 1987; Gimenez et al., 1997; Passioura, 2006). All management options that increase T relative to other soil water balance components, and therefore biomass production, also increase the efficiency of water use (Loomis, 1983). Generally, net water savings are achieved only if consumptive use (ET) is reduced. This only occurs if E reductions would be achieved, as reducing T would also decrease biomass production. Until recently, because of the difficulties in measuring E and T separately, there has been uncertainty in the relative magnitude of both components of ET (Loomis, 1983). A robust, functional model for calculating E (Ritchie, 1972) has been thoroughly tested and is now widely used to estimate E. One option to reduce E relative to T is to achieve full canopy cover quickly (Loomis, 1983). In rainfed systems, barley has shown an advantage over other cereals along these lines (López-Castañeda and Richards, 1994). Soil evaporation in barley, which grows and develops faster than other winter cereals, was found to be 10% less than that of wheat (López-Castañeda and Richards, 1994). Subsequent work has focused on improving seedling shoot vigour by combining genetic improvement with agronomic practices to hasten canopy cover that reduced *E* and thus increased *T* and WUE (Richards, 2006). Small improvements in canopy expansion rates at the initial developmental stages have a strong influence in the partitioning of ET, because the canopies expand exponentially and small growth rate improvements are magnified as time goes on (Hsiao, 1993). In addition, shoot vigour may be associated with root vigour and enhanced water and nitrogen uptake (Section 4 in Chapter 13). Appropriate management practices that improve seedling vigour, optimise sowing densities and provide sufficient nutrients and water are key to improving WUE by minimising *E* and maximising *T* in cereals and in row crops (Cooper et al., 1987; Section 2 in Chapter 2). In rainfed systems, however, high *T* early in the vegetative phase may lead to severe stress during the critical reproductive stages, decreasing the efficiency of water use (Angus and van Herwaarden, 2001). If irrigation is available, it should target the reproductive stages to avoid this negative effect.

It should be pointed out that *E* and *T* are not completely independent of each other; dry surface soil (low *E*) may induce higher *T* than would occur if the surface soil is wet. Ritchie (1983) and Villalobos and Fereres (1990) have shown experimental evidence of this partial compensation in *T* by varying *E* in several row crops. Such compensation occurs primarily under partial (20–60%) ground cover. As the canopy closes, the relative importance of *E* declines and the compensatory effect of low or high *E* on *T* can hardly be detected (Villalobos and Fereres, 1990). There are many reports where the partitioning of *E* and *T* has been experimentally determined. Canopy size and soil wetting frequency are the two main factors determining the relative magnitude of *E*. Seasonal *E* estimates for annual crops vary from more than 50% of ET in rainfed systems to less than 25% of ET in intensive, irrigated systems (Villalobos and Fereres, 1990). In irrigated systems, the goal is to achieve complete canopy cover as fast as possible and crop management is optimised to achieve that goal. Once most of the radiation is intercepted by the crop, *E* from soil is limited to less than 10% of ET, even when the soil is wet (Villalobos and Fereres, 1990). Thus, the opportunities to reduce *E* in annual crops under irrigation is limited to the period from sowing to full cover. There, irrigation method and frequency are the primary factors determining *E*. The reduction of *E* by wetting only a small fraction of the soil surface is perceived as one of the primary advantages of drip irrigation. Only few studies have assessed experimentally the reduction in *E* by drip. In processing tomatoes, the ET of daily drip irrigation was compared against that of furrow irrigation, applied every 10 days (Pruitt et al., 1984). Measured ET of the furrow irrigation lysimeter was about 35% higher than that of the drip irrigation lysimeter on the day of furrow irrigation (Pruitt et al., 1984). As time went on and the surface soil dried in the furrow lysimeter, its ET declined relative to that of the daily drip lysimeter and by day 5 after irrigation, it was only about 90% of the drip lysimeter, maintaining that difference until the date of the next furrow irrigation. The compensation between the two parts of the drying cycle resulted almost in identical seasonal ET in drip and furrow irrigation (Pruitt et al., 1984). Because in irrigated cropping systems the canopies are managed to achieve full cover as fast as possible, the opportunities to reduce *E* are thus limited. The exception would be to use subsurface drip irrigation where *E* is very small unless there is rainfall. To our knowledge, no rigorous studies have been conducted in annual crops under subsurface drip to assess the *E* savings and the degree of compensation that the virtual elimination of *E* may cause by increasing *T* due to the surrounding dry environment. In tree crops and vines, the relative importance of *E* depends on canopy size, method of irrigation and management. Separate estimates of *E* and *T* may now be achieved by measuring *T* with sap flow techniques (Smith and Allen, 1996) and *E* with microlysimeters (Bonachela et al., 1999). As drip is being adopted worldwide for tree and vine irrigation, *E* is of small magnitude relative to *T* in perennial crops (Bonachela et al., 2001), except in the case of young trees or vines where canopy cover is small.

If the opportunities for reducing *E* are limited, the options remaining to save water in irrigated agriculture are a reduction in *T* and a reduction in applied irrigation water. Reducing *T* requires the imposition of water deficits through deficit irrigation (Fereres and Soriano, 2007). Reducing applied irrigation water while maintaining high productivity needs accurate irrigation scheduling and uniform distribution of water. From the standpoint of the chain of efficiencies described in Section 2.3, reducing *T* and applied irrigation water while maintaining productivity would require the improvement of two of the ratios in Eqs. 4 and 5. One is the ratio between harvestable yield and biomass, known as harvest index (HI; $M_{\mathrm{yl}}/M_{\mathrm{bm}}$). The other is $W_{\mathrm{rz}}/W_{\mathrm{fe}}$, the ratio between the water applied and that that is stored in the root zone for its use in ET, known often in the literature as irrigation efficiency.

3. MAXIMISATION OF HARVEST INDEX TO IMPROVE WATER PRODUCTIVITY

Our understanding of the processes that determine yield is limited. The decline in whole-plant physiological research of the last two decades prevents us to attain further insight on the mechanisms leading to high yields. A recent controversy is an example of our present limitations (Sinclair and Jamieson, 2008; Fischer, 2008). Without sufficient knowledge on how crops achieve high yields under optimal conditions, it is difficult to make further progress in water-limited environments. Water deficits limiting crop yields affect many different processes at several levels of organisation, from cell to whole plant (Hsiao, 1973). Three key processes are affected at the crop level. First, the high sensitivity of expansive growth to water deficits influences intercepted radiation and diminishes biomass production and therefore yield (Hsiao et al., 1976). Second, water deficits can directly induce abortion of flowers and fruits (Salter and Goode, 1967; Boyle et al., 1991; Passioura, 2006). If this occurs, the effect on yield may be more detrimental than the effect on biomass production. Finally, water deficits hasten leaf senescence, and hence reduce intercepted radiation, biomass and yield (Hsiao et al., 1976). The last two responses impact directly reproductive development and thus the HI, normally decreasing it below that observed when water is not limiting. Passioura (1977) emphasised the role of HI in achieving high WP in water-limited conditions, making it one of three components of water-limited yield. It is therefore crucial to explore how to avoid the detrimental effects of water deficits on HI under water scarcity.

3.1. Harvest index and water productivity in water-limited situations

Although HI is considered to be fairly constant within cultivars in the absence of environmental constraints (Hay, 1995), there is ample evidence that in many annual crops, HI is reduced by water deficits. Fereres and Soriano (2007) reviewed the HI response to water deficits in several crops and found that HI was more or less constant until the stress was sufficient to reduce biomass production by 30–40%, under progressive stress. The relative decline in biomass production is used as indicative of the stress level, and no causal relation between the decline in B and the changes in HI is implied. Cotton and sorghum were an exception in that HI increased under moderate stress relative to non-stressed crops. Passioura (1977) showed that the pattern of water use in the pre- and post-anthesis periods determines the HI of wheat. Sadras and Connor (1991) found that the HI of sunflower and wheat was maintained nearly constant as the fraction of water transpired after anthesis decreased up to a limit, below which it declined, reflecting the need to maintain canopy photosynthesis under water deficits in that period. Kemanian et al. (2007) proposed that HI is related to the fractional post-anthesis phase growth (f_G), defined as the ratio between aboveground biomass produced post-anthesis and that produced from emergence to maturity, instead of the fraction of post-anthesis water use developed by Sadras and Connor (1991). The advantage of this approach is that it provides a conceptual framework for the analysis of source- and sink-limited as well as for the source-sink co-limited situations. It has important implications for management in dry environments, as earlier flowering should allow a longer grain-filling period that may result in higher HI. Species and even varieties differ on the type of response of HI to f_G, depending on the balance between yield components (Kemanian et al., 2007).

How is HI related to WP? This relationship depends on many factors, including the metabolic pathway of carbon assimilation and the composition of biomass (Sadras and Connor, 1991). On a normalised scale, however, the proportionality between WP and HI seems similar for diverse species including maize, sorghum, wheat, rice, sunflower and cotton (Figure 3a). The positive correlation between yield and WP has been extensively documented in many agricultural systems and is illustrated in Figure 3b. In rainfed systems a similar relationship is found, even when it is reported in inverse or colourful terms (Rockström and Barron, 2007). Figure 3 highlights the importance of avoiding water deficits at critical stages that would decrease HI, yield and, therefore, WP (Richards et al., 2002). In rainfed systems, Kirkegaard et al. (2007) highlighted the importance of healthy cereal roots for subsoil water extraction and Chapter 13 emphasised the role of root vigour for late-season water uptake; both root health and vigour are also important for crops under deficit irrigation.

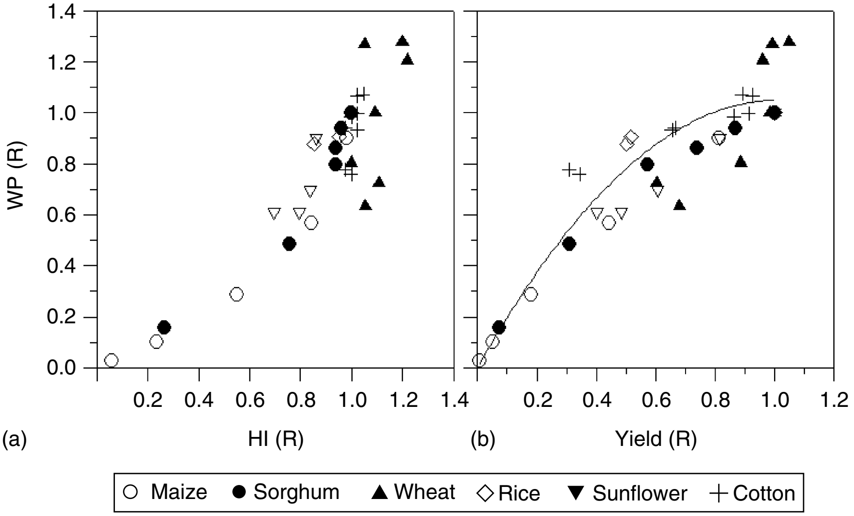

FIGURE 3

Relationship between relative water productivity [WP(R)] and (a) relative harvest index [HI(R)] and (b) relative yield [Y(R)]. All variables are relative to well-watered conditions. Data sources: maize and sorghum, Farre and Faci (2006); wheat, Ilbeyi et al. (2006); rice, Zhang et al. (1998); cotton, Orgaz et al. (1992) and sunflower, Alvarez de Toro (1987). Line in (b) corresponds to the relationship found in wheat by Musick et al. (1994), adapted to a relative scale.

If irrigation supply is restricted below the full ET requirement, water management must be directed at maximising *T* for the supply available and at achieving the highest possible HI. How can HI be maintained or even enhanced under water deficits? To answer this question, the underlying physiological processes involved in yield determination under water deficits are explored in the following section.

3.2. Yield formation and reproductive structures

Boyer and McLaughlin (2007) pointed out that meiosis, anthesis, pollen fertility, pollination, female fertility and early zygote development were all susceptible to water deficit. Flowering is thus in general a period very sensitive to water deficits (Kramer and Boyer, 1995) partially due to the susceptibility of cell enlargement (Westgate and Boyer, 1985). Chapter 15 (Section 3.2.2) describes the well-defined time windows of maximum sensitivity to stress in major grain crops. The intensity of water deficit required to affect these reproductive processes is, in comparison, less clear as often parts of reproductive organs are insulated and protected from mild water deficits. Kernel number is reduced in proportion to the inhibition of photosynthesis by water stress (Schussler and Westgate, 1991; Egli, 2006). Modifying source activity during flowering and fruit set invariably changes seed number (Egli, 2006). The reduction in grain number is especially damaging because it is irreversible and sets an upper limit to yield (Boyer and McLaughlin, 2007).

The large plasticity that exists in many crop plant species on seed number contrasts with the narrow range of seed weight, although there are variations among species. Sadras (2007) has shown, from an evolutionary standpoint, the fitness benefit of variable seed numbers so that the resources available are matched to produce viable seeds above a minimum size. If irrigation water is limited, an optimal balance between seed number and seed size must be sought to prevent imbalances between pre- and post-anthesis water use. Although seed size is conservative, water deficits severe enough can reduce seed weight significantly and thus HI, as it occurs often in cereals under terminal drought (Angus and van Herwaarden, 2001).

Nevertheless, abortion of reproductive structures is one of the main causes of yield reduction under water stress, and irrigation management must avoid water deficits during critical reproductive stages. This fact was greatly emphasised in the early literature (Salter and Goode, 1967), but in some specific cases, plant breeding has reduced the risks of crop failure due to water stress during flowering and fruit set. In maize, reducing the interval between anthesis and silking has increased kernel set (Bolaños and Edmeades, 1996). Passioura (2006) suggests that future genetic improvement of WP should focus on how to reduce further the detrimental effects of water deficits on flowering and fruit set processes.

During seed filling, HI depends on the processes controlling seed growth rate and duration. Water stress shortens the seed-filling period, with minor effects on seed growth rate (Egli, 2004). It has been observed that the longer the grain-filling period, the higher the HI (Yang and Zhang, 2006). Selection for long seed-filling period increased yield in several crops, although it seems to be generally compensated by growth rate. Increase in duration should be associated with early flowering or with delayed maturity that may be advantageous in long-growing season environments (Egli, 2006). Faster filling would also have some advantages if the season is limited, as under water-limited conditions (Yang and Zhang, 2006). Water deficits during grain filling shorten duration by hastening leaf senescence; similarly, N stress also reduces grain-filling duration, probably through the same effect (Egli, 2006). Nitrogen uptake during seed filling plays an important role in maintaining green leaf area, and thus assimilate supply to the growing seeds (Egli, 2004). While emphasis has often been placed on the carbon flow to the growing seeds, the role of N in determining HI is equally important (Sinclair, 1998). Limited irrigation programs must also consider N management to optimise the use of both resources towards the goal of maintaining or enhancing HI. Greater insight on the mechanisms that determine the balance between seed number and seed size in crops is needed, and is unlikely to be obtained through correlative analyses at the field level; research at lower levels of organisation is needed to uncover causal relationships among the factors controlling yield.

3.3. Carbon and nitrogen supply to grain: actual assimilation and reserves

Once grain number is established, carbon and nitrogen assimilation during seed filling and translocation from reserves and senescing organs will set the final yield (Wardlaw, 1965; Schnyder, 1993; van Herwaarden et al., 1998a, 1998b; Hall et al., 1989, 1990; Takami et al., 1990; Chapter 15). The dynamics of carbon and nitrogen are, however, closely linked, as discussed in Chapter 8.

Water deficit hastens leaf senescence (Palta et al., 1994; Yang et al., 2001); maintenance of green leaf area is therefore essential to grain filling and yield under water stress. In the experiments of Foulkes et al. (2007), flag-leaf persistence was the trait which showed the highest correlation with maintenance of yield in wheat during drought. Close correlations between yield and green leaf area duration from anthesis to harvest have been reported for maize (Wolfe et al., 1988) and sunflower (Hall et al., 1985). Yield was also closely correlated to grain-filling duration in rice (Yuan, 1994; Yang et al., 2002), highlighting the importance of delaying senescence on yield formation. Similar results have been found in wheat when leaf area index did not exceed that required for complete light interception (Evans et al., 1975), and also in cotton (Jackson and Gerik, 1990).

Some stay-green sorghum genotypes can maintain green leaf area through the whole grain-filling process (Henzell et al., 1992). Under some growing conditions, delayed senescence in stay-green types can leave much unused carbohydrates in the straw and reduce HI in comparison to fast-maturing genotypes (Gong et al., 2005). Nevertheless, stay-green genotypes generally outyield genotypes without this trait under water stress (Rosenow et al., 1983; Borrell and Douglas, 1996; Chapter 15). Borrell and Hammer (2000) found that stay-green cultivars had a better balance between the N demand from the grain and the N supply from soil and remobilisation from leaves suggesting this trait is related to more fundamental root and shoot traits. There is little doubt that the maintenance of green leaf area in the face of water deficits leads to higher yields

(Borrell et al., 2000; Harris et al., 2007); the physiology and role of stay-grain as a trait for tolerance to water and heat stress is further discussed in Chapter 15 (Section 3.2.3).

Pre-anthesis assimilates contribute to grain filling in both well-watered and stressed crops. In well-watered conditions, the contribution to yield of pre-anthesis assimilates is normally less than in stress conditions, about 10–20% of the final grain weight under the experimental conditions of Hall et al. (1989, 1990) and Yang and Zhang (2006). Remobilisation of reserves compensates partly for the decline in photosynthesis during grain filling in stressed plants, but this compensatory flow seems to be less effective during the early reproductive stages, when the sensitivity to water stress is high (Kramer and Boyer, 1995). The benefits from remobilisation of reserves for grain filling are more significant in relative terms when water shortage decreased the photosynthetic rate after anthesis (Wolfe et al., 1988; Asseng and van Herwaarden, 2003; Hall et al., 1989, 1990). In their model of HI, Sadras and Connor (1991) assumed that the contribution of pre-anthesis assimilates to yield decreases linearly as the fraction of water transpired after anthesis increased.

In contrast to carbon, pre-anthesis assimilation is the main source of nitrogenous compounds for grain filling in most crops. The actual contribution of reserves to final grain nitrogen, however, varies with species, cultivar and growing conditions, for example from 63 to 100% in wheat, 11 to 100% in soybean, 49 to 64% in sorghum and 41 to 69% in maize (Egli, 2004). Chapter 8 outlines physiological explanations for differences between species in the contribution of pre- and post-anthesis nitrogen for grain fill. It appears that, although water deficits during the reproductive phase tend to decrease HI, mild water deficits may enhance slightly HI in some crops and that the N nutrition is an important factor interacting with the level of water supply to determine the nature of the response.

Xue et al. (2006) found that the decrease in HI in wheat due to sustained water deficits could not be compensated for by the increase in translocation of pre-anthesis assimilates; enhancement of reserve translocation is necessary but not sufficient to compensate for the decline in post-anthesis carbon assimilation: nitrogen supply to grain also needs to be maintained. In field conditions, water deficit may limit N uptake, mainly because of the disruption of N fluxes from soil to roots (Garwood and Williams, 1967). Chapter 8 (Section 3.5) illustrates some of the nitrogen-mediated responses to water deficit and expands on crop responses to water by nitrogen interactions. In some cases, excess nitrogen reduces the soluble carbohydrate pool available for translocation, as in the phenomenon called 'haying-off' in wheat (van Herwaarden et al., 1998a). Excess nitrogen during the vegetative phase delays senescence and inhibits the remobilisation of assimilates to grain in cereals (Yang and Zhang, 2006). Yang et al. (2000, 2001) assessed the effect of remobilisation on grain filling in wheat and rice in relation to water and nitrogen application. They showed that HI was not reduced or slightly increased when water was withheld due to the enhanced remobilisation of reserves relative to the slight decline in photosynthesis. The contribution of carbohydrates from reserves increased with the withholding of water, as photosynthesis was inhibited. This positive effect on HI was mitigated by high N application, as excess N delayed senescence (Yang and Zhang, 2006).

In summary, an irrigation strategy to favour high WP should aim at (i) avoiding water stress at the critical stages of grain number determination (Section 3.2.2 in Chapter 15) and (ii) balancing post-anthesis photosynthesis against the enhancement of remobilisation to achieve high HI and yield, and hence a high WP (Figure 3). Water and N management could be manipulated to incline the delicate balance between remobilisation and carbon assimilation towards the maintenance or even the enhancement of HI, although substantial information on the environment and on the crop response would be needed to strike the right balance under field conditions.

4. FIELD IRRIGATION MANAGEMENT AND EFFICIENT WATER USE

Understanding the factors that affect efficiency of irrigation and the potential for improvement requires knowledge of both irrigation methods and of crop response. Judicious irrigation management is based on an in-depth knowledge of these somewhat unrelated subjects, and it is unfortunate that advanced training in higher education institutions on such expertise has or is being abandoned. Following is a brief description of the interactions between irrigation management and crop responses.

Irrigation has been carried out by surface water application for thousands of years. Innovative, pressurised irrigation methods were developed early in the second half of the twentieth century, but their expansion and widespread adoption is much more recent. Sprinkler irrigation followed by microirrigation have caused a revolution in the water application techniques in irrigated agriculture. In surface methods, the soil itself controls the depth of infiltrated water, and due to the spatial variability in soil water properties, surface methods have generally less control of the water applied and cannot apply shallow depths of water uniformly to soils of variable properties. Farmers have found that pressurised methods are much easier to manage than the traditional surface systems, in particular when variable depths of water need to be applied to match crop needs. Also, frequency of application is no longer an issue in terms of irrigation costs with permanent sprinkler and drip irrigation systems. High application frequency offers the option of irrigating marginal soils of very low water holding capacity with high efficiency. When water supply is limited, all of these advantages should make the use of pressurised methods the preferred option for efficient water use, despite their high capital costs and higher energy requirements.

4.1. Optimising crop water supply under limited water

Crop water supply has three components: rainfall, irrigation and soil water depletion. Irrigation scheduling should aim at achieving the ET rate targeted by the manager, for which it is critical to have knowledge of crop ET (Allen et al., 1998). The technical procedures for irrigation scheduling are based on ET information, which may be supplemented with the use of soil- or plant-based indicators (Martin et al., 1990). When precision irrigation is needed, soil and/or plant indicators are used for local calibration of regional ET estimates (Fereres, 1996). Spatial variability makes the use of soil water indicators difficult, but new developments for their application in horticulture are promising (Thompson et al., 2007). Plant-based indicators are becoming more popular, following decades of much research and little application. The plant indicator most commonly used in horticulture is the xylem water potential, measured with a pressure chamber (Shackel et al., 1997). Because of its operational difficulties, other indicators and sensors have been developed and used with variable success. The basic limitation of all indicators and sensors is the measurement variability in relation to established thresholds. Goldhamer and Fereres (2001) have proposed the use of a signal-to-noise ratio to assess the potential value of plant indicators for irrigation scheduling, where the signal is the magnitude of the indicator (e.g. maximum daily trunk diameter) and the noise is its coefficient of variation.

It is likely that the use of plant-based indicators will expand as water becomes scarce. Under limited irrigation, some knowledge of crop water status is essential to avoid risk of undesired water stress, and to exploit stored soil water most effectively. Crops can extract substantial amounts of water from the root zone before water stress limits transpiration. In a typical irrigated soil, 100–200 mm may be extracted at the end of the season, representing a significant fraction (15–30%) of the crop ET. Deficit irrigation practices should be designed to take advantage of stored soil water, extracting the maximum amount possible, and leaving the profile dry for subsequent replenishment by rainfall (Fereres and Soriano, 2007). Monitoring the crop response to the irrigation deficit to avoid unwanted stress becomes of paramount importance in these situations.

Once the depth of irrigation is calculated, as precisely as possible to avoid waste, the other critical issue at the field scale is to distribute the water as uniformly as possible, in particular when water is limited. The established indicator of uniformity is the ratio of the volume applied in the low quarter of the field to the average volume applied over the entire field (DU_{lq}; Burt et al., 1997). If the distribution of water is known, it is possible to obtain statistical expressions of uniformity and to relate them to the standard DU_{lq}. To emphasise the importance of uniformity, Figure 4a shows typical field distributions of irrigation water computed as fractions of the total area, from the lowest to the highest amounts of applied water. Line A depicts the water distribution when the required amount or more is applied to half of the field. Half of the field then has a deficit. Line B shows the same distribution when the manager attempts to reduce the under-irrigated area to

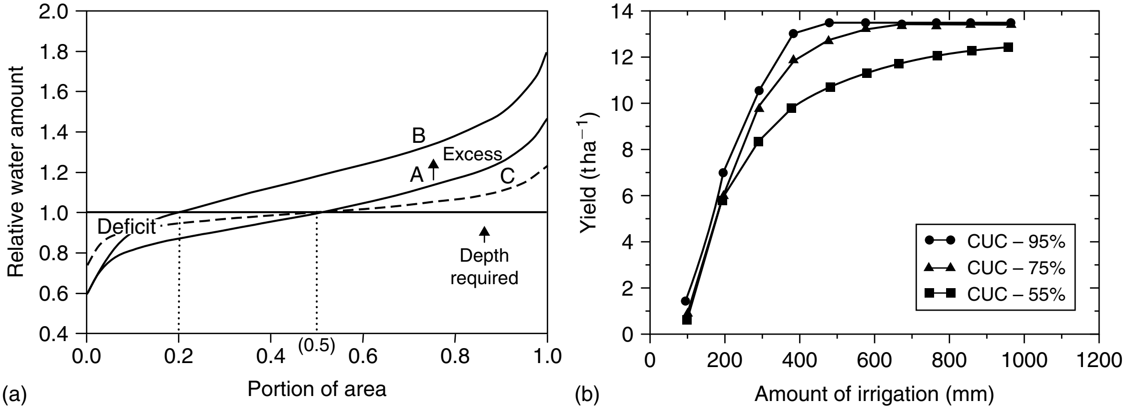

FIGURE 4

(a) Field distributions of irrigation water computed as fractions of the total area. (Source: Clemmens and Molden, 2007.) (b) Simulated relation between corn yield and seasonal irrigation applied for three Christiansen uniformity coefficient (CUC) using CERES model. (Source: Mantovani et al., 1995; used by permission.)

only one quarter of total. Both distributions have a CV of 20%, typical of standard irrigation systems. Line C shows how by reducing the CV from 20 to 10%, the amount of extra water needed as well as the losses are largely reduced (Clemmens and Molden, 2007). Because of the spatial variations in applied water, supplying the required amount to 100% of the area is not feasible, as there is always a fraction that will receive less (Figure 4a) unless large volumes of water are applied to other areas, risking water-logging problems. When the distribution functions are combined with yield response functions, the role of uniformity in determining area yields becomes evident. Figure 4b shows that as uniformity decreases, a substantial amount of additional water is needed for a certain yield level. Managers must then set certain uniformity criteria that are commensurate with the anticipated water available.

Depending on the DU_{lq}, that low quarter of the area may receive a depth that could be yield limiting over a significant fraction of the field (Figure 4a). As water becomes more expensive or scarce, the emphasis will be placed on new irrigation systems with very high uniformity, with concomitant increases in irrigation costs. However, for a realistic assessment of the impact, in terms of yield loss, of a given DU_{lq}, what is needed is to quantify on a given spot in the field the impact of an insufficient depth of irrigation. That is not easy task, given the spatial variability of soil water properties, the ability of root systems to capture water, the variations in evaporative demand within a field and the plasticity of crop plants in their yield response to water. Two technological developments can assist agronomists in this difficult assessment. One is the increased accuracy in remote sensing techniques for water stress detection and mapping (Sepulcre-Cantó et al., 2006). It is now possible to fly over fields on a daily basis, collecting thermal and multispectral information at a very small scale (pixels of less than 50 cm) from unmanned aerial vehicles (Berni et al, 2009). Mapping the spatial development of water deficits over a field is thus technically feasible and will soon be commercially available. Crop simulation modelling is another tool that can be useful in mapping the anticipated variations within a field (Debaeke and Aboudrare, 2004). If all this knowledge about spatial variability becomes available, instead of attempting to achieve very high, impractical DU_{lq} levels, it may be more desirable in economic terms to apply variable depths of water within a field management unit, a practice termed precision irrigation (Sadler et al., 1998). Precision farming is a concept that developed some time ago to cope with the continuous enlargement of management units due to mechanisation. As single units increased in size, the use of uniform applications of fertilisers and other agrochemicals caused environmental concerns, as spatial variation in many soil properties tend to increase with field size. Just as precision agriculture is expanding for fertility and herbicide management (Lamb and Brown, 2001), it is very likely that travelling irrigation systems that can apply variable depths to different areas of the field in response to management objectives (such as minimum deep percolation losses) will expand in the future (Evans and Sadler, 2008). Chapter 19 discusses in detail the challenges and recent developments in the science and technology of management of spatial variation in farming systems.

5. CONCLUDING REMARKS

Until now, many farmers in irrigated agriculture tend to apply excess water to avoid the yield loss associated with the risks of water deficits of an unknown magnitude. Recent and future advances in crop water status monitoring should permit future improvements in precision irrigation, by combining very uniform water application with the accurate determination of water needs. However, in situations of water scarcity, improving IE by combining advances in engineering and management would not be sufficient, simply because water supply would not be enough. In such cases, the use of deficit irrigation strategies will be the only viable alternative to sustain irrigated production, particularly in drought years. Knowledge of the crop responses to water deficits will then be invaluable to decide on the timing and the degree of water deficits that may need to be imposed as a consequence of a reduced water supply.

While ample information exists in the main crops to quantify the effects of water deficits on canopy growth and development, and on canopy photosynthesis, knowledge on how HI, and thus yield, is affected by water deficits is limited. Empirical and correlative information on the relations between yield and water use abounds, but causal relationships based on greater insight of the basic physiological processes determining yield are still lacking. Multidisciplinary work at more than one level is required to uncover how to manipulate water supply to crop plants in the field, with the goal of reducing transpiration while maintaining or even increasing farmers' net profits. Such improved knowledge will definitely contribute to much progress towards reducing the consumptive use requirements of irrigated agriculture.

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CHAPTER 7

Crop Radiation Capture and Use Efficiency: A Framework for Crop Growth Analysis

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1. INTRODUCTION

Radiation-use efficiency (RUE), defined as crop biomass produced per unit of total solar radiation or photosynthetically active radiation (PAR) intercepted by the canopy, is a fundamental component of a framework to analyse crop growth based on resource capture and use efficiency. This framework is applied in other chapters of this book to account for (i) the effects of nitrogen deficiency on crop growth (Section 3.2.1 in Chapter 8), (ii) avenues to genetically improve yield potential (Sections 3.2.2 and 5.1 in Chapter 15), (iii) the environmental and genetic influences on grain quality attributes (Chapter 16), (iv) environmental influences on the competitive ability of crops and weeds (Section 6.3.1. in Chapter 18) and (v) growth and yield responses to increased ambient CO_2 concentration (Section 4.1 in Chapter 20).

The concept of capture and efficiency in the use of radiation and its application to assess the relative performance of crops under different environments and management practices have been the subject of excellent articles (e.g. Monteith, 1977) and reviews (e.g. Sinclair and Muchow, 1999). Readers are encouraged to review these two sources. It is useful to contemplate these and other articles in historical context; we can safely assume that many young readers or graduate students may not have been exposed to the so-called classical growth analysis of Watson (1952). Essentially, it considers growth as the product of net assimilation rate per unit leaf area and total leaf area. This approach is conceptually correct but presents some limitations as discussed by Monteith (1994) and perhaps in an overly critical tone by Sinclair and Muchow (1999). The current framework to analyse crop growth based on radiation capture and RUE targets the canopy instead of a representative leaf area section, as implied in the net assimilation rate. The leaf area index (LAI), instead of being a focal point of the analysis, acts as an intermediate variable determining radiation capture and distribution throughout the canopy. The importance of making abstractions at a useful level of aggregation for studying plant communities is argued by Hammer et al. (2004).

The radiation capture and RUE framework can be formalised as follows:

$$B = \mathrm{RUE}\, f_{\mathrm{is}}\, S_{\mathrm{t}} \qquad (1\mathrm{a})$$

$$Y = \mathrm{HI}\, \mathrm{RUE}\, f_{\mathrm{is}}\, S_{\mathrm{t}} \qquad (1\mathrm{b})$$

where B is biomass produced ($\mathrm{g\,m^{-2}}$), RUE a crop/cultivar-specific parameter ($\mathrm{g\,MJ^{-1}}$), f_{is} the fraction of the incident solar radiation intercepted by the canopy, S_{t} total incoming solar radiation ($\mathrm{MJ\,m^{-2}}$) in a given time interval, Y yield ($\mathrm{g\,m^{-2}}$) and HI the harvest index or ratio of harvestable material to total biomass at harvest (usually calculated based on shoot biomass for grain crops and on total biomass for root and tuber crops).

The use of the RUE concept as presented in Eq. 1a was introduced at least four decades ago (Warren Wilson, 1967). This framework is useful for the interpretation of agronomic experiments (e.g. Sadras et al., 2005) and has been extensively used for modelling biomass production (Williams et al., 1984; Jones et al., 1998). Nonetheless, while the literature reporting RUE is large, few articles combine theory, experimentation and modelling to get an understanding of RUE and growth variation based on hypothesis-driven analysis (e.g. Hall et al., 1995; Sadras et al., 2005). The reported RUE estimates are often snapshots of what happened, leaving unanswered why it happened, rendering an incomplete understanding of the system functioning. Furthermore, environmental factors, canopy architecture, stress and other factors obscure the interpretation of RUE.

Our objective in this chapter is to summarise the use of RUE to analyse crop growth in agronomy, breeding and modelling. Limitations that may constrain the utility of the RUE concept are also discussed. Our purpose is neither to present an encyclopaedic review of RUE applications nor a manual to determine RUE.

Throughout this article, solar radiation S_{t} is taken as the basis for the calculation of RUE ($\mathrm{RUE_S}$), unless otherwise stated. It is definitively appropriate to use PAR as the basis for RUE ($\mathrm{RUE_{PAR}}$), as photosynthesis is powered by radiation in the visible spectrum (although most of the absorbed energy in the PAR waveband is dissipated as heat), and it should be preferred if incident PAR is available. However, PAR is usually derived from the most commonly recorded $\mathrm{S_t}$. Appropriate conversion factors between $\mathrm{RUE_S}$ and $\mathrm{RUE_{PAR}}$ are provided and discussed.

2. ESTIMATION OF RUE BY SCALING UP FROM LEAF TO CANOPY

RUE is a canopy-level variable that in principle can be obtained by scaling up net photosynthesis from leaf to canopy and properly accounting for maintenance and biosynthesis or growth respiration. Examples of this approach are available in the literature (e.g. Norman and Arkebauer, 1991; Hammer and Wright, 1994).

Scaling up the calculation of RUE from leaf to canopy helps understanding the expression of leaf-level properties and processes affecting carbon and energy exchange, as well as the impact on RUE of properties exclusive of the foliage (or population of leaves), such as canopy size and architecture. It also highlights the interaction between weather variables and RUE. As discussed by Stockle et al. (2008), for any given time step of integration, the following set of equations apply, where Eq. 1 is written in terms of PAR:

$$\mathrm{RUE_{PAR}PPFD}f_{\mathrm{ip}} = F\int_{l=1}^{l=n}\int_{\lambda=1}^{\lambda=m}\left\{\min\begin{bmatrix}J_{\mathrm{E}}\\J_{\mathrm{C}}\\J_{\mathrm{S}}\end{bmatrix} - R_{\mathrm{d}}\right\}dL_{l\lambda} = F\int_{l=1}^{l=n}\int_{\lambda=1}^{\lambda=m} g_c(c_a - c_i)dL_{l\lambda} \tag{2}$$

$\mathrm{RUE_{PAR}}$ is in $\mathrm{g\,B\,\mu mol^{-1}}$ PPFD; PPFD is the photosynthetic photon flux density (above canopy, $\mathrm{\mu mol\,m^{-2}}$ ground); f_{ip} is the fraction of PPFD intercepted by the canopy (in this case applied to photon flux not to energy); F is a conversion factor from net $\mathrm{CO_2}$ fixation to biomass ($\mathrm{g\,B\,\mu mol^{-1}\ CO_2}$); l is canopy layer number; λ is leaf azimuth and inclination angle class number; $dL_l\lambda$ is the leaf area (only one side) in canopy layer l and leaf angle class λ; J_{E} and J_{C} are light- and rubisco-limited photosynthetic rate; J_{S} is the rate imposed by sucrose synthesis ($\mathrm{\mu mol\ CO_2\ m^{-2}}$ leaf); R_{d} is dark respiration ($\mathrm{\mu mol\ CO_2\,m^{-2}}$ leaf); g_{c} is the combined stomatal, leaf boundary and turbulent conductance to CO_2 transfer (mol CO_2 $m^{-2}\,s^{-1}$); and c_a and c_i are the atmospheric (bulk air) and internal (leaf) atmospheric CO_2 concentration (μmol mol^{-1}).

The middle equation represents the biochemical capacity for CO_2 fixation by photosynthesis (Collatz et al., 1991), and the right-hand-side equation represents the diffusion of CO_2 from bulk air to the leaf sub-stomatal cavities. Leaf net photosynthesis is integrated for n number of leaf angle classes per canopy layer and m number of canopy layers to obtain canopy net photosynthesis. The coefficient F converts fixed CO_2 to crop biomass, depending on factors affecting maintenance and growth respiration such as biomass composition, canopy size and temperature. A given c_i value reflects the equilibrium between CO_2 demand and supply. The reader is referred to Collatz et al. (1991, 1992) for details in the evaluation of J_E, J_C, J_S and R_d.

Given the large number of physiological and environmental factors affecting g_c, c_i and the biochemical capacity for CO_2 fixation by photosynthesis, and the interaction of these factors with crop canopy characteristics, RUE changes continuously, even for crops well supplied with water and nutrients. A variety of factors such as water and nutrient shortage also affects RUE. Using radiation capture and RUE as a framework to assess crop agronomic performance or the impact of crop breeding requires careful consideration of the RUE controls, particularly in comparisons across locations with significant differences in climate.

3. ESTIMATING RADIATION-USE EFFICIENCY OF CROPS FROM MEASUREMENTS OF BIOMASS PRODUCTION AND RADIATION INTERCEPTION

The field determination of RUE is straightforward. It requires measuring intercepted radiation and biomass at time intervals adequate for accurate estimations of intercepted radiation and biomass accretion. From Eq. 1a, RUE is the ratio between biomass accumulation and radiation interception during the time interval considered. To remove sampling variability, RUE estimates are often obtained as the slope of the linear regression between cumulative biomass and cumulative intercepted radiation for a given period of interest. A detailed account of factors that contribute to uncertainty and errors in the determination of RUE is given by Sinclair and Muchow (1999).

Crop and soil variability are important sources of uncertainty. Collecting sufficient samples to measure biomass with acceptable statistical confidence while minimising disruption of crop growth can be challenging. Ideally, the measurement of radiation interception should be done continuously throughout the period of interest, which is logistically and economically problematic. Fortunately, reasonable estimates of radiation interception can be obtained from discrete measurements. The field protocol should carefully consider the frequency of measurements, time of day and sensor placement to provide correct daily integration of radiation interception (or absorption). Radiation interception measurements in canopies with a marked row structure when the sun is at the same azimuth as the row can underestimate daily radiation interception by 15% or more, depending on the row dimensions. Simple radiation transfer models that allow correcting for this error in row crops are available (Fuchs and Stanhill, 1980; Boote and Loomis, 1991; Campbell and van Evert, 1994).

4. SOLAR AND PAR-BASED RADIATION-USE EFFICIENCY

The solar radiation reaching the earth surface contains approximately 3–4% of the energy in the ultraviolet waveband (UV, $< 0.4\,\mu m$), and roughly an equal fraction of the remaining energy in the PAR (0.4–$0.7\,\mu m$) and infrared (IR $> 0.7\,\mu m$) wavebands. Most of the IR radiation reaching the earth surface is in the near-infrared (NIR, 0.7–$1.4\,\mu m$). The UV and PAR fractions can be higher when the radiation is mostly diffuse, but the exact spectral quality of the global solar radiation is difficult to predict due to the interactions among solar elevation, turbidity and cloudiness of the atmosphere (Monteith and Unsworth, 2008). The ratio S_{PAR}/S_t is customarily taken as 0.5, but a ratio closer to 0.45 has been reported by Howell et al. (1983). Separating the solar spectrum in NIR and PAR is convenient because the optical properties of leaves greatly differ for these two wavebands.

Radiation interception measured with PAR or total solar radiation sensors renders different fractional interception because single-leaf absorptivity (α) and transmissivity for PAR and NIR differ: For a single leaf, $\alpha_{\mathrm{PAR}} \sim 0.85$ and $\alpha_{\mathrm{NIR}} \sim 0.15$ (Ross, 1975). The fraction of radiation transmitted through the canopy (τ) depends on the relative absorption and reflection of both PAR and NIR. Due to the low contribution of UV radiation to the total solar radiation spectrum, the UV radiation balance is usually ignored. It should be noted that since α_{UV} is even higher than α_{PAR}, the foliage elements act almost as black leaves at that waveband; however, in clear-sky days UV radiation is more diffuse than PAR.

Canopy absorptivity is higher than single-leaf absorptivity because a beam transmitted through a leaf has multiple opportunities to interact with the rest of foliage. The ratio of UV to PAR above and below the canopy are reasonably similar (Shulski et al., 2004), but the radiation reaching the soil is enriched in NIR, compared with the incoming radiation due to the efficient absorption of PAR and UV by the canopy. The actual enrichment ratio depends on the canopy size and architecture; therefore, it is no trivial task to convert $\mathrm{RUE}_{\mathrm{PAR}}$ to $\mathrm{RUE}_{\mathrm{S}}$. Bonhomme (2000) remarked on common mistakes that appear in the literature when doing these conversions and analysed the variations on the conversion coefficients due to different radiation dynamics (equatorial and temperate), canopy size and geometry. Similar calculations are reported by Campbell and van Evert (1994).

Goudriaan (1977, pp. 26–27 and Table 5) showed that an exponential model provides a reasonable approximation for radiation scattering by crop canopies. Following Goudriaan, the fraction of radiation transmitted through the canopy (τ) for each waveband is reasonably well represented by $\tau = \exp(-\alpha^{0.5}k_{\mathrm{b}}\mathrm{LAI})$, where the product $\alpha^{0.5}k_{\mathrm{b}}$ is the extinction coefficient k for each waveband and k_{b} is the extinction coefficient for black leaves ($\alpha = 1$). As discussed by Campbell and van Evert (1994), daily k can be calculated assuming that the daily integral of beam radiation transmission is closely approximated by the transmission of diffuse radiation. The k_{S} ranges from 0.35 to 0.60 from vertical to horizontal leaf angle distributions, with most k_{S} around 0.44–0.50 (e.g. Kemanian et al., 2004); for k_{PAR}, the range is roughly 0.45–0.9. It should be noted that for a constant leaf angle distribution, k varies with LAI; therefore, constancy of k throughout the growing season implies a gradual change in leaf angle distribution (see Campbell and van Evert, 1994, Figure 3.2). If daily k_{PAR} is available, the daily k_{S} can be approximated by $k_{\mathrm{S}} = 0.62{k_{\mathrm{PAR}}}^{0.86}$ (and $k_{\mathrm{PAR}} = 1.62{k_{\mathrm{S}}}^{1.16}$). It is convenient, however, to calculate solar radiation interception based on both PAR and NIR interception separately.

Conversion coefficients from $\mathrm{RUE}_{\mathrm{PAR}}$ to $\mathrm{RUE}_{\mathrm{S}}$ calculated with a detailed canopy radiation transfer model for both horizontal and upright leaves are presented in Table 1. The model calculates sub-hourly PAR and NIR interception as a function of latitude, canopy architecture and size and fractions of beam and diffuse radiation. It is based on equations by Campbell and Norman (1998), Goudriaan (1977) and Goudriaan and van Laar (1994), and accounts for changes in reflectivity as the canopy size increases. The conversion coefficients are not sharply affected by canopy geometry but are moderately affected by canopy size. Results are comparable to those given by Bonhomme (2000); the differences are explained by $\alpha_{\mathrm{PAR}} = 0.8$ and $\alpha_{\mathrm{NIR}} = 0.2$ used by this author while we used 0.85 and 0.15 (Ross, 1975). For high LAI, $\mathrm{RUE}_{\mathrm{PAR}}$ is about twice $\mathrm{RUE}_{\mathrm{S}}$.

5. RADIATION-USE EFFICIENCY OF MAIN CROPS

The RUE reported in this section is based on S_t ($\mathrm{RUE}_{\mathrm{S}}$). Theoretical analyses of expected RUE were performed by several authors and are discussed by Sinclair and Muchow (1999, p. 221). Maximum $\mathrm{RUE}_{\mathrm{S}}$ of 1.4 and $2.0\,\mathrm{g\,MJ^{-1}}$ for C_3 and C_4 species were proposed by Monteith (1977, 1978). Piedade et al. (1991) reported a $\mathrm{RUE}_{\mathrm{S}}$ of $2.3\,\mathrm{g\,MJ^{-1}}$ for the C_4 grass *Echinochloa polystachya*, growing in the seasonally flooded

Table 1 Coefficients to Convert Radiation-Use Efficiency Values Based on Intercepted PAR to Values Based on Intercepted Total Solar Radiation

LAI	Upright Leaves		Horizontal Leaves	
	RTM	Bonhomme (2000)	RTM	Bonhomme (2000)
0.5	0.68	–	0.68	–
1	0.66	0.61	0.66	0.60
2	0.63	–	0.62	–
3	0.60	0.55	0.59	0.56
4	0.58	–	0.57	–
5	0.56	–	0.55	–

The radiation transfer model (RTM) refers to the model briefly described in the text, and Bonhomme (2000) refers to a similar table presented by that author.

Amazonian floodplain, including roots. This grass accumulated mostly stem mass (~80–85%), which has a relatively high biosynthesis conversion efficiency of ~0.80 g biomass g^{-1} CH_2O, and grows in optimal conditions for C_4 photosynthesis with vapour pressure deficit (VPD) <1 kPa. Beale and Long (1995) also reported RUE_S of 2.3 g MJ^{-1} (3.9 g MJ^{-1} intercepted PAR) for the C_4 grass miscanthus (*Miscanthus x giganteus*) growing in the cool climate of England. These are likely the highest seasonal RUE_S reported, and the maximum RUE_s for other species should equate or scale down from those reported for *E. polystachya* and miscanthus, depending on the maximum leaf photosynthetic rates and biosynthesis cost.

Table 2 presents a summary of maximum RUE_S for different species. It is a synthesis and an update of the review by Sinclair and Muchow (1999). Unless otherwise stated, only shoot biomass is considered. To consider roots, proper adjustments of RUE_S in Table 1 are needed. These adjustments can differ among species, particularly between perennial and annual species, growing conditions and phenological stage (e.g. Brown et al., 2006). Reviews such as that by Amos and Walters (2006) for maize (*Zea mays* L.) should be used for this purpose. In crops with high oil or protein accumulation, RUE_S in biomass terms should be corrected for the energetic cost of synthesis, which depends mostly on the oil or protein concentration of the newly generated biomass and the source of nitrogen.

Maximum values reported or calculated for other C_4 grasses are in broad agreement with that for *E. polystachya*. Sinclair and Horie (1989) estimated that the maximum maize RUE_S should be 1.8 g MJ^{-1}. A recent estimate by Lindquist et al. (2005) for maize was 3.8 g MJ^{-1} absorbed PAR, considering only shoot biomass, which is equivalent to a RUE_S of 2.0 g MJ^{-1} as proposed by Monteith (1977, 1978). A correction for below-ground carbon allocation approaches maize RUE to that of *E. polystachya*. Similarly, Muchow et al. (1997) reported a maximum RUE_S of 1.8 g MJ^{-1} for sugarcane, considering only shoot biomass. Kiniry et al. (1999) reported switchgrass RUE equivalent to those of *E. polystachya* (2.0–2.4 g MJ^{-1}), even without considering roots, and larger by a factor of two than that of three other perennial C_4 grasses in the same experiment (a slight underestimation of radiation interception may have caused a RUE overestimation). Grain sorghum (*Sorghum bicolor* L. Moench) RUE seems to be slightly lower than that of other annual C_4 crops such as millet (*Pennisetum glaucum* L. R. Br.) or maize, while sweet sorghum seems to have one of the highest RUE.

For C_3 crops, maximum RUE was reported for sugar beet (*Beta vulgaris* L.) (Malnou et al., 2008) and potato (*Solanum tuberosum* L.) (Manrique et al., 1991), which is consistent with crops accumulating mostly simple sugars or starch and low protein or oil. The winter cereals barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.) and wheat (*Triticum aestivum* L.) show similar values near 1.7 g MJ^{-1}, that is, approximately 15% lower than maximum values for C_4 crops. Based on the reported data, rice (*Oryza sativa* L.) and the non-grass non-legume C_3 crops growing

Table 2 Radiation-Use Efficiency for Several Plant Species

Reference	Crop	RUE	Comments
C_3 annual grasses and crops			
Kemanian et al. (2004)	Barley	1.5–1.7	Review of several sources
Muurinen and Peltonen-Sainio (2006)	Oat	1.2–1.7	Undistinguishable from barley and wheat in the same study
Kemanian et al. (2004)	Wheat	1.6–1.7	Review of several sources
Mitchell et al. (1998)	Rice	1.2–1.5	Review of several sources
C_3 perennial grasses			
Duru et al. (1995)	Fescue	1.3	
Kätterer et al. (1998)	Phalaris	1.4–1.6	Average temperature 8 – 15°C
Akmal and Janssens (2004)	Ryegrass	1.7–2.3	Includes roots; highest estimate from pot experiment
Duru et al. (1995)	Orchard grass	1.1	
C_4 annual grasses and crops			
Lindquist et al. (2005)	Maize	2.0	Irrigated, five growing seasons
Kiniry et al. (1998)	Sorghum	1.7–1.8	Sinclair and Muchow (1999) argued for 1.4 g MJ^{-1}
Mastrorilli et al. (1995)	Sweet sorghum	1.9–2.5	Shoot biomass 32 Mg ha^{-1} at harvest
Van Oosterom et al. (2002)	Pearl millet	1.9	
C_4 perennial grasses			
Muchow et al. (1997)	Sugarcane	1.7–1.8	Seasonal values; daily maximum likely $>2.0\,\text{g MJ}^{-1}$
Kiniry et al. (1999)	Switchgrass	2.0–2.4	Rainfed, three growing seasons
Beale and Long (1995)	Miscanthus	2.0	2.3 g MJ^{-1} for total biomass
C_3 oil crops			
Marcos (2000)[a]	Canola	1.3–1.5	Reported value corrected by 1.29
D'Antuono and Rossini (1995)	Flax	1.7	RUE during seed growth = 0.7 g MJ^{-1}
Rosenthal and Gerik (1991)	Cotton	1.5	Similar values reported later by other authors
Trapani et al. (1992)	Sunflower	1.7–2.0	Highest estimate includes roots, strong response to f_i; lower value by Steer et al. (1993), strong relation RUE-ontogeny
Marcos (2000)[a]	Safflower	1.3–1.6	May be affected by mild water stress, reported value corrected by 1.29
Legume grain crops			
Rochette et al. (1995)	Soybean	1.0	1.1 g MJ^{-1} when considering roots
Kiniry et al. (2005)	Peanuts	1.2	Pod mass 'corrected' using a factor of 1.65
Lecoeur and Ney (2003)	Peas	1.5	Strong seasonal pattern; 1.5 was the maximum RUE
Brown et al. (2006)	Alfalfa	1.1	~1.6 g MJ^{-1} when considering roots

(Continued)

Table 2 Continued

Reference	Crop	RUE	Comments
Tuber, root and other non-grain storage organ crops			
See Sinclair and Muchow (1999)	Potato	1.6–1.7	Manrique et al., (1991) show values up to 1.9 g MJ^{-1}
Malnou et al. (2008)	Sugar beet	1.9	Total biomass, maximum of three years reported here
Rizzalli et al. (2002)	Garlic	1.6–1.8	Canopy with vertical leaf angle distribution

These values are based on shoot biomass and on intercepted solar radiation and should be considered appropriate for atmospheric CO_2 of 360–380 μmol mol^{-1}. Larger RUE by up to 20% may be expected under conditions of moderate radiation or high fraction of diffuse radiation.

[a] *The canola and safflower RUE reported by Marcos (2000) were multiplied by 1.29, which is the ratio of 1.7 g MJ^{-1} maximum RUE for wheat to that reported in Marcos (2000).*

in summer have a slightly lower RUE, with the exception perhaps of sunflower (*Helianthus annuus* L.). This may reflect a lower photosynthetic efficiency due to CO_2 photorespiration losses in the summer months. Perennial C_3 grasses show lower RUE than annual C_3 grasses, but the differences are probably negligible when allocation of biomass to underground organs is considered. Section 6.8 considers in detail the influence of shoot–root partitioning on RUE.

Legume crops show lower RUE than those of other C_3 crops. Soybean (*Glycine max* L. Merr.) and peanut (*Arachis hypogaea* L.) have RUE_s of 1.0–1.2 g MJ^{-1}, while pea (*Pisum sativum* L.) seems to have slightly higher RUE_s (1.5 g MJ^{-1}, Lecoeur and Ney, 2003), only 15% lower than that of C_3 cereals. Marcos (2000) reported, however, spring pea RUE 25–30% lower than that of wheat in an experiment growing these two crops side by side. In addition, in a study by Lecoeur and Ney (2003), RUE_s of pea varied throughout the growing season, ranging roughly from 0.7 to 1.6 and averaging 1.3 g MJ^{-1}. Alfalfa RUE is in the lower end of that reported for C_3 perennial grasses. The extent of the difference between soybean and peanut RUE, compared with that of other C_3 crops, seems to be larger than that expected from the energetic cost of reducing N_2. Sinclair and Muchow (1999) pointed out that, in general, legumes have low RUE. The reason for lower RUE in these crops is not fully understood; a sink control of RUE may partially explain these low values (Section 5.1.2 in Chapter 15; Lecoeur and Ney, 2003; Haro et al., 2007).

6. RADIATION-USE EFFICIENCY RESPONSE TO ENVIRONMENTAL, PLANT AND MANAGEMENT FACTORS

Despite the apparent simplicity of the RUE concept, the environmental, plant and management factors affecting RUE are not fully understood or are treated with confusion in the literature. Like both gross and net photosynthesis, RUE can be affected by environmental factors such as temperature, radiation and air humidity, or by plant factors such as nutritional and water status, ontogeny and source–sink regulation. When integrated through the canopy, leaf-level responses are dampened or buffered, and accordingly, the RUE responses to these factors are moderated. Furthermore, canopy-level properties, in particular canopy structures, can have a significant impact on RUE.

The effect of management factors must be interpreted as manipulations of the plant environment or physiological processes that affect RUE. Plant density or seeding date do not have an inherent effect on RUE or any other process: They operate through physiological mechanisms that are independent of the management practice. This distinction is sometimes blurred in the literature, particularly in experiments with an agronomic interest.

Below, we briefly review the effect of environmental and plant factors on RUE. Without a clear understanding of these responses, agronomical interpretations of RUE variation are bound to be incomplete or confounded. The management of the crops and crop environment to improve RUE and overall productivity are also discussed.

Here, and later in this chapter, we introduce results from computer simulations to illustrate the behaviour of RUE in response to a range of conditions that would be prohibitive to obtain experimentally (Box 1).

6.1. Radiation environment

Theoretically, RUE should increase with a decrease in the proportion of leaf area operating at saturating light (Sinclair and Horie, 1989). This proportion depends on factors such as irradiance, fraction of diffuse to total radiation (f_d) and LAI. Increase in RUE is expected with a decrease in irradiance and an increase in f_d because, in both cases, the proportion of photosynthetic area operating at non-saturating irradiance increases. These effects have been demonstrated by using simulation models (Allen et al., 1974; Norman and Arkebauer, 1991; Sinclair et al., 1992; Choudhury, 2000), and a small effect was documented in sunflower by artificially varying the radiation environment (Bange et al., 1997). In maize, Rochette et al. (1996) measured 25% higher net canopy photosynthesis in overcast than in clear-sky days for PAR up to $1000\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$. Loomis and Connor (1992) summarised the crop photosynthesis response to irradiance of several species from which it can be inferred that RUE decreases gradually as S_t increases, with a sharp drop for some C_3 species for $S_t > 400\,\text{W}\,\text{m}^{-2}$ (Figure 10.8 of Loomis and Connor, 1992). Canopy size and architecture can also affect the radiation environment within the canopy and RUE, as discussed later.

Under field conditions, irradiance and f_d are associated with variations in temperature and vapour pressure. Overcast conditions are associated with both high f_d and low S_t, small thermal amplitude due to moderated cooling at night and heating at daytime and low VPD. Similarly, high irradiance is associated with low f_d and, in many cases, rather high VPD. Rodriguez and Sadras (2007) modelled RUE in eastern Australia and claimed that f_d and irradiance explain the latitudinal variation on RUE and that the inverse relationship between RUE and VPD found in that modelling exercise was a consequence of the correlation of VPD with those variables. While the explanation is feasible for both eastern Australia and other locations, the analysis hinges on the assumptions of their model, which computes photosynthesis based on radiation, thus effectively decoupling photosynthesis from any explicit stomatal control. Nonetheless, the point here is that the isolation of effects through simulation modelling helps quantify the relative impact on RUE of factors that are difficult to isolate under field conditions (e.g. Hammer and Wright, 1994).

The eruption of Mount Pinatubo in June 1991 injected SO_2 in the atmosphere, causing an increase in sulphate aerosol and consequently f_d (Gu et al., 2003). These authors persuasively discuss evidence indicating that photosynthesis in the hardwood Harvard Forest was enhanced in the two years following the eruption due to the increase of diffuse radiation. In the summer after the eruption, the diffuse component of irradiance at noon increased from approximately 70 to $140\,\text{W}\,\text{m}^{-2}$, and the direct component was reduced by approximately $70\,\text{W}\,\text{m}^{-2}$ from $\sim 970\,\text{W}\,\text{m}^{-2}$, compared with the years after the effect of the eruption in the atmosphere subsided. This equates to an increase in f_d from approximately 0.07 to 0.13 at noon. The authors argued that this change caused an increase in gross canopy photosynthesis on the order of 20%, a substantial increase, which essentially implies a similar increase in RUE.

6.2. Canopy size and architecture

Since, as discussed above, RUE should increase with the proportion of LAI operating at non-saturating irradiance, an increase in LAI and f_i should increase RUE. In annual crops, this effect should be evident in the first stages of development, when both LAI and f_i are low. Gallagher and Biscoe (1978) first suggested this effect on barley and wheat, but it was explicitly studied by Trapani et al. (1992) on sunflower. They found a twofold

BOX 1 Modelling Radiation-Use Efficiency

We used a two-leaf (sunlit and shaded leaf fractions) canopy transpiration and photosynthesis (CTP) model (Kremer et al., 2008) to obtain simulated RUE for maize and wheat. The main features of the CTP model are: (1) partitioning of the canopy in sunlit and shaded fractions; (2) calculation of canopy solar radiation interception and average solar and PAR irradiance; (3) computation of canopy transpiration using a big–leaf approach; (4) calculation of gross photosynthesis by balancing the biochemical capacity for CO_2 assimilation (demand) and the CO_2 flux from the bulk air (supply); (5) calculation of average leaf stomatal conductance as a function of light, temperature, atmospheric CO_2 concentration, air VPD and plant water status; and (7) simulation of plant water uptake and the effect of plant water stress on stomatal conductance. Calculations are made separately for sunlit and shaded leaf fractions, with nested iterations to close the energy balance and conserve the mass balance.

To consider a diverse set of conditions in the simulations, daily weather data from eight locations were selected, encompassing the period day of the year (DOY) 120 through 239 (with proper adjustment for southern hemisphere location), for a year selected at random in seven locations (Concepcion del Uruguay, Argentina; Landriano, Italy; Pullman and Prosser, Washington, USA; Temple, TX, USA; Ankara, Turkey; and Aleppo, Syria), and for DOY 166 through 239 in Maricopa, Arizona, USA. The main climatic characteristics of the selected period at each location are presented in Table 3. We do not imply that the crops are grown or can be economically grown in the locations and periods selected for this exercise. For the CTP simulations, LAI was set to 4 (unless otherwise noted), the root–top biomass partitioning to 0.4 (including carbon rhizodeposition) and soil water content to field capacity, except for simulations involving water stress. These conditions were invariant during the simulations to focus solely on environmental effects on RUE.

Table 3 Average Maximum and Minimum Temperature (T_x, T_n), Solar Radiation (S_t), Maximum and Minimum Relative Humidity (RH_x, RH_n), Wind Speed (WS), Reference Evapotranspiration (ET_o) and Daytime Vapour Pressure Deficit (D_a) for Eight Different Locations and Selected Periods of 4 Months Starting from May and November in the Northern and Southern Hemisphere, Respectively

Location	T_x (°C)	T_n (°C)	S_t ($MJ\,m^{-2}$)	RH_x	RH_n	WS ($m\,s^{-1}$)	ET_o ($mm\,d^{-1}$)	D_a (kPa)
Aleppo 36°1′N 37°18′E 430 m a.s.l.	34.7	17.5	27.2	0.67	0.26	4.8	9.0	2.6
Ankara 40°7′N 32°59′E 948 m a.s.l.	27.9	14.3	21.1	0.63	0.32	1.8	5.0	1.8
Concepción 32°28′S 58°16′W 20 m a.s.l.	27.8	16.9	21.5	0.99	0.65	3.0	4.3	0.8
Landriano 45°18′N 9°15′E, 78 m a.s.l.	26.0	14.2	22.5	0.86	0.47	1.2	4.3	1.0
Maricopa 33 °49′N 112°1′W 359 m a.s.l.	38.9	24.3	27.6	0.79	0.25	2.2	7.7	3.2
Prosser 46°N 119°7′W 380 m a.s.l.	27.0	9.3	25.7	0.62	0.43	1.5	4.8	1.3
Pullman 46°45′N 117°1′W 756 m a.s.l.	22.6	8.4	23.3	0.81	0.33	2.1	4.4	1.1
Temple 31°7′N 97°4′W 208 m a.s.l.	31.2	20.6	21.1	0.92	0.48	2.7	5.3	1.5

increase in RUE when f_i (PAR) > 0.8, compared with canopies with f_i < 0.8. This result contrasts with the theoretical considerations of Sinclair and Horie (1989) and Choudhury (2000) that indicate that this effect is quantitatively marginal; the planophile habit and heliotropic behaviour of sunflower leaves may explain the results of Trapani et al. (1992). Rochette et al. (1995) reported low RUE for soybean when LAI < 1.

Artificially varying the radiation environment above the canopy is rather impractical, but the irradiance normal to the leaf surface can be manipulated through variations in the leaf angle distribution. Less explored is the light scattering produced by the long awns of some cereals such as two-row barley, which can intercept and scatter a large fraction of the incoming radiation, potentially increasing the RUE of the underlying foliage. It has been extensively argued that in canopies with f_i > 0.8 (or LAI~3), vertical leaf angles will increase RUE. Classical references regarding canopy photosynthesis and by implication RUE are the articles by Duncan et al. (1967) and Loomis and Williams (1969). Based on the discussion above, canopies with more vertical leaf angles (a spherical leaf angle distribution is already on the vertical side) are advantageous in locations where the sun elevation or irradiance or the beam component of irradiance are high.

In conditions of no water or nutritional stress and low LAI, it is convenient for crops to intercept as much radiation as possible; therefore, horizontal, non-overlapping leaves are ideal. As LAI and f_i increase, roughly when daily f_i~0.8, there is an advantage of canopies that gradually move from horizontal to more vertical leaf angle distributions. Therefore, the ideotype crop would have a canopy that is mostly horizontal after emergence and gradually switches to vertical as LAI increases. The authors have observed barley and oat genotypes that resemble that behaviour. Under conditions of water stress, the advantage of vertical canopies might not be an increase in RUE but a reduction in radiation interception and therefore in the energy load.

Figure 1 shows simulated RUE for different LAI of a generic C_3 crop at Temple, TX, plotted as a function of the ratio of average projected areas of canopy elements on horizontal and vertical surfaces (x) as defined by the ellipsoidal model introduced by Campbell (1986), where $x = 0$ corresponds to an entirely vertical canopy, $x = 1$ to a spherical or random canopy and $x > 1$ (up to infinity) to progressively horizontal canopies. Campbell and van Evert (1994) suggested x values of 0.8–2.5 for maize, 1 for wheat, 1.2 for barley and

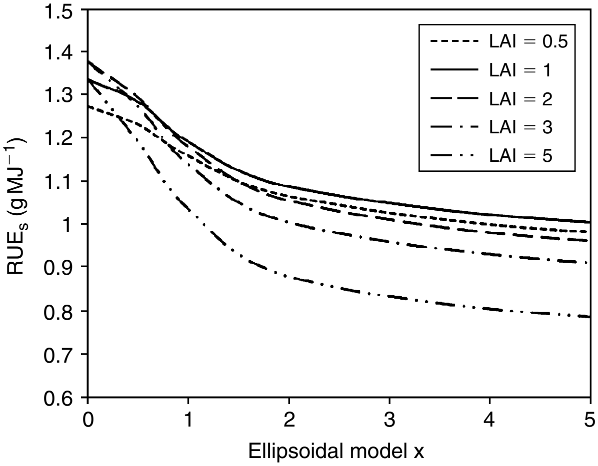

FIGURE 1

RUE of a generic C_3 crop at Temple, TX, simulated by the CTP model for different leaf area indices and x values from 0 to 10, where x is the ratio of average projected areas of canopy elements on horizontal and vertical surfaces as defined by the ellipsoidal model introduced by Campbell (1986), where x = 0 corresponds to an entirely vertical canopy, x = 1 to a spherical or random canopy and x > 1 (up to infinity) to progressively horizontal canopies.

1.4 for sorghum. The figure illustrates the advantage of vertical canopies. It also shows the increase in RUE when LAI increases from initial low values ($0.5\,m^2\,m^{-2}$ in the case of Figure 1) to higher values ($2–3\,m^2\,m^{-2}$), particularly for vertical canopies ($x < 1$).

Although canopy architecture is seemingly a mandatory stop when discussing increases in canopy photosynthesis and RUE (e.g. Reynolds et al., 2000; Long et al., 2006; and references above), caution must be exercised when considering canopy architecture because 'vertical canopy' and 'vertical leaf angle distribution' are often confounded or not clearly defined. Vertical canopies are often used to define canopies with vertical leaves on the top of the canopy that gradually become horizontal towards the bottom of the profile, resembling a yucca plant with 'radiating' leaves (see Figure 1 in Long et al., 2006). This leaf array is hardly vertical but rather strongly anisotropic; however, it can maintain a relatively high RUE while effectively intercepting incident radiation, thus being more desirable than canopies with vertical and isotropic leaf angle distributions.

Overall, despite the fact that canopies optimised for RUE are definable, there are limitations in the manipulation of traits such as canopy architecture due to genetic linkages and pleiotropy, as discussed by Rasmusson (1991) for barley. Chapter 15 (Section 5.1) discusses the role of improved RUE in genetic improvement of yield potential.

6.3. Temperature

Leaf-level photosynthesis has a marked response to temperature. In regular field conditions, leaves may experience a range of temperatures from sub-optimal to optimal to supra-optimal within a single day. The daily pattern of temperature follows that of radiation, with a shift of 1–2 h, and is associated also with the daily variation on VPD. Differences between consecutive days or weeks can be marked due to differences in weather. We show in Table 4 the 10-day average temperature, radiation, daytime VPD and reference evapotranspiration (ET_o) for the typical period of growth of spring crops (barley, wheat, peas, lentils) in the Palouse area of the Pacific Northwest. Intra-year and inter-years variations can be dramatic and are well within the biologically sensitive range for photosynthesis. Leaf temperature is related to atmospheric evaporative demand through the energy balance so that leaves (particularly sunlit leaves) can be a few degrees below air temperature due to evaporative (transpiration) cooling or a few degrees warmer than the surrounding air if transpiration is limited.

Table 4 Summary of Meteorological Conditions[a] for the Growing Season of Spring Crops (Barley, Wheat, Peas, Lentils) for Two Years (2000 and 2001) in Pullman, WA

Calendar Day	Maximum Temperature (°C)		Minimum Temperature (°C)		Solar Radiation ($MJ\,m^{-2}\,day^{-1}$)		Daytime Vapour Deficit (kPa)		ET_o (mm)[b]	
	2000	2001	2000	2001	2000	2001	2000	2001	2000	2001
130	16.9	19.9	5.6	7.2	24.0	19.7	0.8	1.0	41.3	42.5
140	20.1	27.9	9.4	8.7	23.9	28.2	1.0	2.1	48.8	58.1
150	20.1	20.4	7.4	6.3	26.6	22.8	1.0	1.1	47.6	43.5
160	18.1	16.8	7.4	7.4	20.9	23.9	0.6	0.7	37.5	41.4
170	23.7	22.4	8.8	10.2	29.4	23.8	1.3	1.1	54.6	46.1
180	23.6	27.3	9.2	12.3	25.8	28.9	1.3	1.6	49.7	56.2
190	27.3	25.8	7.9	12.4	29.9	24.9	1.8	1.5	55.6	51.9
200	29.6	26.4	11.6	11.1	28.2	25.7	2.1	1.5	58.5	53.3
210	33.4	26.9	13.0	13.0	27.3	23.0	2.9	1.7	60.5	51.5
220	29.6	34.2	9.1	15.8	26.6	24.8	2.5	3.2	56.1	63.7

The data brackets approximately the period from emergence to maturity ±15 days.

[a] *Calendar day indicates the first of a 10-day interval. Temperature, radiation and vapour pressure deficit are averages; ET_o is cumulative.*

[b] *Reference evapotranspiration (Allen et al., 1998).*

Several authors have identified RUE responses to temperature. Andrade et al. (1993) reported a positive response of maize RUE to temperature in the range of 16–21 °C (intercept $= -1.0\,\mathrm{g\,MJ^{-1}}$, slope $= 0.15\,\mathrm{g\,MJ^{-1}\,°C^{-1}}$); extrapolation provides an estimated RUE = 0 at ~7 °C, which is consistent with the base temperature of this crop (Ritchie and NeSmith 1991). Maize RUE seems to stabilise between 20 and 25 °C (Kiniry et al., 1989). Figure 2 shows simulated $\mathrm{RUE_S}$ versus VPD for maize with all data included and data with mean temperature <25 °C excluded. The former shows significant reductions of daily $\mathrm{RUE_S}$ for VPD < 2, mainly due to low temperatures, while the latter shows a more typical correlation between $\mathrm{RUE_S}$ and VPD (Stockle and Kiniry, 1990; Kiniry, 1999).

Brown et al. (2006) reported a temperature response for alfalfa in the range of 6–18 °C with a lower slope than maize (slope $= 0.09\,\mathrm{g\,MJ^{-1}\,°C^{-1}}$) and $\mathrm{RUE_S} = 0$ at 0 °C. In wheat and barley, typical temperatures experienced for spring-grown crops seem to have little effect on RUE. Kemanian et al. (2004) showed that temperature was unrelated to the observed variation in seasonal RUE, with minimum temperature ranging from 9 to 12 °C and the maximum ranging from 23 to 28 °C.

The complexity of factors affecting RUE is inferred from the results obtained by Awal and Ikeda (2003) in peanuts. They found a positive response of RUE to soil temperature in the 21–26 °C range, with RUE = 0 at 10 °C. The exact cause of that response is not clear and may involve interactions with the plant nutritional status or root–shoot relationships. This article also highlights the impact of the root environment on RUE.

Low temperatures can impair photosynthesis due to photoinhibition. In clear-sky days, early in spring, both soil and air temperatures can be low and irradiance can be high, causing photoinhibition (Long et al., 1983). If the temperature–radiation combination causes photoinhibition, RUE should be lower than expected.

6.4. Air humidity

Stomata tend to close with increasing VPD (Schulze and Hall, 1982; Dai et al., 1992) likely due to increasing transpiration (Mott and Parkhust, 1991; Monteith, 1995), providing a simple mechanism for the RUE

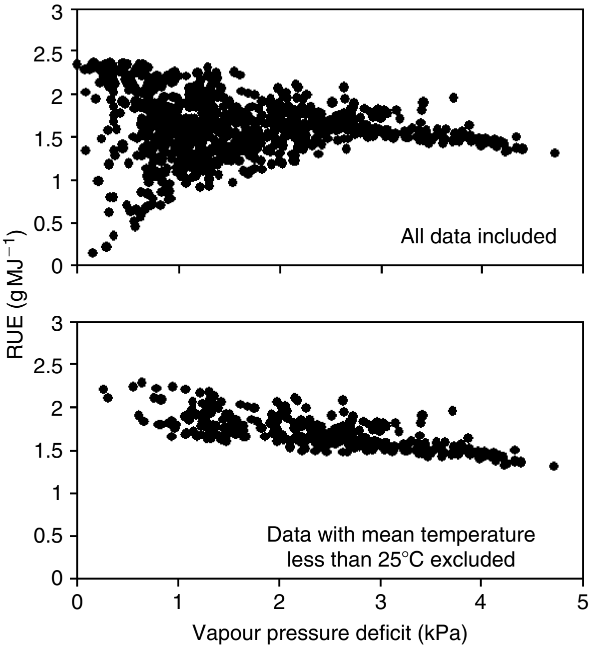

FIGURE 2

Daily RUE versus vapour pressure deficit simulated for maize in eight locations and 120 days per location.

response to air humidity, independent of the effect of radiation level and f_d on photosynthesis. It can also be argued that stomatal closure reflects some degree of water stress, for example, at midday; therefore, what is being observed is simply a decrease in RUE due to water stress (Hammer, personal communication).

There is no known air humidity sensor in leaves that can be manipulated to trigger physiological responses. Stomata respond to a complex net of regulations that maintain a favourable plant water balance and carbon uptake. It is therefore difficult to isolate the effect of air humidity alone under field conditions. Nevertheless, RUE has been found to correlate negatively with VPD (Stockle and Kiniry, 1990; Kiniry, 1999; Manrique et al., 1991), and Kemanian et al. (2004) showed that RUE corrections by temperature, S_t, or f_d did not remove the detected relationship between RUE and VPD. Manrique et al. (1991), on the contrary, found correlations between RUE and S_t, temperature and VPD (Figure 3).

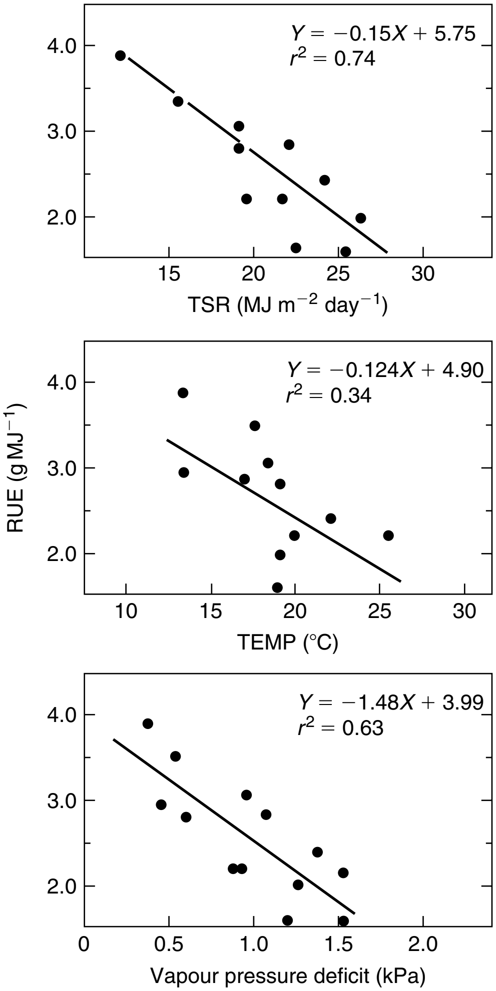

FIGURE 3

Observed RUE of potatoes plotted as a function of total solar radiation (TSR), temperature (TEMP) and vapour pressure deficit (VPD) (Source: Manrique et al., 1991, reproduced with permission).

Figure 4a shows simulated daily wheat RUE as a function of VPD. Although a correlation between the two variables is evident at VPD $>$ 2 kPa, the correlation is weak at lower VPD. When only data with mean temperature $>$ 15 °C and $f_d > 0.84$ (maximum is 0.88) are plotted, the correlation between RUE and VPD is stronger (Figure 4b). Similarly, when plotting RUE against f_d for data with VPD $<$ 1.2 kPa a good correlation also emerges (Figure 4c). This illustrates that both VPD and f_d affect RUE somewhat independently. There is general agreement that it is unlikely that one factor alone would control the expression of RUE. However, using one or two variables to adjust RUE, say f_d and VPD, which indirectly account for other effects (e.g. Figure 3), is a reasonable approach to allow inter-location or inter-year comparisons of RUE and facilitate interpretation of crop performance.

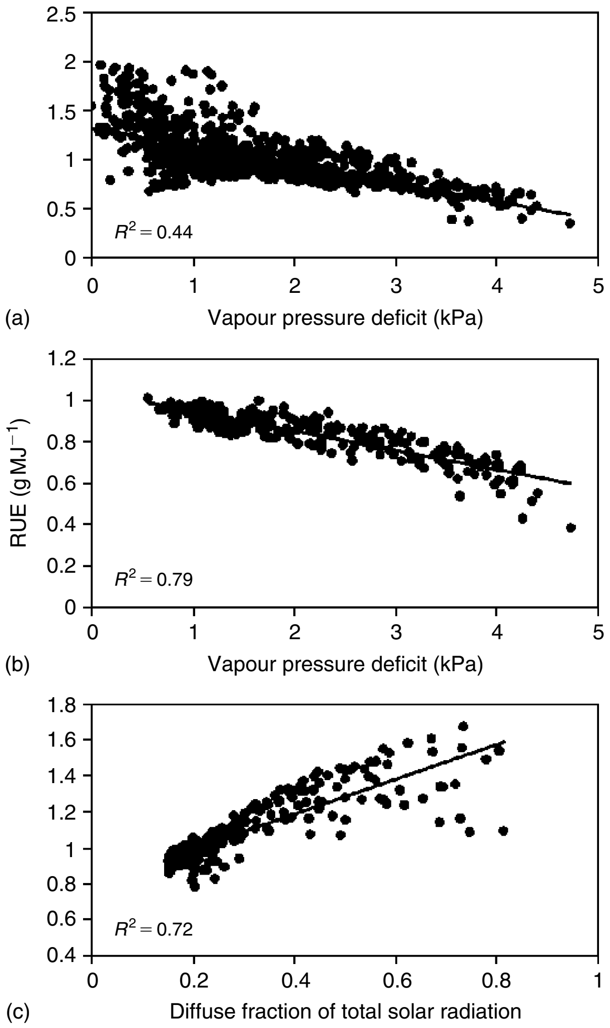

FIGURE 4

Simulated daily RUE of wheat in eight locations and 120 days per location: (a) RUE as a function of vapour pressure deficit using all data, (b) RUE for days with mean temperature > 15°C and a fraction of diffuse radiation > 0.84 as a function of vapour pressure deficit, and (c) RUE for days with vapour pressure deficit < 1.2 kPa as a function of the fraction of diffuse radiation.

6.5. Water stress

Water stress reduces leaf photosynthesis and therefore RUE. Lower RUE under water stress has been reported for barley (Jamieson et al., 1995), sweet corn (Stone et al., 2001), maize (Earl and Davis, 2003) and peanut (Collino et al., 2001). Water stress not only reduces RUE but also affects canopy expansion and therefore radiation capture (Jamieson et al., 1995; Stone et al., 2001).

Crop water status depends on the balance between crop water demand and the supply for transpiration. Water stress can reduce leaf photosynthesis (and RUE) via stomatal and non-stomatal effects. Water stress can cause stomatal closure that limits the supply of CO_2 within the leaf, may enhance photoinhibition since photosynthesis can be impaired by non-stomatal effects under low leaf water potentials and may reduce photosynthesis due to overheating caused by reduced transpirational cooling (Valladares and Pearcy, 1997).

Figure 5 presents the ratio of stressed to unstressed daily wheat RUE as a function of actual to potential transpiration ratio simulated with the CTP model, and shows that RUE reduction due to water stress is not linearly related to the decrease in the actual to potential transpiration ratio, as often assumed. The reason is that, at early stages of water stress, photosynthesis decreases less than transpiration. While stomatal closure reduces transpiration almost proportionally (thermal effects aside), the internal leaf CO_2 concentration also decreases due to photosynthesis, resulting in larger leaf-to-air CO_2 gradient than under no water stress.

6.6. Crop nutritional status

To the extent that nutrition affects net photosynthesis, RUE should decrease under nutritional stress. Based on a theoretical analysis of RUE, Sinclair and Horie (1989) concluded that RUE should decrease as nitrogen stress increases, and that the decrease should be closely linked to a decrease in leaf photosynthetic rate. In agreement with theory, low RUE in nitrogen-stressed crops has been widely documented (Gallagher and Biscoe, 1978; Garcia et al., 1988; Fischer, 1993). A unique response of RUE to nutritional status should not, however, be expected.

The response of maximum photosynthetic rate (A_{max}, μmol $CO_2\,m^{-2}\,s^{-1}$) to the specific leaf nitrogen content (SLN, $g\,N\,m^{-2}$) is well established and is analysed in Chapter 8 (Section 3.2.3). At low light intensity, A_{max} is less relevant at determining the net photosynthesis rate. As LAI increases, more of the radiation transmitted by the sunlit leaf area can be utilised by shaded leaves, which in turn will be operating at non-saturating light intensities. Thus, the RUE response to SLN will depend on LAI. In addition, the nitrogen distribution in the canopy tends to allow an optimal use of light for photosynthesis (Section 3.3.3 in Chapter 8). The upper parts of the foliage, which are more likely to be sunlit, have in general higher SLN (and are younger) than those that are shaded. Thus an average SLN for the foliage does not necessarily

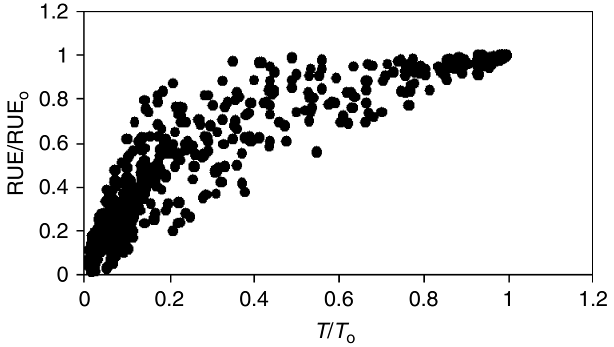

FIGURE 5

Simulated ratio of stressed to unstressed daily RUE of wheat as a function of actual to potential transpiration.

represent with accuracy the SLN needed to calculate RUE. Hammer and Wright (1994) have shown through an elegant simulation analysis that nitrogen distribution within the canopy affects RUE when the average SLN is low.

Phosphorus deficiency may also affect RUE. Rodriguez et al. (2000) found evidence of reductions in plant leaf area of wheat due to phosphorus deficiency affecting both leaf expansion and reduced availability of assimilates for leaf growth, resulting in reductions of 63 and 46% in f_i and 21 and 31% in RUE, 61 days after emergence in non-shaded and shaded plants, respectively. On the other hand, Plenet et al. (2000) reported no effect of phosphorus deficiency on maize RUE, even during the period when shoot biomass accumulation was most severely reduced, with the bulk of this reduction caused by reduced LAI (reduced radiation capture) and not by reduced photosynthesis per unit leaf area.

6.7. Ontogeny and leaf age

Leaf photosynthesis rate has been shown to reach a maximum shortly before or after a leaf reaches its maximum area and then decreases with aging in fescue (*Schedonorus phoenix* Scop. Holub) (Jewiss and Woledge, 1967), cotton (*Gossypium hirsutum* L.) (Constable and Rawson, 1980) and wheat (Suzuki et al., 1987). It is reasonable to assume that this is a general pattern for plants. This decrease in photosynthesis is accompanied by a decrease in leaf conductance (Field, 1987). On the other hand, Frank (1981) reported a small or no effect of age in the photosynthesis of three perennial C_3 grasses: *Agropyron intermedium* var. trichophorum (Link) Halac., *A. desertorum* (Fisch. ex Link) Schult. and *Phalaris arundinacea* L.

Under field conditions and for most annual crops, newer leaves are usually in the sunlit part of the canopy. Therefore, as the growing season progresses, the older leaves gradually occupy shaded portions of the canopy while the younger leaves remain sunlit. In this way, the eventual canopy-aging effect on RUE is somewhat moderated, if not erased altogether. Furthermore, Hikosaka et al. (1994) demonstrated that both leaf age and irradiance affect the leaf nitrogen content and the leaf nitrogen content gradient along the canopy. Thus, the effect of aging can be further ameliorated by the light distribution among the canopy elements.

In barley, Kemanian et al. (2004) reported stable RUE from early tillering to well within grain filling; however, both Calderini et al. (1997) and Foulkes et al. (2001) reported a decrease in RUE after anthesis in wheat. A confounding effect is that spikes of barley were shown to intercept 30–40% of the incoming PAR radiation (Kemanian et al., 2004) and can contribute significantly to canopy photosynthesis (Blum, 1985), taking the role of new photosynthetic elements on top of the canopy during the first half of grain filling. As discussed above, the light scattering produced by the awns can increase f_d and therefore the RUE of the underlying leaves. Thus, at least in annual crops, the effect of leaf age may express late in the growth cycle, without major effects on overall biomass accretion.

Circumstantial evidence that RUE is related to ontogeny is discussed by Hall et al. (1995) in sunflower. The authors found a curvilinear relationship between RUE (biomass corrected for biosynthesis costs) and time after emergence that was not fully related to changes in SLN. They suggested that a variable respiratory load per unit leaf area (and perhaps per unit of stem and root mass) may explain the observed pattern; if that is the case, it points to a major gap in understanding the controls of respiration. If RUE is related to ontogeny, the mechanism behind that response must be understood.

6.8. Biomass partitioning between shoot and root

Most RUE determinations are based on shoot biomass. Fewer RUE estimates use micrometeorological methods that account for the net canopy CO_2 exchange, therefore including root growth and root exudates (Rochette et al., 1996), or include direct root sampling (e.g. Brown et al., 2006; Section 3.3.1 and Table 2 in Chapter 8). Both approaches have caveats: Micrometeorological methods require estimates of microbial soil respiration to compute the crop carbon balance, and root sampling ignores root exudates and root turnover, which can be a significant portion of the crop carbon budget (Amos and Walters, 2006).

In alfalfa, the pattern of plant carbon allocation to above or below ground is markedly seasonal, and RUE determinations based on shoot biomass are grossly misleading, as shown by Brown et al. (2006). The root–shoot partitioning can partially explain relatively low RUE in early growth for annual crops when only sampling shoot biomass. Trapani et al. (1992) found that neglecting sunflower roots led to a RUE underestimation of about 20% during early growth (LAI < 1.7) but of only 4% during the linear growth phase.

Determination of RUE during early growth has received far less attention than after canopy closure. One reason is the difficulty to install radiation sensor bars below small plants, although inversion techniques based on remote sensing can provide accurate estimates of f_i. A second reason is that when RUE is estimated based on cumulative biomass and radiation interception by least square error parameter fitting, low biomass and radiation interception during early growth affect little the parameter estimate. Whenever possible, RUE should be determined for time intervals in which f_i varies little, which indeed is difficult to achieve during early canopy growth. Analysis of RUE during early canopy growth is clearly an area in which research is needed.

6.9. Source–sink control of RUE

Accumulation of unused photosynthetic products in leaves can down-regulate photosynthesis (Paul and Peliny, 2003). It follows that RUE can depend on the capacity of the growing organs and the transport system to deplete the leaves from photosynthetic products. The control or stimulation of photosynthesis during grain filling by a high number of grains per unit leaf area (or per unit leaf mass or per unit of leaf nitrogen) has been discussed earlier by Geiger (1976) and more recently by Reynolds et al. (2005). In fact, the concept applies to any growing organ such as stems and roots.

In both sunflower (Sadras et al., 1991) and wheat (Miralles and Slafer, 1997), RUE seems to be related to the source–sink balance during grain filling, with RUE increasing as that ratio decreases. Broader experimental evidence in this regard is highly desirable. Grain filling offers a relatively simple experimental setup to control the source–sink balance because by artificially modifying the number of growing grains, the source-to-sink ratio is easily altered. Alternative ways of modifying this balance are by increasing the radiation load per unit leaf area while minimising perturbations in the canopy or the root environment. Modifications that allow a large-scale manipulation such as removal of entire rows to increase light penetration also affect the root environment and the energy balance, and less invasive practices such as moving plants to low/high-CO_2 environments may be impractical. The control of RUE by source–sink relationship remains one the most unexplored and interesting aspects of canopy-level control of photosynthesis. It may be the basis of the observed differences in the growth rate of annual and perennial grasses early in the fall in temperate zones – where the growth rates of annual grasses such as oats or barley are much higher than those of orchard grass fescue, phalaris or perennial bromegrass – or the observed differences in RUE corrected by biosynthesis costs of C_3 legumes and grains crops.

7. RADIATION-USE EFFICIENCY RESPONSE TO ATMOSPHERIC CARBON DIOXIDE CONCENTRATION

Atmospheric dioxide concentration has increased since the start of the Industrial Revolution from 275 to the current (2008) ~385 μmol CO_2 mol^{-1} air, and it is expected to reach 550 and 700 μmol mol^{-1} by 2050 and 2100, respectively (IPCC, 2007). As a reference, during the last 420,000 years the atmospheric CO_2 concentration fluctuated between 180 and 300 μmol mol^{-1} (Petit et al., 1999).

Elevated CO_2 concentration increases net photosynthesis of C_3 plants and therefore increases RUE. This results from both rubisco-increased carboxylase and rubisco-reduced oxygenase activity (reduced photorespiration, Gutteridge, 1990). A reduction in photoinhibition may also contribute to the enhancement of photosynthesis under high CO_2 concentration in the C_3 grass *Dactylis glomerata* (Hymus et al., 2001). These effects are much lower in C_4 plants because the (dissolved) CO_2 concentration in the bundle sheath chloroplasts already saturates rubisco. Stomatal conductance decreases in both C_3 and C_4 plants at increased CO_2 concentration (Morison and Gifford, 1983).

Increasing CO_2 concentration from ~350 to 550 μmol mol^{-1} in Free-Air Carbon Dioxide Enrichment (FACE) experiments have shown an average increase in shoot biomass accumulation of ~12% for C_3 grasses, ~3% for C_4 grasses, 24% for clover and 32% for cotton and grape (Kimball et al., 2002). The analysis of FACE experiments by Long et al. (2004) gives an average increase in biomass production of ~20% for C_3 and ~3% for C_4 plants. Kimball et al. (2002) reported a biomass accumulation increase of 8 and 11% for rice in FACE experiments with ample water and nitrogen, but the increase was 17 and 14%, respectively, when very high N treatments were included. Specific data on RUE changes in response to elevated CO_2 concentration are mostly not available, and observed biomass increases can be partially attributed to increases in radiation capture and RUE. The increase in biomass production and RUE for FACE-grown cotton was 32±1 and 28±1%, respectively (Kimball et al., 2002).

Figure 6 presents relative changes of RUE for wheat and maize simulated with the CTP model for two contrasting locations (Landriano, low VPD, and Aleppo, high VPD) as CO_2 concentration raises from a baseline of 365 to 700 μmol mol^{-1}. As expected, RUE of wheat shows important increases in response to CO_2 concentration in both locations, while the increase for maize is much lower. At a CO_2 concentration of 550 μmol mol^{-1}, the CTP model simulated increases of 17 and 27% for wheat in Landriano and Aleppo, respectively, and 3 and 4% for maize. The increase in RUE for wheat is larger than the 12±1% increase reported by Kimball et al. (2002) for wheat with ample water and nitrogen, but in agreement with overall increase of 20% reported for C_3 plants by Long et al. (2004). Simulated RUE increases for maize are in agreement with FACE data. The larger RUE increase in Aleppo results from already reduced stomatal conductance due to high VPD that minimises additional reduction due to elevated CO_2 concentration, thus taking advantage of the larger CO_2 gradient. There is evidence that plants may acclimate to growth in elevated CO_2 concentration due to the loss of rubisco amount and activity, although this loss appears to cause no or very little loss of stimulation of photosynthesis across FACE experiments (Long et al., 2004).

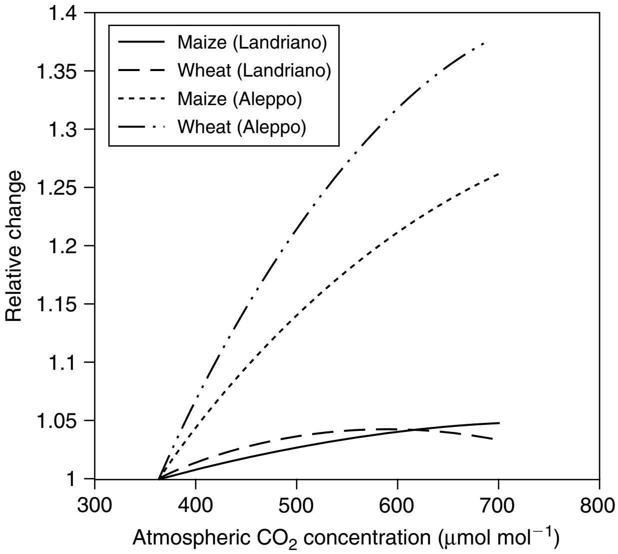

FIGURE 6

Relative change of RUE for wheat and maize simulated with the CTP model for two contrasting locations (Landriano, low VPD, and Aleppo, high VPD) as CO_2 *concentration increases from a baseline of 365–700* μ*mol mol*$^{-1}$.

Using the initial slope of change for wheat in Figure 6, we can estimate that RUE may have increased 6 and 9% from 1975 to 2008 in high-humidity (Landriano) and low-humidity (Aleppo) sites, respectively. These do not represent very large changes but add uncertainty when comparing RUE reported in the literature. If these changes were to translate directly into yield increases, it means a background yield increase of ~2% per decade in C_3 crops; this rate of increase gradually levels off as CO_2 saturates rubisco.

8. IMPROVING RADIATION CAPTURE AND USE EFFICIENCY: AGRONOMY AND BREEDING

As in any economic activity, farming seeks to increase profits and reduce risks. When these objectives align with increasing physical production, improvements in radiation (or water or nutrients) capture and use efficiency are critical. This can be achieved, at least in principle, through improved management or through the use of superior cultivars. While the resource capture and use efficiency framework is helpful from a crop physiology perspective, the farming systems management is substantially more complex, for it involves socio-economic, agronomic and environmental considerations. Breeding programs focus in general on improving yield or quality attributes for one species. For farming systems researchers, who can be thought as farming systems breeders, cultivar selection is one more option to improve resource capture and use efficiency. Cultivar choice is in many instances subordinated to weed and disease control or other aspects of the enterprise (Chapters 2–5).

The economic yield Y can be increased by gains in HI, RUE_S and $f_{is}S_t$ (Eq. 1b). Increases in one component, say $f_{is}S_t$, can be compensated by losses in other components, say HI. Annual crops well supplied with water and nutrients intercept approximately 55–60% of the incident solar radiation during the growing season (Figure 7). Increasing $f_{is}S_t$ during early growth can be achieved by several means through agronomic management and breeding. Increasing fertilisation rate and plant density or distributing plants more regularly (e.g. narrow rows) can accelerate canopy closure, but excess early growth may lead to decreases in HI. Individual cohorts (plants, tillers) require a minimum size or growth rate to produce reproductive structures (e.g. Vega et al., 2000); therefore, an excessive number may decrease HI. Furthermore, early use of limited water

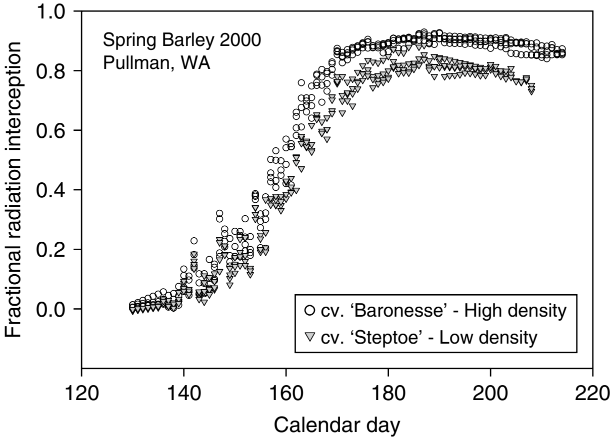

FIGURE 7

Fractional radiation interception of two cultivars of spring barley during the 2000 growing season in Pullman, WA. The first days of radiation interception were interpolated from actual measurements. Radiation below the canopy was measured continuously with tube solarimeters (see Kemanian et al., 2004 for details). Baronesse intercepted 60% and Steptoe 54% of the incident radiation from emergence to maturity.

may cause post-anthesis stress and low HI (Passioura, 1977; Sadras and Connor, 1991; Kemanian et al., 2007; Section 5 in Chapter 6). Provided that water is available, a longer growing season may allow larger $f_{is}S_t$ and increases in yield. In the inland Pacific Northwest of the United States, the six-row and short-cycle cultivar of barley 'Steptoe' was displaced by the higher-yielding two-row cultivar 'Baronesse' (an introduction from Germany), which has longer cycle, similar RUE and lower HI than Steptoe (Kemanian et al., 2004).

An important concept rarely acknowledged in the literature is the distribution of the intercepted radiation among plants or cohorts. In individual plants, HI increases sharply above a threshold minimum biomass required for producing seeds and then tends to decrease in the largest plants (Vega et al., 2000) with differences among species. In species that tiller aggressively, it is better to consider each cohort rather than each plant, but the concept still applies. Crop plants or tillers with uneven sizes may render low HI. It follows that it is more convenient to distribute light homogenously among cohorts than to concentrate interception in main tillers, a difficult task for it involves concerting the dynamics of tiller appearance, leaf area growth and canopy architecture. Increases in early vigour in wheat have been proposed as a way to increase early radiation interception, reduce soil evaporation and increase transpiration (Richards and Townley-Smith, 1987; Regan et al., 1992). This approach may be adequate in some environments, but this must be achieved by distributing radiation homogenously among tillers to preserve or improve the HI. In practical terms, it implies minimising the main tiller shading of the new tillers, which can be achieved by both more upright leaves and by tillers that 'escape' the shade of existing leaves and tillers. The mathematical modelling of radiation interception by individual tillers and leaves within a tiller is complex but largely feasible, and the subtleties of within-plant light distribution are hidden when considering canopy-level properties such as the extinction coefficient. A better understanding of desirable canopy architecture traits during early growth is a promising avenue for increasing radiation capture without sacrificing RUE and HI.

Increasing RUE is another avenue to increase productivity. As discussed above, RUE should gradually increase in response to the rise in atmospheric CO_2 concentration, particularly in C_3 crops. It is convenient to separate the analysis of RUE improvements in situations with and without water (or nutrients) stress. RUE is related to water and nutrient (generically represented by X_n) use efficiency as follows:

$$\mathrm{RUE_S} = \mathrm{TUE}\,\frac{T}{f_{is}\,S_t} \tag{3}$$

$$\mathrm{RUE_S} = X_n\mathrm{UE}\,\frac{X_n}{f_{is}\,S_t} \tag{4}$$

where TUE is transpiration use efficiency (kg B kg^{-1} H_2O), T transpiration (kg $H_2O\,m^{-2}$) and X_nUE the use efficiency of nutrient X_n (kg B kg^{-1} X_n). The ratio of T to f_iS_t reflects the fraction of net energy absorbed by the canopy partitioned to latent heat (in energy terms, it is around 0.55–0.7 J J^{-1} at VPD~1 kPa in crops well supplied with water), and is therefore an indication of canopy conductance.

When water is not limiting, $\mathrm{RUE_S}$ can be increased by increasing TUE or T or by reducing f_iS_t, while maintaining the other factors constant. The latter option should be discarded as reducing radiation interception will likely penalise B (Eq. 1a). To increase T while maintaining TUE constant implies, essentially, a higher stomatal conductance while maintaining c_i constant, thus increasing net canopy photosynthesis. To increase TUE while maintaining T constant implies a lower c_i and a higher net photosynthetic rate. In a study in sunflower, Sadras et al. (1991) found genetic differences in RUE among hybrids in the post-anthesis phase, and this difference was associated to lower c_i, given that the ratio $T(f_iS_t)^{-1}$ did not vary among hybrids.

Systematic analysis of the alternatives to increase photosynthesis are presented by Reynolds et al. (2000) and Long et al. (2006, their Table 3 and related discussion). Long et al. (2006) strongly argued for decreases in c_i through genetic engineering by reducing the oxygenase activity of rubisco, increasing rubisco catalytic activity, reducing the time of recovery from the xanthophylls-driven photoprotection of photosystem II in the thylakoid and increasing capacity to recover ribulose biphosphate. Long et al. (2006) speculated that these changes can collectively increase RUE by 50%, and that such improvement can be introduced in commercial cultivars in <20 years. These figures seem rather optimistic, and one is left to ponder why mutation and DNA recombination and subsequent natural selection have not already rendered such benefits in terrestrial plants (Box 1 in Chapter 9). Other authors are more cautious (Sinclair et al., 2004). Although we do not advocate for direct selection for RUE, there is no advance in considering a complex trait such as RUE intractable; improvements from genetic engineering and from traditional breeding are to be expected by dissecting the traits that ultimately control RUE.

Gains in RUE can be indirectly obtained by decreasing the source-to-sink ratio. This argument was developed by Reynolds et al. (2000) and has been briefly discussed above. Borrás et al. (2004) presented a strong case for sink limitation of yield during post-anthesis, particularly in wheat, which implies that under some circumstances, the photosynthetic machinery is idling. A decrease in the source-to-sink ratio can be obtained by an increased demand for stem, spike or grain growth, and in forage crops, through the number and size of growing meristems.

When water is limiting, increasing RUE is directly linked to an increase in TUE, but increases in grain yield are likely related to increases in HI. Under Mediterranean-like conditions, in which crops will have some degree of water stress during flowering or grain filling and rely on stored water, a balance must be found between using the water for growth and saving the water for grain filling to preserve the HI. The seasonal management of RUE (and TUE) rather than the growing season RUE seems more relevant; for TUE, this has been addressed by Condon et al. (1993, 2002) for wheat in southern Australia. When both water shortage and water excesses are rather unpredictable, or predictable but with an even frequency, options are more limited and a defensive management to minimise losses seems in order. Simulation modelling can help define the probability of water stress and systematically explore management options to increase RUE (Chapman et al., 2003; Chapter 10).

The quantification of radiation capture and RUE provides a useful framework for generalised analyses of crop productivity. However, its use for in-depth assessment of crop performance or to evaluate the progress of breeding programs in providing productivity gains can be confounded by numerous factors and limitations of field measurements already discussed. An excellent example of a thorough RUE analysis is that of Hall et al. (1995) in sunflower. These authors compared expected modelled and measured RUE, showing weaknesses in the cross-level compatibility between leaf-level photosynthesis and RUE as proposed by Sinclair and Horie (1989). A good example of RUE used for hypothesis-driven research was presented by Sadras et al. (2005). The authors proposed testable hypotheses regarding resource capture versus resource use efficiency to explain soil compaction effects on wheat growth. Straightforward and thoughtful approaches like this can greatly facilitate the interpretation of agronomic experiments.

9. CONCLUDING REMARKS

Separating RUE and radiation capture provides a transparent and robust framework for crop growth analysis and treatment comparisons. Major differences in the physiology of C_3, C_4 and legume crops are captured in the maximum RUE for different species. The radiation capture and RUE framework also offers a simple way of simulating crop growth by modelling biomass accrual as the product of intercepted radiation and RUE, provided that environmental and other factors affecting RUE are considered. For agronomic or breeding applications, the use of that framework provides a powerful tool for comparison among treatments on the same location; comparisons among locations require more caution but are still feasible.

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CHAPTER 8

Quantifying Crop Responses to Nitrogen Deficiency and Avenues to Improve Nitrogen Use Efficiency

Gilles Lemaire and F. François Gastal

1. INTRODUCTION

Over the last 40 years, the worldwide use of mineral N fertilisers increased sevenfold in parallel with the doubling of agricultural food production. The use of N fertilisers in agriculture is therefore one of the key elements for producing sufficient food to meet the demand of increasing human population (Angus, 2001; Eickhout et al., 2006). Nevertheless, production of N fertilisers through the Haber–Bosch process is extremely consuming in fossil energy with large emission of greenhouse gases. Moreover, the use of large amount of N in intensive agricultural systems has led to important environmental impacts such as the eutrophication of freshwater (London, 2005) and marine ecosystems (Beman et al., 2005) and gaseous emission of N oxides and ammonia into the atmosphere (Ramos, 1996; Stulen et al., 1998) through nitrogen cascades (Galloway and Cowling, 2002). Problems associated with climate change, biofuel production and global food security also question the efficiency of use of N fertiliser in agricultural systems (Cassman, 2007).

For many years, a relatively high grain-to-fertiliser price ratio, particularly in subsidised agricultural systems, incited farmers to apply excess N to allow for high yield and profit. This assurance strategy led to a progressive increase in soil N accumulation and an elevated risk of N leaching (Addiscott et al., 1991). This effect, combined with the long residence time of N within the soil organic matter suggests that the pollution of ground water that we observe today could well be the delayed consequence of the intensification of cropping systems one or two decades ago (Mariotti, 1997). Adoption of a more restricted strategy for supply and timing of N fertilisers on crops is difficult because we have a limited capacity to predict weather, which determines both soil N mineralisation and crop growth potential. In most of the agricultural area in the world, uncertainty of rainfall is an important factor for decisions related to fertiliser application (see Section 2 in Chapter 19) either for lack of rainfall reducing crop growth and soil N mineralisation or for excess of rainfall increasing the risk of nitrate leaching (Sadras, 2002; Sadras and Roget, 2004; de Koeijer et al., 2003; Cabrera et al., 2007). In consequence a reduction in N application rates to avoid excess of N in soils would increase the likelihood of temporary crop N deficiency, that is when soil N availability does not meet plant N demand. Management techniques and breeding approaches to improve N use efficiency are required under both conditions that favour over-fertilisation, for example subsidised economies, intrinsically high fertility, high grain-to-nitrogen price, and systems where shortage of nitrogen is chronic, for example semi-arid and arid regions in poorer countries. Therefore, understanding the processes that govern crop N uptake and distribution in plants is of major importance for optimising crop production with the use of minimum N input to reduce environmental hazards (Cassman et al., 2002).

For most of the crop species, the plant life cycle can be simplified into two main phases: (i) the pre-anthesis phase, when plant develops its leaf area and root system, and young developing leaves and roots behave as sinks, and (ii) the reproductive phase after anthesis, when senescing leaves are sources of carbohydrates and reduced N for developing storage organs such as seeds, fruits or tubers. Therefore, we need a better understanding of the control of N uptake and N partitioning within the plant during these two distinct phases. First, it is necessary to evaluate the dynamics of plant and crop N demand in relation to growth potential during the crop cycle. In a second stage, it is necessary to analyse the physiological and morphological responses of the plant to N deficiency. A better understanding of the regulatory mechanisms controlling these responses to N deficiency at both plant and crop levels should allow the identification of plant physiological and morphological traits which can be used to improve the efficiency in the use of nitrogen through both breeding and crop management (Good et al., 2004).

This chapter develops the case for the ecophysiological understanding of the drivers of plant and crop N nutrition. This focus means that important aspects of the nitrogen economy of crops are beyond the scope of this chapter. Biological fixation is not treated per se as a symbiotic process, but it is shown that once within the plant, biologically fixed N behave exactly as N originating from mineral N absorption (Oti-Boateng et al., 1994; Peoples and Baldock, 2001; Kahn et al., 2002). Chapter 9 (Section 6) deals with N_2-fixation from the viewpoint of evolutionary conflict, that is traits that maximise microbe fitness are not necessarily those that maximise host-plant fitness involving microbial mutualists. The dynamics of N in soil is also not directly considered here (see Powlson et al., 1992; Mary and Recous, 1994; Murphy et al., 2003; Garnier et al., 2003). Another important point not discussed within this chapter is the interactions between plant N nutrition and biotic stresses; readers can refer to White (1993) and Waring and Cobb (1992) for plant–insect interactions and to Delin et al. (2008) for fungal diseases. Chapter 18 (Section 6) discusses the effects of nitrogen supply on crop–weed interactions and nutrient-use efficiency.

This chapter develops a general theoretical framework of the regulation of N uptake and distribution at two levels of organisation: the individual plant and the plant population (i.e. the crop). The aim is to identify the buffering effect on some physiological traits when scaling up from organ to whole plant and to crop. From this theoretical framework, we derive a functional tool for the determination of N status of plant and crop, and then to quantify the degree of N deficiency. Using this diagnostic tool we analyse quantitatively the response of important physiological processes to N deficiency. In the final section, we examine the concept of nitrogen use efficiency (NUE) in the light of the theory developed; avenues for improving NUE through plant breeding and agronomic strategies are identified.

2. CROP N DEMAND: ITS REGULATION AT PLANT AND CROP LEVELS

In this section we develop a general framework based on both empirical relationships and theory that allows for the regulation of plant N uptake in relation to plant growth potential and soil N supply. From this general framework, a diagnostic tool of plant and crop N status is derived to quantify the intensity and the timing of N deficiency during the crop developmental cycle.

Crop N demand at any time of the crop cycle can be defined as the result of maximum crop mass and the critical plant N concentration. The critical plant N concentration is defined as the minimum plant N concentration corresponding to maximum crop mass (Greenwood et al., 1990). Thus, crop N demand corresponds to critical N uptake that is the minimum crop N uptake necessary to achieve maximum crop mass. This concept of critical N can be applied in dynamic terms, such that the daily crop N demand (or critical N uptake rate) is the quantity of N required each day for the crop to maintain its potential growth rate over a given period of time. This dynamic approach of crop N demand has been used extensively on perennial forage crops such as alfalfa and grasses (Lemaire and Salette, 1984a, b; Lemaire et al., 1985) and further extended to annual crops such as wheat (Justes et al., 1994), maize (Plénet and Lemaire, 1999) and canola (Colnenne et al., 1998). All these studies bring convergent results that have been assembled within consistent theory (Greenwood et al., 1990; Lemaire and Gastal, 1997; Gastal and Lemaire, 2002).

2.1. N dilution and N uptake dynamics

The N dilution process within growing crop has been initially approached empirically by plotting plant or crop N concentration with plant or crop mass. Further a theoretical framework is presented to provide eco-physiological evidence supporting such empirical relationships.

2.1.1. Empirical approach

The actual plant N concentration in a crop stand declines even under favourable N supply as the crop mass increases (Greenwood et al., 1986). This decline can be described empirically by a negative power function (Lemaire and Salette, 1984a,b) relating plant N concentration ($\%N$) to crop mass (W in $\mathrm{t\,ha^{-1}}$) during the vegetative growth period (before anthesis):

$$\%N = aW^{-b} \tag{1}$$

The coefficient a represents the plant N concentration for $W = 1\,\mathrm{t\,ha^{-1}}$. Its value depends on the level of steady-state N supply and should also be affected by the species considered. Coefficient b is dimensionless and it represents the ratio between the relative decline in plant $\%N$ and the relative crop growth rate. From Eq. 1 it is possible to derive the relationship between crop N uptake (N) and crop mass (W) during the vegetative growth period of crops:

$$N = a'W^{1-b} \tag{2}$$

The coefficient a' corresponds to the crop N uptake for $W = 1\,\mathrm{t\,ha^{-1}}$. Its value is equal to $10a$ when N is expressed in $\mathrm{kg\,ha^{-1}}$. So, as for a, a' depends on the rate of the steady-state N supply of the crop. The allometric coefficient $1 - b$ is the ratio between the relative N uptake rate and the relative growth rate of the crop.

When N supply is maintained at the minimum necessary for achieving the maximum crop growth rate during all the crop growth period, then it is possible to define the critical N dilution curve:

$$\%N_c = a_c W^{-b} \tag{3}$$

where a_c is the critical plant $\%N$ for a crop mass of $1\,\mathrm{t\,ha^{-1}}$. An example of the determination of the critical dilution curve for a maize crop is represented in Figure 1. In the same way it is possible to define the evolution of critical crop N uptake:

$$N = a'_c W^{1-b} \tag{4}$$

where a'_c is the critical crop N uptake for a crop mass of $1\,\mathrm{t\,ha^{-1}}$.

The values of coefficients a_c or a'_c and b have been established for the main cultivated species according to the method developed by Justes et al. (1994) (Table 1). For a given species coefficients a_c (or a'_c) and b remain constant in a large range of climatic conditions. Lemaire et al. (2007) showed that for wheat, maize, canola, sorghum and sunflower the coefficients of Eq. 4 established in temperate conditions hold in sub-tropical situations. So coefficients a_c and b can be considered as a crop species characteristic. Coefficient b varies between 0.25 for canola and 0.52 for rice with a majority of values around 0.30–0.40 as for perennial grasses, alfalfa, pea, maize and sorghum (Table 1). Due to uncertainty in the determination of b, a common average of 0.35 is proposed. No clear differences appear between C_3 and C_4 species neither between monocots and dicots.

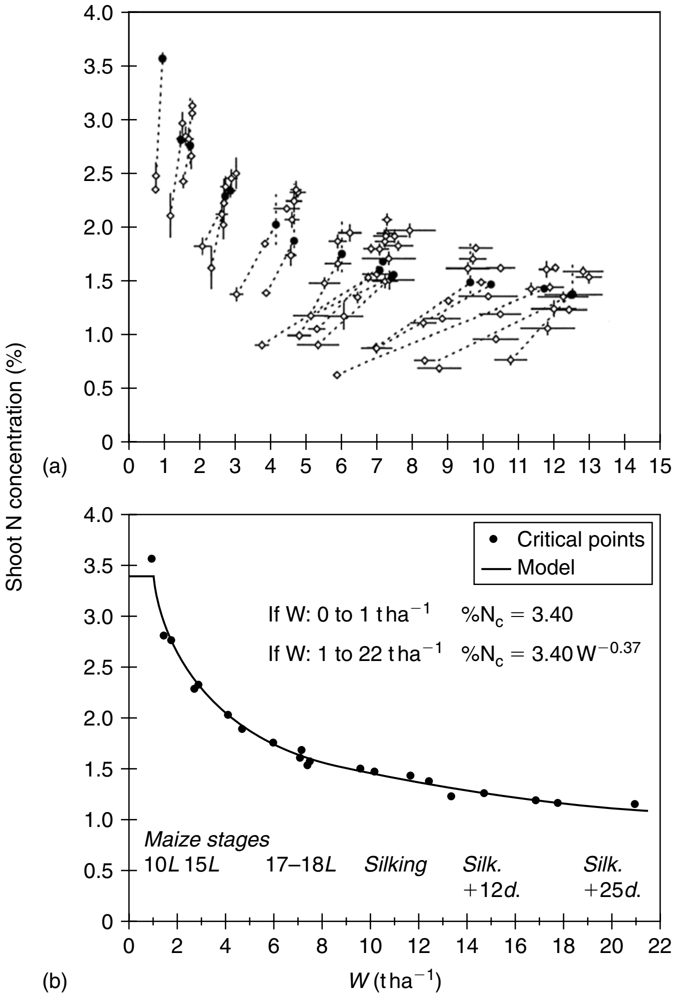

FIGURE 1

Determination of the critical dilution curve from data obtained with different N fertilisation rate experiments in maize. (a) Open symbols are the different experiments. Dark symbols are the critical N concentration calculated as the intersection of the oblique line representing response of crop mass to increased plant N concentration and the vertical line representing the increases in plant N concentration without any increase in crop mass (accumulation of excess of N). (b) The critical dilution curve of maize. (Source: Plénet and Lemaire, 1999.)

The coefficient a_c is lower in C_4 than in C_3 species, in correspondence with the difference in leaf N content according to the difference in photosynthetic pathway (Brown, 1978). Within each of the metabolic groups it is difficult to observe clear differences between species, as pointed out by Greenwood et al. (1990). Due to the tendency to have correlation between a_c and b, Eqs 3 and 4 are relatively close together for species of the same metabolic group (Gastal and Lemaire, 2002).

Table 1 Coefficients a_c and b of the Critical Dilution Curve $\%N = a_c W^b$ for Different Crop Species

Crop Species	a_c (kg N ha^{-1})	b (Dimensionless)	References
Temperate grasses (C3)	4.8	0.32	Lemaire and Salette (1984a, b)
Lucerne (C3)	4.8	0.33	Lemaire et al. (1985)
Pea (C3)	5.1	0.32	Ney et al. (1997)
Wheat (C3)	5.3	0.44	Justes et al. (1994)
Canola (C3)	4.5	0.25	Colnenne et al. (1998)
Rice (C3)	5.2	0.52	Sheehy et al. (1998)
Tomato (C3)	4.5	0.33	Tei et al. (2002)
Maize (C4)	3.4	0.37	Plénet and Lemaire (1999)
Sorghum (C4)	3.9	0.39	Plénet and Cruz (1997)
Tropical grasses (C4)	3.6	0.34	Duru et al. (1997)

Crop *N* demand can be analysed in dynamic terms at daily intervals. The derivative of Eq. 4 relates the daily crop *N* demand to the daily crop growth rate:

$$\frac{dN}{dt} = \frac{dN}{dW}\frac{dW}{dt} = a_c(1-b)W^{-b}\left(\frac{dW}{dt}\right) \tag{5}$$

Hence the daily crop N demand follows the daily crop growth rate, but for a similar daily crop growth rate, the daily crop N demand declines as the crop mass *W* increases.

In conclusion, for a given species at any moment of its vegetative growth period:

- **(i)** the dynamics of the crop dry matter accumulation determines both the critical plant %*N* and critical N uptake;
- **(ii)** crop growth rate determines crop N demand;
- **(iii)** the relationship between critical crop N uptake (the crop N demand) and crop growth rate is fairly independent of external variables such as soil and climate;
- **(iv)** this relationship is slightly variable among species of the same metabolic group, but it reflects the metabolic difference between C3 and C4.

2.1.2. Physiological principles

Greenwood et al. (1990) and Lemaire and Gastal (1997) developed a theory to account for the empirical observations in Section 2.1.1. Following the assumption of Caloin and Yu (1984), plant mass *W* is composed of two compartments: (i) W_m, the metabolic tissues directly involved in plant growth processes (photosynthesis and meristematic activity) with a high N concentration ($\%N_m$), and (ii) W_s, the structural tissues necessary for plant architecture with a low N concentration ($\%N_s$). Then

$$W = W_m + W_s \tag{6}$$

and the plant N concentration (%N) is

$$\%N = \frac{1}{W}(\%N_\mathrm{m}W_\mathrm{m} + \%N_\mathrm{s}W_\mathrm{s}) \tag{7}$$

If we assume that W_m increases allometrically with W, then

$$W_\mathrm{m} = kW^{\alpha} \tag{8}$$

and

$$\%N = k(\%N_\mathrm{m} - \%N_\mathrm{s})W^{\alpha-1} + \%N_\mathrm{s} \tag{9}$$

Equation 9 represents a negative power function between plant N concentration and crop mass provided that $\alpha < 1$ and is equivalent to the empirical relationship of Eq. 2. The main difference between the empirical and theoretical models is the small positive asymptote ($\%N_\mathrm{s} \approx 0.8\%$) in Eq. 9, but the difference between the two equations is small (Lemaire and Gastal, 1997). Hence $\alpha - 1$ in Eq. 9 is close to $-b$ in Eq. 1.

Following Hardwick (1987) and considering that W_m is dominated by photosynthetic tissues, it is postulated that W_m scales with plant area. It is then possible to establish an allometric relationship between leaf area index, LAI, and W:

$$W_\mathrm{m} = p(\mathrm{LAI}) \tag{10}$$

and according to Eq. 8:

$$\mathrm{LAI} = \frac{k}{p}W^{\alpha} \tag{11}$$

The coefficient k/p is the LAI for $W = 1\,\mathrm{t\,ha^{-1}}$ that corresponds also to the leaf area ratio (LAR) at this crop stage. It has been called 'leafiness' coefficient by Lemaire et al. (2007), representing the intrinsic plant shape and architecture through its LAR. When the crop develops, Eq. 11 predicts a decrease in the plant LAR with W, this decline being more or less rapid depending on plant density. Lemaire et al. (2007) have compared α in Eq. 11 and $1 - b$ in Eq. 4 for different crops such as maize, sorghum, wheat, canola and sunflower, growing in sub-tropical and temperate environments near the critical N status. They concluded that $\alpha \approx 1 - b$; with this assumption, a relationship between crop N uptake dynamics and LAI expansion was derived from Eqs 2 and 11:

$$N = \frac{a'p}{k}\mathrm{LAI} \tag{12}$$

Such proportionality between N uptake and LAI has been empirically observed for wheat (Sylvester-Bradley et al., 1990; Grindlay et al., 1993) and alfalfa (Lemaire et al., 2005). Jamieson and Semenov (2000) used such a relation for modelling N uptake of wheat crops. Lemaire et al. (2007, 2008) showed that the coefficient of proportionality between crop N uptake and LAI depends not only on crop N status through coefficient a', but also on plant shape and architecture through the leafiness coefficient k/p that is very variable among crop species. Equation 12 therefore has a less general use than Eq. 2 for simulation of crop N demand. Lemaire et al. (2007) wondered if the dynamic of N uptake (or of N dilution) is dominated by crop mass accumulation (Eq. 2) or LAI expansion (Eq. 12). They concluded that both are incomplete representations of the same global process. For the same crop mass increment, the corresponding increment in N uptake should not be exactly the same if this biomass is mainly composed of leaf tissue (high W_m content) or stem tissue (high W_s content). This accounts for the finding by Angus (2007) that phenologic stages that govern leaf/stem ratio in wheat have an important influence of N dilution curves when comparing cultivars with different timing of stem elongation.

Lemaire et al. (2005, 2007) showed that the dilution of N with plant growth in isolated plants was less marked than for plants in dense stands. These authors showed that $1 - b$ and α from seedling emergence until LAI≈1, that is the period where the plants can be considered as near isolated, are in a range 0.90–0.95, indicating a low decrease in plant %*N* and LAR with increasing plant mass. For LAI > 1, as competition for radiation increases, both $1 - b$ and α decline rapidly to a common value of 0.60–0.70 indicating a parallel acceleration of both plant %*N* and LAR decreases, as shown in Figure 2 for wheat. Theoretically, coefficient α in Eq. 11 should be two-thirds if three conditions are met: (i) plant mass *W* scales with plant volume, (ii) plant mass per unit volume is constant and (iii) plant growth is isometric, that is the plant grows with the same relative rate in the three dimensions (Niklas, 1994). Lemaire et al. (2007) provided evidence favouring the notion of $\alpha \approx 2/3$ for the majority of crop species.

For isolated plants, α is a little bit lower than 1; $\alpha = 1$ would have implied that the plants grew only in two dimensions, that is in area but not in height or in thickness. The value of 0.90–0.95 indicates that plants tend to optimise their leaf area expansion when they are near isolated, while in a dense stand, plants invest more in the third dimension allowing for the placement of their leaves within the illuminated layers at the top of the canopy. As the growth in the third dimension, that is in height, implies more structural tissues with low N concentration, the decline in plant %*N* is accelerated as the radiation environment changes in growing canopies (Pons et al., 1989; Tremmel and Bazzaz, 1995). So, one of the causes of the plant %*N* decrease with increasing crop mass is the architectural and morphological changes of plants in response to the presence of neighbours.

Early plant-to-plant interactions are related to the perception of the presence of neighbouring plants via changes in light spectrum including sensing red:far red ratio (R:FR) of light by phytochrome and blue light

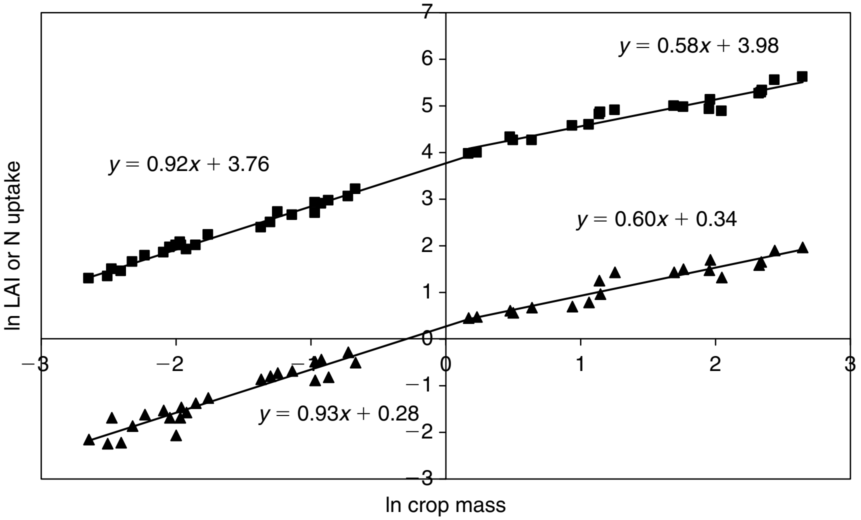

FIGURE 2

Relationships between LAI (▲) or N uptake (■) and crop mass in an ln–ln scale ($R^2 > 0.91$). Data for vegetative wheat crops grown under non-limiting N supply. (Source: Lemaire et al., 2007.)

by cryptochrome (Ballaré et al., 1995, 1997). This allows plants to anticipate competition for radiation through modifications of their architecture (tillering, internodes and petiole elongation, size of sheath and lamina) and strategies for shade avoidance (Aphalo and Ballaré, 1995; Bahmani et al., 2000; Héraut-Bron et al., 1999; Gautier et al., 1998). This response leads to an increase in the proportion of structural tissues (W_s), and then to an acceleration of the N dilution process as crop mass increases.

Another cause of the N dilution is the decrease of N concentration of shaded leaves as the canopy develops. The vertical pattern of foliar N is associated with the light extinction in the canopy and has been interpreted in terms of optimisation of canopy photosynthesis, as discussed in Section 3.3.3.

In conclusion, this theoretical framework shows that the N dilution process operates at different levels of organisation: the organ (e.g. leaf and stem), the whole plant and the canopy. N dilution has to be considered as an ontogenetic process and its expression in terms of crop mass accumulation allows an overall simple representation of complex processes. In this way, critical N dilution curves generically capture most of the environmental sources of variation as well as variations among the metabolic groups C_3 and C_4.

2.2. Co-regulation of plant N uptake rate by both N soil availability and plant growth rate potential

The empirical approach described in Section 2.1.1 seems to indicate that plant growth itself regulates plant N uptake. This appears contradictory with physiological processes indicating that plant growth is the consequence of plant N uptake and not the reverse. To reconcile these two points of view we have to consider that (i) plant N uptake is directly related to N availability to roots, and then to N supply in soil, and (ii) plant N uptake is also feedback controlled by the crop growth rate. As reviewed in Lemaire and Millard (1999) plant N uptake is feedback regulated by shoot N and C signalling irrespective of the source of soil N, that is nitrate, ammonium or N_2 fixation (Ryle et al., 1986; Gastal and Saugier, 1989; Tourraine et al., 1994; Oti-Boateng et al., 1994). A positive regulation comes from a C signal corresponding to photosynthetic assimilate transported by phloem from leaves to roots, and a negative signal comes from organic N re-circulated from shoots to roots (Lejay et al., 1999; Forde, 2002). This latter regulation acts as an N satiety signal, repressing the N uptake of the plant when its capacity to store organic N compounds within new growing organs becomes saturated.

Thus, an increase in plant growth rate increases (i) the leaf area and then the plant photosynthesis rate, leading to a positive C signal to the root transport system for nitrate absorption, and (ii) the sequestration of N organic compounds in new growing organs (leaves, stems and roots), leading to a reduction in the negative N signalling to root nitrate transport systems. At the reverse, a decrease in plant growth rate leads to a decrease in the positive C signalling and to an increase in the organic N compounds re-circulating down in the phloem and repressing N absorption by the roots. Therefore, the actual N absorption rate of a plant is co-regulated by both the soil N supply and its own growth rate potential. Two groups of transport systems, with low and high affinity for nitrate operate in plants (Glass et al., 2002). Devienne-Baret et al. (2000) have proposed a model accounting for the co-regulation of plant N uptake by soil nitrate concentration and plant growth rate:

$$\frac{dN}{dt} = a_c(1-b)W^{-b}\left(\frac{dW}{dt}\right)_{\max}\left[V_H\frac{C}{K_H + C} + V_L\frac{C}{K_L + C}\right] \tag{13}$$

where V and K are the coefficients of the Michaelis–Menten formula and subscripts describe the high (H) and the low (L) affinity transport systems for nitrate; C is the actual NO_3^- concentration in soil solution, W is the crop mass and $1 - b$ is the allometric coefficient of Eq. 2.

Lemaire et al. (2007) discussed whether leaf expansion or crop mass accumulation is the variable that best describes the feedback control of crop N uptake. They concluded that biomass accumulation and LAI expansion are two faces of the same regulation process. Nevertheless, the slope of the N uptake versus LAI relationship (Eq. 12) is relatively more variable across species than the variation in N uptake versus crop mass relationship (Eq. 4) when crops are maintained near the critical N supply. The variation of plant morphology and leafiness across crop species induces variation in N uptake plant capacity per unit of LAI indicating that leaf area expansion is not the only way by which the plant can sequestrate organic N compounds, but that stem growth or leaf thickness can be also a means for plant to store reduced N, delaying the retro-inhibition of absorption of N by roots.

Equation 13 represents the crop N uptake versus crop mass trajectories for different steady-state N supply conditions, that is C = constant. The four trajectories in Figure 3 correspond to rates of N supply for the agronomic range between highly limiting N to saturated plant capacity to sequestrate organic N. Each trajectory represents a 'virtual' constant plant N status maintained by a steady-state N supply, whereas a 'real' crop in a changing environment could move from one trajectory to another according to changes in soil supply conditions with time. The dotted lines As-Af-Ac-Am and Bs-Bf-Bc-Bm represent two response curves of the crop to increased N supply for either (i) different time during crop growth, (ii) different genotypes at the same time having different growth potential, or (iii) different environments (e.g. temperature) modulating crop growth rate. So whatever the cause of the variation in crop mass provided that N supply remains at steady state, any increase in crop mass (ΔW) is accompanied by a corresponding increase in crop N uptake

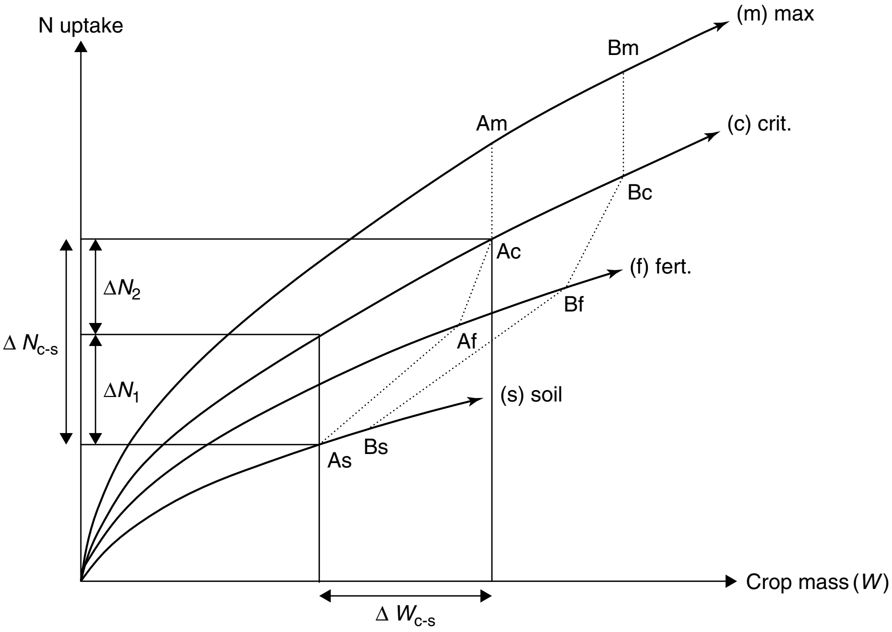

FIGURE 3

N uptake versus crop mass trajectories for different steady-state N supply corresponding to (s) non-fertilised crops representing a highly limiting N condition, (f) a sub-optimal fertilisation rate, (c) the critical N uptake and (m) the maximum N uptake where the capacity of the plant to sequestrate organic N according to its growth rate is saturated. (A) and (B) represent either (i) two growth stages of the same crop, (ii) two crops having different growth rate, or (iii) an environmental effect. The dotted lines represent the response curves to increased N supply for the situations A and B.

(ΔN) according to Eq. 13 (C constant). So the corresponding $\Delta N/\Delta W$ represents the effect of the increment in crop mass (W) on the corresponding increment in crop N uptake (N) along a given N uptake versus crop mass trajectory; this reflects the feedback effect of plant growth on plant N uptake. Then increase in plant N uptake can be considered a consequence of the increment in plant growth as shown in Eq. 2. When N supply increases from situation (s) to situation (c) then, at a given time, we can observe an increment in N uptake, $\Delta N_{\text{c-s}}$, that can be related to the corresponding increment in crop mass $\Delta W_{\text{c-s}}$ considered as the direct consequence of the increment in crop N uptake. But in fact, as shown in Figure 3, $\Delta N_{\text{c-s}}$ can be seen as the sum of two components: (i) ΔN_1, the increment in N uptake necessary for the plant to achieve its critical N status hence its potential growth rate, and (ii) ΔN_2, the supplement of N uptake corresponding to the increase in crop growth rate. This is an illustration of the co-regulation of plant N uptake by both soil N supply and plant growth capacity. As soil N supply increases, plant N uptake increases according to the increase in C, the soil mineral N concentration (Eq. 13) and as a result of the increase in plant N status, plant growth rate is accelerated and then, as a feedback consequence, a supplement quantity of N is taken up according to Eq. 2. So at any moment crop growth rate is the consequence of crop N uptake and vice versa.

In conclusion, the close relationship between N uptake and crop mass accumulation as expressed by Eq. 2 reflects the feedback regulation of root mineral N absorption by shoot growth dynamics. Thus, the co-regulation of N uptake by both soil N supply and plant or crop growth rate as shown by Eq. 13 is an emerging property of the whole plant–soil system.

2.3. Diagnostic of plant N status in crops: nitrogen nutrition index

The main consequence of the theory developed in section 2.1.2. is that neither the plant N concentration nor the crop N uptake per se can indicate unequivocally the crop N nutrition status. Equations 1 and 2 indicate that both plant N concentration and crop N uptake have to be interpreted in relation with crop mass. The critical N dilution curve as determined by Eq. 3 for each crop species (Table 1) allows the separation of the actual N status of crops in two situations as illustrated in Figure 4: above the critical N curve the crops

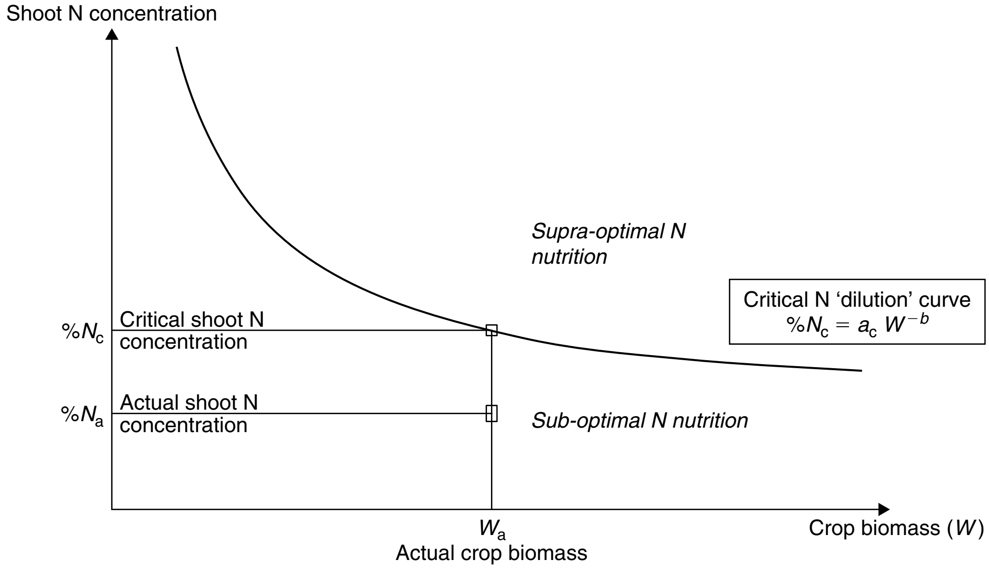

FIGURE 4
The critical N dilution curve and the calculation of the nitrogen nutrition index (NNI) (see text for further details on NNI).

are in N luxury consumption, and below the critical curve the crops are in deficient N supply. It is necessary to measure simultaneously the plant N concentration and the crop mass at any moment of the vegetative growth period of the crop. Lemaire and Gastal (1997) proposed a nitrogen nutrition index (NNI) to quantify the intensity of both N deficiency and luxury consumption of a given crop. NNI is calculated as the ratio between the actual plant N concentration of the crop ($\%N_a$) and the critical plant N concentration ($\%N_c$) corresponding to the actual crop mass (W_a):

$$\mathrm{NNI} = \frac{\%N_a}{\%N_c} \tag{14}$$

When NNI is close to 1, the plant N status is considered as near optimum. Departures from 1 indicate deficiency ($\mathrm{NNI} < 1$; intensity of deficiency $= 1 - \mathrm{NNI}$) or excess nitrogen ($\mathrm{NNI} > 1$; intensity of excess $= \mathrm{NNI} - 1$).

Nevertheless, this approach does not take into account that the minimum plant N concentration is not 0 but $\%N_s$, the N concentration of the structural compartment of the plant mass (Eq. 9). As stated, $\%N_s$ should correspond to the minimum N content for the plant to stay alive. Angus and Moncur (1985) already postulated the existence of such a minimum plant N concentration with a parallel evolution of $\%N_s$ with $\%N_c$. Determination of $\%N_s$ in field conditions is very difficult because even under very severe N deficiency the minimum plant N concentration is not achieved. Even, because the N deficiency is generally lower at early growth stages, such estimation tends to indicate a decrease in $\%N_s$ with plant mass as shown by Plénet and Lemaire (1999) on maize. Lemaire and Gastal (1997) used Eq. 9 to derive $\%N_s$ of 0.77% for wheat and 0.82% for maize. So a common value of about 0.8% can be used. The theory developed above postulates that $\%N_s$ should be stable all along the crop growth cycle. In absence of any contrary indication we can use a constant value of 0.8% for $\%N_s$. Then an NNI that reflects this physiological attribute can be calculated:

$$\mathrm{NNI}' = \frac{\%N_a - \%N_s}{\%N_c - \%N_s} \tag{15}$$

NNI′ is therefore physiologically more robust than NNI, but involves a greater degree of uncertainty related to the actual value of $\%N_s$, which has not been documented for many crop species.

The simpler NNI allows for the interpretation of the response of crops to N nutrition in agronomic experiments. Lemaire and Meynard (1997) showed that the same rate of N application could lead to very different plant N status, depending on plant growth potential, soil N mineralisation rate and overall soil N availability (dry soil for example). So the determination of the plant N status at target stages of the crop growth period is a prerequisite for studying crop response to N deficiency. NNI estimates the instantaneous crop N status when plant $\%N_a$ and actual crop mass (W_a) have been determined. But under changing N supply in the field it is necessary to determine NNI several times during the growth period of the crop. Jeuffroy and Bouchard (1999) used NNI to characterise the N deficiency of wheat crops in terms of intensity, duration and timing. They showed that such an integrated NNI explained 96% of the variation in grain number of wheat within a large experimental data set, while a single NNI observed at anthesis explained only 92% of this variation (Justes et al., 1997). The difference in percentage of variance explained was significant but small indicating that in these temperate conditions the temporal changes in soil N supply were relatively smooth. Determination of NNI at anthesis is too late for management of N fertiliser aimed at yield improvement. The possibility to predict the crop NNI evolution through the use of dynamic crop models combined with in situ crop measurements appears a very promising solution (Naud et al., 2008).

Despite its high informative value as diagnostic tool for N crop status, NNI is difficult to use in field conditions and it remains more a research than an agricultural management tool. NNI determination is time-consuming because of the necessity to determine both actual crop mass and plant N concentration. Therefore it is necessary to develop non-invasive, cost-effective methods for a rapid determination of plant N status and use NNI as a reference for calibration.

The theory developed in the preceding text for explaining N dilution with plant growth in dense canopy shows that the decrease in plant N concentration is the result of two processes: (i) the decline in plant leaf area ratio as crop mass increases, and (ii) the preferential allocation of N to the well-illuminated upper layer of leaves as canopy develops (see Section 3.3.3). Therefore, Lemaire et al. (1997) suggested that while plant N concentration declines with crop mass accumulation the N content per unit of leaf area within the upper layer of leaves was more stable and would correlate well with the NNI. This assumption was verified by Farrugia et al. (2004) for grasslands, indicating the diagnostic value of N content of leaves in the upper canopy layer.

Chlorophyll measurement is a practical, commonly used method for the estimation of the upper leaf N concentration (Piekelek and Fox, 1992; Feibo et al., 1998; Reeves et al., 1993; Matsunaka et al., 1997, among many others). Peng et al. (1996) showed that chlorophyll measurements were well correlated with leaf colour chart estimations. Caviglia and Sadras (2001) showed that NNI and chlorophyll measurements provided consistent measures of crop nitrogen deficiency in wheat. But all these methods gave large variation of calibration according to genotypes used and environmental conditions.

Promising methods to assess crop nitrogen status are being developed with the aid of remote-sensing tools (e.g. Houlès et al., 2007; Babar et al., 2006). Chapter 19 (Section 2) analyses these methods in detail.

2.4. Intra- and inter-specific interactions within plant stands

The theory developed earlier allows the scaling up from isolated plant to the plant within a dense stand. But the latter is only considered as the average of plant population. More interesting is to analyse how plant–plant interactions would impact on N acquisition and repartition in individual plant within canopies.

Lemaire et al. (2005) analysed the N uptake dynamics of individual plants within an alfalfa stand according to their hierarchical position within the canopy: dominant, intermediate or suppressed plants (Figure 5). Dominated plants showed a lower plant N concentration than dominant plants at a similar plant mass (Figure 5a). This difference was entirely explained by a lower leaf mass:shoot mass ratio (Figure 5b). So within a plant stand allocation of N among individual plants reflected the contribution of individual plants not to the whole biomass but to the total leaf mass and probably to the total leaf area. The dominated plants had a lower leaf:shoot mass ratio associated with the shade-avoidance syndrome promoting greater allocation of resources to stem growth and height (Section 2.1). Hence, competition for light and photomorphogenetic adaptations within dense canopies leads to differences in repartition of N among individual plants according to their hierarchical position.

In mixed grass–legume stands, it is of interest to analyse the influence of the legume on the N nutrition of grasses. Cruz and Lemaire (1986) proposed an experimental design allowing the distinction of the intra- from the inter-specific competition (Figure 6a). Figure 6b shows that the inclusion of alfalfa rows between cocksfoot rows led to an increased N concentration of cocksfoot. A classical interpretation of this is that alfalfa provides N to grass. The analysis in terms of dilution curve avoids this misinterpretation: the increase in grass N concentration in the mixture was due to the reduction in the biomass accumulation of grass in the presence of alfalfa (Figure 6c). Moreover, at the same grass biomass, the grass N concentration was lower in the presence of alfalfa, indicating a ‘competition’ effect of alfalfa. Cruz and Lemaire (1986) showed that the application of N fertiliser did not change this effect, and thus they concluded that the influence of alfalfa on N nutrition of the grass was not due to a depletion of soil N mineral by alfalfa. As cocksfoot was dominated by alfalfa, its N demand was depressed because it shifted its morphology in response to the light and soil environment under competition, including greater investment in structural tissues with less N concentration. Figure 6d shows that alfalfa N nutrition was not affected by the presence of neighbour rows of cocksfoot while the presence of a neighbour row of alfalfa depressed substantially alfalfa N concentration.

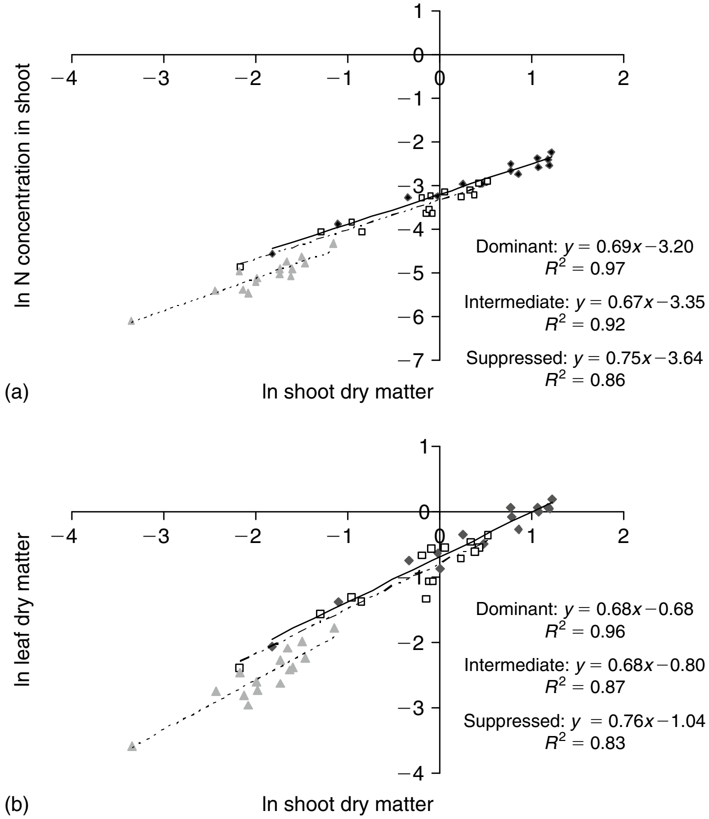

FIGURE 5

Relationships between (a) ln N concentration in shoot and ln shoot dry matter and (b) ln leaf dry matter accumulation and ln shoot dry matter in plants having different hierarchical positions within a lucerne canopy during a regrowth period under field conditions. Hierarchies are dominant (◆), intermediate (□) and suppressed (▲). (Source: Lemaire et al., 2005.)

As alfalfa was in this experiment the dominant species, intra-specific competition of alfalfa was stronger than inter-specific competition with cocksfoot.

Hence, intra- or inter-specific interactions in dense stands lead to hierarchical N resource sharing among plants according to their hierarchical position for light interception. So these plant–plant interactions have to be taken into account for understanding the competition for soil N resources. In complex plant communities, a dominated species with high intrinsic N uptake capacity could still have a low competitive ability for mineral soil nitrogen. Hence N resource sharing among plants in dense stands is dominated by competition for light under high N supply, and is dominated by intrinsic N uptake capacity of plants under low N supply (Dybzinski and Tilman, 2007).

3. RESPONSE OF PLANTS AND CROPS TO N DEFICIENCY

Once the timing and the intensity of N deficiency has been quantified for a crop, it is possible to analyse the crop responses to a varied range of N deficiency through the different functions leading to crop mass

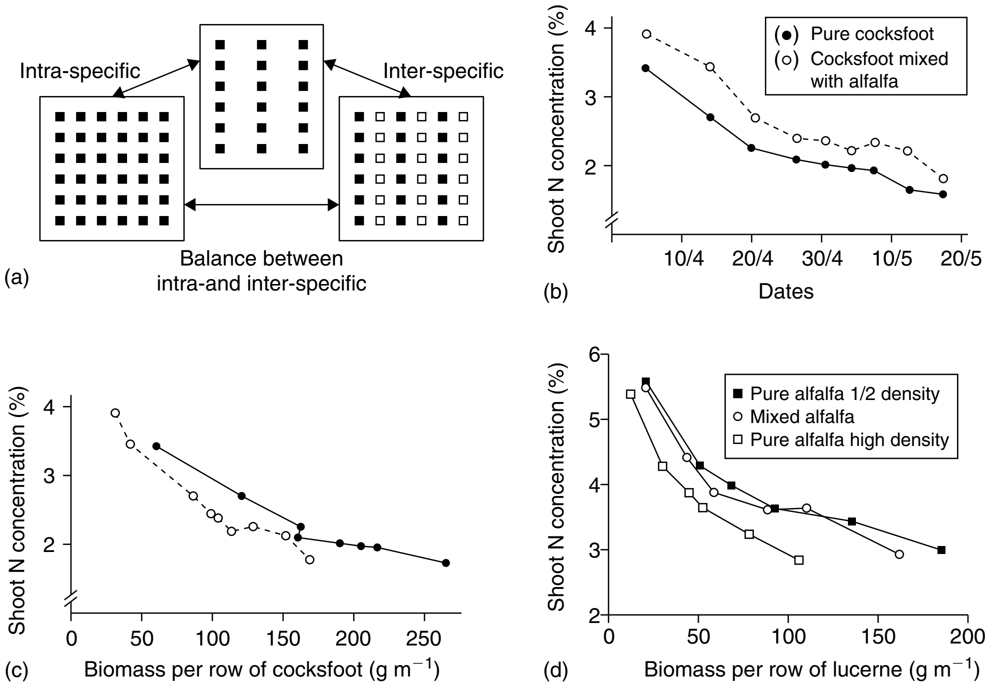

FIGURE 6

(a) Experimental design for studying the combined effect of intra- and inter-specific interference in mixed crops. The row of one species in double-spaced row plots can be compared with row within pure crop in single-spaced row (intra-specific effect) or with row within mixture (inter-specific effect). Evolution during spring growth of plant N concentration of a pure double-spaced row of cocksfoot compared with row of cocksfoot in mixture with alfalfa either on (b) time basis or (c) dry matter basis. (d) Evolution of plant N concentration of alfalfa rows in pure stand with single-spaced rows, in pure stand in double-spaced rows and in mixture with cocksfoot. (Source: Cruz and Lemaire, 1986.)

accumulation: (i) the interception of light (leaf expansion processes and leaf senescence) and (ii) the radiation use efficiency (RUE; photosynthesis and respiration), and its allocation patterns within plants [e.g. shoot vs. root and harvest index (HI)].

3.1. Crop life cycle and plant N economy

Here we present selected comparisons between grain crops (wheat and rice vs. maize) and between grain and forage crops to illustrate differences and similarities between species. In most crop species in arable cropping systems, the plant life cycle with regard to N nutrition can be divided into two main phases: the vegetative phase, from seedling emergence until flowering, and the reproductive phase, from fecundation to maturity. In unstressed crops, the end of the vegetative phase often coincides with peak leaf area, stem height and branching (tillering), but peak leaf area is anticipated in relation to flowering under stressful conditions. In the reproductive stage, leaves, stems and roots behave predominantly as net sources of N organic compounds for seed development and grain filling. This N recycling is associated with leaf senescence that leads to a progressive decline in crop photosynthesis and C supply. During this post-anthesis period, plant N uptake can provide an additional source of N for grains.

Pearson and Jacobs (1987) tested the effects of large changes in N availability during pre- and post-anthesis phases on the amount of N remobilised to grain. In wheat (Palta and Fillery, 1995; Habash et al., 2006) and rice (Mae, 1997; Tabuchi et al., 2007), 60–95% of the grain N at harvest comes from remobilisation of N stored in roots and shoots before anthesis. In maize, this proportion is only 45–65% (Ta and Weiland, 1992; Rajcan and Tollenaar, 1999a, b; Gallais and Coque, 2005). Under conditions of good water supply, wheat and rice can develop a larger LAI (7–8) compared to maize (4–6); this, according to Eq. 12, allows a greater capacity of storage of organic N compounds in shoots. This corresponds to the double function of leaves: as organs of C assimilation and as temporary storage of N in rubisco (Sinclair and Sheehy, 1999; Thomas and Sadras, 2001). Lemaire et al. (2007) showed that the capacity of shoot N storage per unit LAI at optimum N supply is 37 kg N ha^{-1} for wheat and 30 kg N ha^{-1} for maize, reflecting differences in both metabolic pathway and intrinsic LAR between the two species. Then the total capacity of shoot N storage at anthesis can reach 250 kg N ha^{-1} for wheat and only 140 kg N ha^{-1} for maize. As a result maize grain yield is more dependent on plant N uptake capacity after anthesis than wheat or rice grain yield.

Canola has the capacity to accumulate a large quantity of N in vegetative parts at the beginning of flowering (Lainé et al., 1993). However, grain yield of canola is low in comparison with the total crop mass, and then an important part of the N stored in the vegetative organs is not used for grain production (Rossato et al., 2001).

For perennial vegetative plants such as grasses and legumes cultivated as forage, the plant life cycle is interrupted by cutting before flowering and then the plant N economy is entirely dominated by the accumulation of N within leaves and stems. Remobilisation of N from shaded leaves at the bottom of the canopy to well-illuminated leaves at the top occurs as the crop LAI develops (Lemaire et al., 1991; Section 2.1.2). For regrowth after defoliation, plants remobilise organic N stored in roots and stubbles (Avice et al., 1996, 1997; Ourry et al., 1996). In these species, perenniality is related to the capacity to restore N root reserve during regrowth (Lemaire et al., 1992). As a consequence the dynamics of N accumulation in shoot during regrowth does not reflect exactly the dynamics of N absorption and assimilation.

The selected comparisons of wheat and rice versus maize and between annual grain crops and perennial forage crops demonstrate that plant N economy differs substantially according to crop species and management. But, despite these differences, a common feature can be pointed out across crop species: the necessity to store sufficient quantities of N in vegetative organs either (i) to produce maximum herbage mass for forage crops and ensure perenniality or (ii) to meet as much as possible the N demand of grains. The more the grain depends on post-anthesis plant N uptake the more the crop is susceptible to terminal stress such as the exhaustion of N in soil and/or reduced soil water content and then N availability. Stay-green types are particularly able to maintain leaf chlorophyll and photosynthetic capacity during grain filling, as discussed in Section 3.4

3.2. N deficiency effects on crop mass accumulation

Maximising harvested production for a crop corresponds in general to maximising crop mass accumulation. This is obvious for forage crops where shoot mass is harvested. It is also the case for most of the grain crop such as cereals where it has been shown that the grain number is very well correlated to crop mass at anthesis (Desmotes-Mainard et al., 1999; Desmotes-Mainard and Jeuffroy, 2004; Uhart and Andrade, 1995).

3.2.1. Radiation use efficiency and PAR interception

According to Monteith (1972), crop biomass accumulation is related to the quantity of photosynthetic active radiation (PAR) intercepted by the crop during its life cycle. Several authors (Gallagher and Biscoe, 1978; Gosse et al., 1984, 1986; Sinclair et al., 1992) have shown that in a first approximation a linear relationship could be established between the accumulation of crop mass and accumulated intercepted PAR during the time course of crop development (Chapter 7). The slope of this relationship represents the average conversion of energy intercepted by the crop in biomass during the crop life cycle and is commonly called the RUE. Bélanger et al. (1992) analysed the effect of N deficiency on the two components of the crop mass accumulation of a tall fescue sward: the quantity of PAR intercepted and the RUE. As shown in

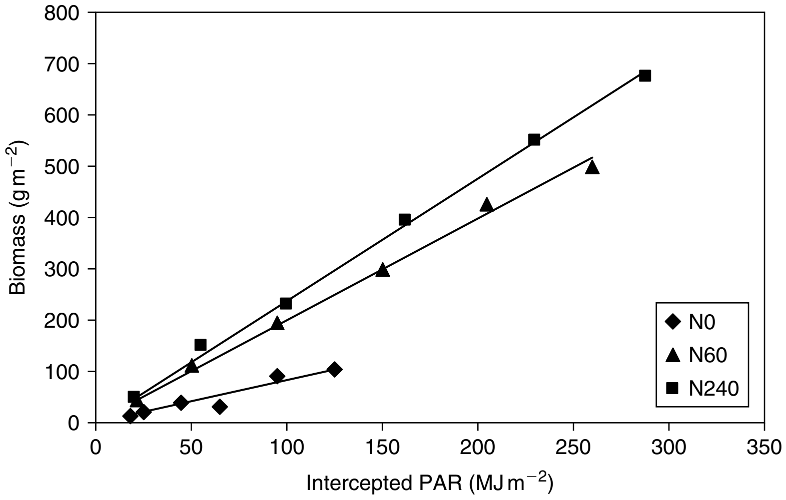

FIGURE 7
Relationships between shoot biomass accumulation and cumulative intercepted PAR during regrowth of tall fescue swards receiving nil, 60 or 240 kg N ha^{-1}. (Source: Redrawn from Bélanger et al., 1992.)

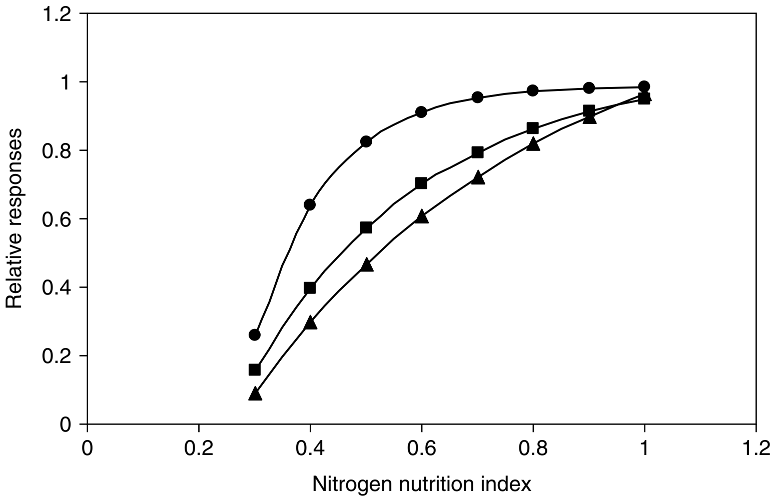

FIGURE 8
Effects of crop N status determined by the nitrogen nutrition index (NNI) of tall fescue swards receiving different N rates and (i) the relative quantity of intercepted PAR, PAR_{act}/PAR_{max} (●), (ii) the relative radiation use efficiency, RUE_{act}/RUE_{max} (■), and the relative LAI, LAI_{act}/LAI_{max} (▲). (Source: Redrawn from Bélanger et al., 1992.)

Figure 7, both components are affected by N deficiency. These authors analysed the responses of RUE and accumulated intercepted PAR to N deficiency using NNI. As shown in Figure 8, in relative terms, RUE was more affected by moderate N deficiency (NNI = 0.6–0.8) than the quantity of PAR intercepted by the crop, but for very severe N deficiency (NNI = 0.3) the response of the two variables converged. Similar results have been obtained by Trápani and Hall (1996) on sunflower and Muchow and Davis (1988) on sorghum and maize. The response of LAI expansion to N deficiency follows a similar pattern as RUE, but with a little bit higher sensitivity: for an NNI of 0.6, RUE was reduced by 30% while LAI was reduced by 40% as compared to their value under critical N supply. The difference in response between LAI and PAR was due to the asymptotic relationship between the radiation interception efficiency (i.e. the ratio between the visible

Table 2 Effects of Nitrogen Supply on Radiation Use Efficiency (RUE) of Tall Fescue Swards

N Rate ($kg\,ha^{-1}$)	(1) RUE_{gp} ($g\,DM\,MJ^{-1}$)	(2) RUE_t ($g\,DM\,MJ^{-1}$)	(2)/(1)	(3) RUE_s ($g\,DM\,MJ^{-1}$)	[(2)–(3)]/(2)
0	4.82	1.78	0.37	1.12	0.37
60	5.03	2.28	0.45	1.73	0.24
120	5.05	2.56	0.51	2.07	0.19
180	5.62	2.65	0.47	2.21	0.17

RUE is calculated on the basis of (1) canopy gross photosynthesis (RUE_{gp}), (2) total biomass (RUE_t) and (3) shoot biomass (RUE_s). The ratio [(2)–(3)]/(2) indicates fractional allocation of dry matter to roots. Source: After Bélanger et al. (1994).

radiation intercepted by a crop and the incident visible radiation) of the crop and the LAI; the reduction in the quantity of PAR intercepted is only important when LAI declines below 3 under severe N deficiency.

The relative effect of N deficiency on both RUE and the quantity of intercepted PAR depends on the timing of the N deficit. An N deficiency before the crop reaches a stage of LAI = 3 is likely to reduce the quantity of PAR intercepted by the crop, while N deficiency occurring after this stage would have only a small effect. This partially accounts for the divergent reports on the relative sensitivity of RUE and light interception in response to N deficiency.

RUE is an integrated variable accounting for photosynthesis and respiration (Chapter 7). However, because RUE is normally estimated on a shoot biomass basis, it is necessary to include allocation of assimilate to roots. Bélanger et al. (1994) analysed the effect of N nutrition on the different components of RUE of tall fescue. Table 2 shows RUE on the basis of (1) canopy gross photosynthesis, (2) shoot biomass and (3) the total (shoot + roots) biomass. Canopy gross photosynthesis was less affected by N deficiency than the accumulation of total biomass: in high N condition, about 50% of assimilated C is used for plant growth while in deficient N conditions this proportion is only 37% reflecting relative higher respiration losses in N-deficient plants (Table 2). The accumulation of shoot biomass was more affected than the accumulation of total biomass reflecting an important change in dry matter allocation to roots, which increased from 17% in crops fertilised with 180 $kg\,N\,ha^{-1}$ to 37% in their counterparts with no fertiliser (Table 2). The lower shoot:root ratio in N-deficient plants is widely documented (Barta, 1975; Robson and Parsons, 1978; Jarvis and Macduff, 1989). The proportional higher root development could be one of the reasons why the respiration losses are higher in relative terms in N stressed swards than under high N supply.

3.2.2. Effect of N deficiency on canopy size and radiation interception

The response of leaf area of plants and canopies to N deficiency is brought about by a large decline in the expansion of individual leaves and on branching or tillering (Wilman and Pearse, 1984; Gastal and Lemaire, 1988; Vos and Biemond, 1992; Trápani and Hall, 1996). These authors showed that the rate of leaf appearance and the duration of individual leaf expansion were little affected by N in many species. The accumulation of non-structural carbohydrates in N-deficient leaves suggests that carbohydrate supply is not the cause of the leaf area expansion reduction under low N supply (Gastal and Lemaire, 2002). N deficiency alters the rates of cell division and cell expansion, while the final cell length is little affected (Mac Adam et al., 1989; Gastal and Nelson, 1994; Fricke et al., 1997; Trápani et al., 1999). In all instances the impact of N on leaf expansion rate of monocots was related more to the effect of N on cell production than cell expansion rate. In dicots, early studies concluded that the shortage of N primarily reduced cell growth rate. Nevertheless, whether the response of leaf growth to N deficiency differs between monocots and dicots, as suggested earlier (Radin, 1983), remains an open question.

Gastal et al. (1992) proposed a quantitative relationship between the leaf elongation rate (LER) of tall fescue and the NNI of the sward:

$$\frac{\mathrm{LER}_{\mathrm{actual}}}{\mathrm{LER}_{\mathrm{critical}}} = 1.39 - 1.9e^{-1.49\mathrm{NNI}} \tag{16}$$

subscript 'actual' refers to sub-optimal N condition while 'critical' refers to non-limiting N condition. This response curve crosses the X-axis at NNI = 0.21 that corresponds to the plant N status at which leaf growth becomes 0. For a severe N deficiency, NNI = 0.4, the actual LER is reduced to about 30% of its maximum value under high N supply.

Lemaire et al. (2008) analysed the response of LAI of different crop species to N deficiency using the allometric relationships between LAI and crop mass W (Eq. 11). This approach allows the separation of the reduction in LAI directly related to the reduction in crop mass from a specific reduction in LAI at a similar crop mass: that is a reduction in plant leafiness coefficient corresponding to (i) a decrease in leaf/stem ratio and/or (ii) an increase in specific leaf weight (SLW). Figure 9 represents the response of LAI of maize and wheat to N deficiency. For about the same level of N deficiency as shown in Figure 9a and 9d, the two crop species behave very differently: the reduction in LAI of maize is entirely linked allometrically to the reduction in crop mass (Figure 9b), while wheat reduced also drastically its LAI at a given crop mass in response to N deficit (Figure 9e). Lemaire et al. (2008) showed that tall fescue behaves like maize while canola behaves like wheat, with sorghum and sunflower having intermediate responses. As a consequence of the response of leaf area per unit of crop mass to N deficiency, the capacity of the crop to accumulate N in canopy per unit of LAI can be either reduced in N-deficient condition as for maize (Figure 9c) or maintained as for wheat (Figure 9f).

Hence classification of crop species in either metabolic group (C_3 vs. C_4) or botanical groups (monocots vs. dicots) does not allow the determination of crop response type: under N deficiency some species such as maize or tall fescue and to a lesser extent sorghum and sunflower tend to maximise light interception by minimising the reduction in crop LAI while other species such as wheat and canola do not. Do these two opposite strategies mean that there exists a trade-off between photosynthesis rate per unit LAI and leaf area expansion? Does maize drop photosynthesis rate per unit LAI more than wheat? Answers to these questions require more analytical studies on response of leaf and canopy photosynthesis to N deficiency.

3.2.3. Effect of N deficiency on leaf photosynthesis

The response of leaf photosynthesis to irradiance is largely dependent on the leaf N content. Photosynthetic proteins, including large amounts of rubisco and, to a lesser extent, light-harvesting complex proteins, represent about 60% of the leaf N content (Evans, 1983; Field and Mooney, 1986; Lawlor, 2002). Leaf photosynthesis at saturating light intensity ($A_{\max}$) increases asymptotically with leaf N content; see Grindlay (1997) for review. This relationship shows a positive intercept on the leaf N content axis, indicating that when leaf photosynthesis rate becomes zero, leaves would still contain significant amount of N, corresponding to structural N (N_s) of Eq. 9 (Field and Mooney, 1986). The variation in the $A_{\max}$/SLN (leaf N content per unit of leaf area) relationship seems relatively limited among cultivated species of the same metabolic group (Evans, 1989; van Keulen et al., 1989). However Sinclair and Horie (1989) show a lower $A_{\max}$ at similar leaf N per unit area for soybean compared to non-legume C3 species. This lower $A_{\max}$ was associated with higher structural N content of leaves, N_s. The variations in $A_{\max}$/SLN relationship among species could be due to (i) differences in nitrogen costs of PEP-carboxylase and rubisco and the relative amounts of these two enzymes per unit leaf area, and/or (ii) the possible accumulation of vegetative storage proteins within legume species such as soybean.

There is a large discussion among crop scientists whether $A_{\max}$ has to be related to leaf N content per unit leaf mass of per unit leaf area basis (Grindlay, 1997). Our opinion is that none of these two approaches are completely right. The two processes of leaf photosynthesis, light harvesting by chlorophyll and CO_2 reduction by rubisco, are affected by leaf N status. Both processes have to be expressed on a volume basis and then leaf thickness becomes an important parameter to be taken into account. But the correlation between

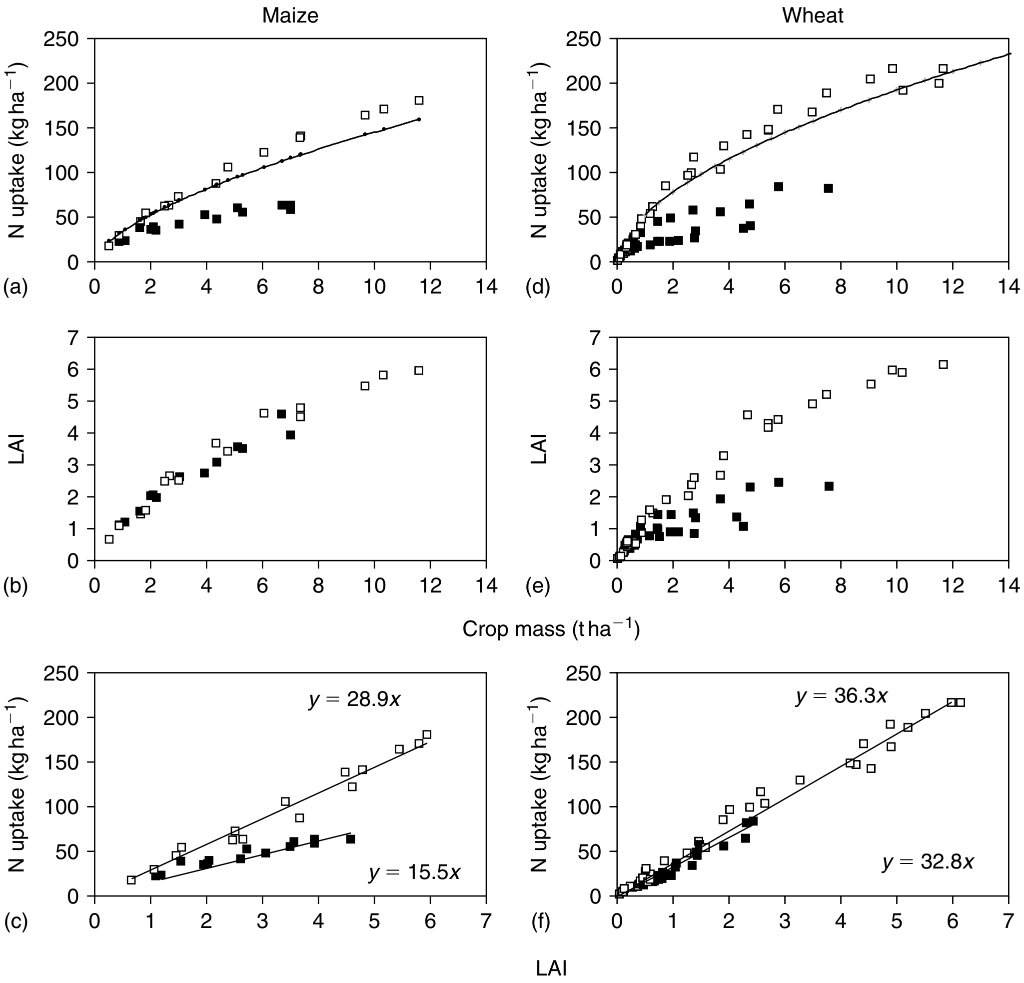

FIGURE 9

Comparison of (a–c) maize and (d–f) wheat responses to non-limiting (□) and limited N supply (■) measured in field crops in France. Relationships between (a, d) N uptake and crop mass, (b, e) LAI and crop mass, and (c, f) N uptake and LAI. In (a) and (c) the line corresponds to the critical N uptake curve. (Source: Redrawn from Lemaire et al., 2008.)

leaf thickness and SLA is weak as SLA varies with non-structural carbohydrate concentrations. A measure of leaf N concentration per unit of leaf volume could be based on leaf water content at saturation (Thornton et al., 1999). This problem reinforces the necessity for scaling metabolic plant processes and for relating them to plant form and size (Enquist et al., 2007).

Data concerning the response of leaf photosynthesis to N at low irradiance, that is the quantum efficiency, are relatively scarce. Gastal and Bélanger (1993) indicated that for tall fescue the effect of leaf N content on the quantum efficiency was low or not significant and always much lower than the effect on $A_{\max}$. Connor et al. (1993) showed no relationship between quantum efficiency and N in sunflower. However Dreccer (1999) found an association between quantum efficiency and leaf N content in both wheat and oilseed rape. Another element of the net C exchange at low light is dark respiration, which seems to increase with increasing N, in association with maintenance (Connor et al., 1993). Hence, in conclusion as the leaves are progressively shaded the effect of N deficiency on leaf net photosynthesis becomes lower.

3.2.4. Integrating from leaf to canopy photosynthesis

Gastal and Bélanger (1993) proposed a quantitative relationship between canopy gross photosynthesis at high irradiance (CGP_{max}) and NNI for tall fescue swards: a reduction in NNI from 1 to 0.4 reduced the relative CGP_{max} from 1 to 0.6. This relative low responsiveness of CGP_{max} to N deficiency was due to the greater number of shaded leaves with increasing canopy size and the decoupling of photosynthesis and leaf N content at low irradiance. The same authors showed that the maximum light yield of the canopy, that is the quantum efficiency of the canopy at low irradiance, was not related to the sward NNI. So when canopy photosynthesis is integrated over a day or over a long period there is only a limited response to N during the periods of low irradiance. For this reason the effect of N deficiency on integrated canopy gross photosynthesis appears relatively limited (Table 2). So genetic variation in A_{max}, if it exists, is in great part buffered when integrated at the level of canopy as previously stated by Sinclair et al. (2004) (Box 1 in Chapter 9).

3.2.5. Trade-off between light capture and radiation use efficiency

Crops can respond to N deficiency through a reduction in light interception, a reduction in canopy photosynthesis rate or both. Sinclair and Horie (1989), Grindlay (1997) and Vos et al. (2005) proposed that these two types of responses represent a trade-off between maintaining resource capture or resource use efficiency. In conditions of limited N supply maintenance of leaf area must lead to a decreased leaf N concentration per unit leaf area (SLN) as in maize (Figure 9b and 9c) whereas maintenance of SLN is expected to be associated with reduced leaf area as in wheat (Figure 9e and 9f). Differences in the critical SLN for LAI expansion and RUE can underlie the differences among species in response to N deficit (Lemaire et al., 2008). For sorghum and maize, the critical SLN for leaf expansion is about $1.0\,g\,m^{-2}$ (Muchow, 1988; van Oosterom et al., 2001) while the critical SLN for RUE is $1.4–1.5\,g\,m^{-2}$ (Muchow and Davis, 1988; Muchow and Sinclair, 1994). Therefore, N deficiency will affect RUE before LAI expansion and maize and sorghum will maintain resource capture rather than resource use efficiency in deficient N conditions. For sunflower, a dicot crop, reported SLN thresholds are $2.0\,g\,m^{-2}$ for leaf size and $1.5\,g\,m^{-2}$ for RUE (Bange et al., 1997). For canola, a dicot species, the quantity of PAR intercepted by the crop is severely decreased by N deficiency while RUE is less affected (Wright et al., 1988). For wheat, a monocot crop, there is also ample evidence that N deficit affects LAI before RUE (Gallagher and Biscoe, 1978; Meinke et al., 1997).

Lemaire et al. (2008) showed consistent differences among crop species in their response to N deficiency in terms of resource capture, the ability of plants to maintain LAI expansion despite N deficiency. Because the specific leaf area (SLA) is not substantially affected by N deficiency when comparisons are made at same LAI, this capacity for maintaining LAI expansion is mainly determined by resource allocation between leaf and stem. These differences among species are not related to either metabolic (C3 vs. C4) or botanical classification (monocot vs. dicot). For resource use efficiency, however, the results show a tendency for C4 species to reduce resource use efficiency more than C3 species. We therefore conclude that the postulated trade-off between resource capture and resource use efficiency is not evident among species.

3.3. N deficiency effects on C and N allocation within the plant and canopy

3.3.1. C and N allocation to roots

Nitrogen deficit increases the root:shoot ratio (Table 2) according to the concept of functional equilibrium (Brouwer, 1962; Thornley, 1977). However, a substantial variation exists between species in the intensity of the root:shoot response to nitrogen deficiency (Robinson, 1994). This response implies a feedback, whereby the increase in root:shoot ratio in response to N deficiency would lead to an increase in plant N uptake that could contribute to limit the crop N deficiency. Local patches of mineral N in soil induce root proliferation while root elongation is enhanced in free mineral N soil zones, leading to a foraging development of roots (Samuelson et al., 1992; Robinson, 1994; Zhang and Forde, 2000).

Root density, root architecture and morphology, and root growth responses to localised mineral N supply differ between species and a large range of root morphological plasticity exists (Fitter, 1991; Grime et al., 1991). Lemaire et al. (1996) stated that differences in root architecture accounted for sorghum's higher N uptake under low soil N in comparison to maize. Intra-specific differences in root architecture have been poorly investigated. Oyanagi et al. (1993) and Oyanagi (1994) investigated genetic differences in vertical root distribution and root angle in wheat. A series of study reported a weak but significant genetic correlation between some root traits, biomass production and yield of maize and wheat under N limiting supply conditions (Guingo et al., 1998; Coque and Gallais, 2006; Laperche et al., 2006).

Recent studies indicate that plant below-ground N may represent 30–60% of the total N for legumes at the pod filling stage and around 35% for cereals at grain filling stage (McNeil et al., 1997; Peoples and Baldock, 2001; Kahn et al., 2002). Hence, some variation in shoot versus root allocation of N organic compounds could explain differences in shoot N recovery between species and genotypes. Total root length and root area per unit of soil volume are important traits related to N absorption. The difference in root length density of cereals and dicots is about twofold, and this is partially associated with a large compensating difference in hydraulic conductivity (Hamblin and Tennant, 1987). Improving our understanding of the relationship between plant growth, plant productivity, and root architecture and dynamics under soil conditions is of major importance (Whu et al., 2005). Chapter 13 (Table 1 and Section 4) deals with the current understanding of root attributes for effective capture of nitrogen and water.

3.3.2. C and N allocation to stems

As discussed in the preceding text, crop species respond very differently to N deficiency in terms of allocation of dry matter to photosynthetic and non-photosynthetic tissue. The effect of N deficiency on the allocation pattern of N is the result of the responses of (i) leaf:stem ratio and (ii) stem N concentration ($\%N_{\text{stem}}$). Species such as wheat and canola reduce proportionally more their leaf growth than their total shoot growth in response to N deficiency, while maize and tall fescue reduce leaf growth in the same proportion than shoot growth, whereas sorghum and sunflower have an intermediate response (Lemaire et al., 2008). Owing to the stability of SLA with N deficiency when compared at similar LAI, the leaf:stem ratio of wheat and canola is sharply reduced by N deficiency while it is not affected in maize. The leaf:stem ratio generally decreases as crop mass increases (Lemaire et al., 1992). Therefore, a progressively greater proportion of C is allocated to the stem as the crop ages. Stems are mainly composed of structural tissues (W_s in Eq. 12) having a low N concentration ($\%N_s$).

As indicated by Eq. 12, N accumulates within the canopy proportionally to LAI. The capacity of a crop to accumulate N in canopy per unit of LAI (N_{LAI}) can be then decomposed in two components, N accumulation in leaves (N_{leaves}) and N accumulation in stem (N_{stems}):

$$N_{\text{LAI}} = \frac{N_{\text{leaves}}}{\text{LAI}} + \frac{N_{\text{stems}}}{\text{LAI}} \tag{17}$$

or

$$N_{\text{LAI}} = \text{SLN} + \frac{N_{\text{stems}}}{\text{LAI}} \tag{18}$$

Figure 10 shows that sorghum and maize responded to N deficiency through a decrease in N allocation to stems per unit LAI, while wheat and canola maintained their N allocation to stems. Reduction in allocation

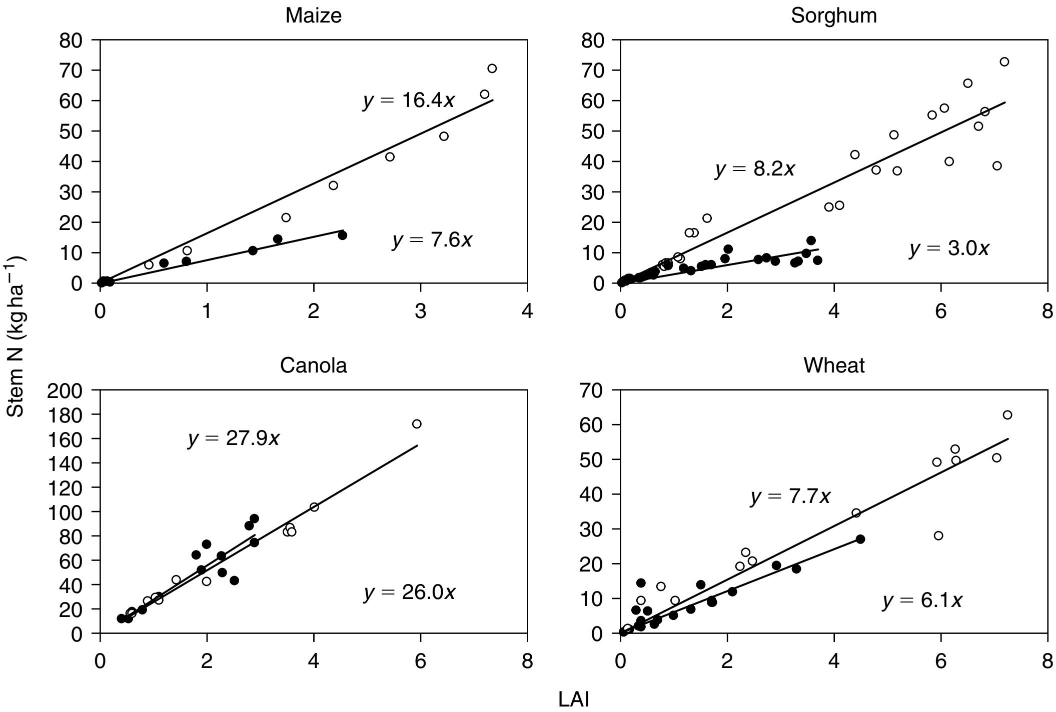

FIGURE 10

Relationship between accumulation of nitrogen in stems and LAI for maize, sorghum, canola and wheat grown under non-limiting (○) or limiting (●) N supply. (Source: Lemaire et al., 2008.)

of N to stem should allow the plant to maintain a high LAI, a high SLN or both, thus favouring light capture and/or RUE under N deficiency. But as stated by Lemaire et al. (2008), the reduction in N allocation to stem could reduce N to reproductive meristems leading then to a reduced grain number and grain yield (Desmotes-Mainard et al., 1999; Vega et al., 2001). If such a hypothesis were confirmed, it would lead to a trade-off between light capture and light use efficiency in one hand, and reproductive growth in the other.

3.3.3. N distribution within the canopies

Numerous studies indicate that N distribution within canopies is not uniform (see review of Grindlay, 1997). This non-uniform distribution can be due to a non-uniform distribution of irradiance within canopies (Hirose and Werger, 1987; Shiraiwa and Sinclair, 1993; Schieving et al., 1992; Lemaire et al., 1991, Anten et al., 1995). Parallel to the extinction of light, there is a gradient of leaf ages in the canopy profile. Hikosaka et al. (1994) and Lemaire et al. (1991) showed that the age effect is less important than the irradiance effect. The relationships between profiles of light and profiles of foliar N in canopies have been analysed in various species: lucerne (Lemaire et al., 1991), sunflower (Connor et al., 1995; Sadras et al., 1993), wheat and oilseed rape (Dreccer, 1999), cotton (Milroy et al., 2001), soybean (Sinclair and Shiraiwa, 1993), *Lysimachia* sp. (Hirose et al., 1988), maize (Drouet and Bonhomme, 1999); *Carex* spp. (Aerts and de Caluwe, 1994).

Rousseaux et al. (1996, 1999, 2000) tried to distinguish the effect of light quality (R:FR ratio) from the effect of light intensity on remobilisation of N from shaded leaves, and found that both signals played a role in determining the start of remobilisation. The adjustment of SLN with irradiance within canopies has been interpreted as a means for optimising canopy photosynthesis through acclimation of the photosynthesis apparatus to the light intensity experienced by individual leaves during their growth (Prioul et al., 1980a). As proposed by Hirose and Bazzaz (1998) the preferential allocation of N to the top of the canopy would correspond to a trade-off between RUE and NUE, that is the increase in dry matter production per unit of supplemental unit of absorbed nitrogen.

This light acclimation of leaves is largely reversible in few days (Prioul et al., 1980b). So young leaves at the top of the canopy with typically high SLN and photosynthesis rate recycle N to growing leaves and drop their SLN as they are progressively shaded by the new leaves. In lucerne (Lemaire et al., 1991) and sunflower (Sadras et al., 1993) leaf N concentration per unit mass basis decreases to a smaller extent than SLN accounting for variations in SLA. The gradient in SLN is more or less steeper within the canopy depending on the light extinction profile that depends on crop species. So some species show an important decline in crop SLN (the average leaf SLN of the canopy) with increasing LAI such as wheat or canola, while species such as maize have a relatively constant crop SLN in relation with their more uniform distribution of light and leaf N throughout the canopy (Lemaire et al., 2008). This inter-specific variation in leaf N profile suggests that species may differ in their acclimation responses to light (Gastal and Lemaire, 2002) leading then to intra-specific variation in the response of canopy photosynthesis to N deficiency.

3.4. Harvest index and components of grain yield

For grain crops, yield is closely correlated to grain number per unit area of soil, which depends on the growth rate in a critical window around flowering (Figure 4 in Chapter 3; Section 3.2.2 in Chapter 15). This period coincides with the maximum rate of crop N uptake (Fischer, 1993). So limitation of crop growth rate by N deficiency at this period decreases grain number and yield in maize (Uhart and Andrade, 1995), wheat (Desmotes-Mainard et al., 1999; Martre et al., 2003) and rice (Mae, 1997). Jeuffroy and Bouchard (1999) established for wheat a relationship between grain number and the severity and duration of the N deficiency before anthesis as calculated by NNI method. In fact N deficiency during the vegetative period has two consequences for the determination of grain number: (i) a lower crop growth rate at anthesis restricting C supply to spikelet primordia and then a decrease in spikelet survival (Arisnaberrata and Miralles, 2004; Desmotes-Mainard and Jeuffroy, 2004) and (ii) a decrease in the N content in the spike stems (Desmotes-Mainard et al., 1999; Desmotes-Mainard and Jeuffroy, 2004) corresponding to a direct effect of N deficiency on floret fertility (Abbate et al., 1995).

The other grain yield component, grain weight, is generally less affected by N deficiency at anthesis than the grain number as shown by Plénet and Cruz (1997) in maize. But it is necessary to take into account the negative correlation between grain weight and grain number: a reduced grain number resulting from pre-anthesis N deficiency can lead to a more favourable source:sink ratio during the grain filling period. Grain filling in both carbohydrates and proteins depends on (i) recycling C and N compounds from vegetative plant organs and (ii) post-anthesis photosynthesis and root N absorption. The relative importance of these two components depends on plant species and probably on genotypes of the same species and their capacity to store C and N compounds in their vegetative organs before anthesis as discussed in the preceding text.

Delaying leaf senescence should allow not only to provide more carbohydrate for grain filling by prolonged photosynthesis, but also to provide C to roots for maintaining N absorption (Dreccer, 2005). So stay-green mutants of maize show a larger source:sink ratio during grain filling with an increased proportion of N derived from soil (Rajcan and Tollenaar, 1999a, b). Using stay-green genotypes in low N supply conditions seems to be beneficial for both grain sorghum (Borell and Hammer, 2000) and maize (Mi et al., 2003).

Recovery of N in grain or nitrogen harvest index (NHI) can be considered as a component of N use efficiency of grain crops (Sinclair, 1998). However breeding progress in NHI has been limited because of the apparent inverse genetic relationship between grain yield and grain protein content in grain crops (Simmonds, 1995; Feil et al., 1990; Canevara et al., 1994). But some recent results show that in maize this inverse correlation can be genetically modulated (Uribelarrea et al., 2007). Chapter 16 reviews the trade-off between yield and grain protein concentration in wheat (Section 4.2).

3.5. Interactions of nitrogen deficit with other resources and stresses

3.5.1. Co-limitation of N with other resources

Crop growth depends on the capture of resources including CO_2, radiation, water, N and other nutrients. So the response of crops to the availability of one particular resource such as N depends on the availability of other resources. In agricultural systems, very often, plant growth is simultaneously limited by several factors (Sinclair and Park, 1993; Sadras, 2005). Kho (2000) developed the concept of limitation index L_i of one resource i, N for example, as being the ratio between the elementary response of crop mass δW to elementary increase in the resource δN, and the use efficiency of this resource W/N:

$$L_i = \frac{\delta W/\delta N}{W/N} \tag{19}$$

This limitation index varies from a maximum of 1 when the N resource is the only limiting factor, to 0 when N becomes non-limiting. This author shows that when several factors are limiting crop growth, then the sum of the limitation index of each factor is equal to 1. Sadras (2005) used the concept of co-limitation following Bloom et al. (1985) who hypothesised that the *plant maximises its growth when growth is equally limited by all resources*. For two resources such as nitrogen and water a co-limitation index CI can then be calculated (Sadras, 2005):

$$\mathrm{CI} = 1 - L_{\mathrm{nitrogen}} - L_{\mathrm{water}} \tag{20}$$

and then maximising crop growth corresponds to maximum CI, that is water and nitrogen are equally limiting. Sadras et al. (2004) showed that, under a given level of stress, crops in SE Australia perform better under conditions of high co-limitation between water and N.

Hooper and Johnson (1999) and Sadras (2005) stressed that co-limitation may arise from variable mechanisms operating at different time scales and at different levels of organisation (molecule, organ, plant, population, community and ecosystem). For instance at the ecosystem level, N × water and N × P interactions reflect the close links between resources mediated by biogeochemical feedbacks (Hooper and Johnson, 1999).

3.5.2. N deficiency – water stress interactions

Sadras (2004) showed that yield and water use efficiency of water and nitrogen stressed wheat crops increase with the degree of water and nitrogen co-limitation. Several studies showed the effect of drought on plant or crop N status (Lemaire and Denoix, 1987; Bassiri Rad and Caldwell, 1992; Karrow and Maranville, 1994; Pratersak and Fukaï, 1997). Reduced crop N uptake under water deficit has been observed for many species: perennial ryegrass (Colman and Lazemby, 1975); rice (Pirmoradian et al., 2004); wheat (Larsson, 1992); and maize (Pandley et al., 2000). It is difficult with these results to determine the relative part of water deficit on (i) reduction in N uptake by diminution of plant growth and hence plant N demand, and (ii) reduction in soil N availability due to soil water deficit. Using N dilution curves, Lemaire and Meynard (1997) showed that drought may create or may increase N deficiency (Figure 11). So when soil is dry, plant N uptake can be reduced more than the decrease of plant N demand, resulting in reduced plant growth by water stress per se. In Figure 11, a reduction in plant growth by water stress only should have led to an increase in plant N concentration due to a lower N dilution effect. So water stress is accompanied by N deficiency. Garwood and Williams (1967) showed that the effect of water deficit on a perennial ryegrass sward was completely removed by an injection of mineral N in a deep (0.6-m) soil layer. This result can be

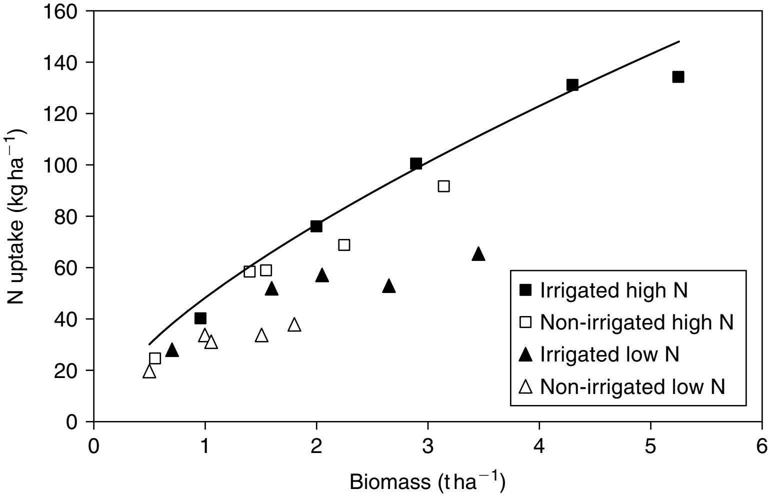

FIGURE 11

Effect of water deficit on N uptake of a tall fescue sward. The curve represents the critical N uptake for temperate grass species with parameters in Table 1. (Source: Redrawn from Lemaire and Meynard, 1997.)

interpreted in terms of a topsoil layer with potentially available mineral N but little water, and a deeper layer with available water but little nitrogen. This has been confirmed by Gonzalez-Dugo et al. (2005), who compared species with different root density profiles. Lemaire and Denoix (1987) on cocksfoot and tall fescue swards showed that during a prolonged drought period when plants depended on water from deeper soil horizons where there is a lack of mineral N, the water use efficiency dropped, indicating that N deficiency increased. This phenomenon has been also observed in maize and sorghum (Lemaire et al., 1996); a greater capacity to extract water from the dry upper layer of soil accounted for sorghum higher rates of N uptake in comparison to maize.

Another factor contributing to co-limitation between water and nitrogen is the effect of soil moisture on soil N mineralisation (Pastor and Post, 1985; Smolander et al., 2005). Birch (1958), Bloem et al. (1992), Franzluebbers et al. (2000) and Austin et al. (2004) showed that soil N mineralisation is rapidly activated during soil re-watering after drought, leading to increased plant N uptake.

3.5.3. N × P × S interactions

Soil phosphorus (P) deficiency is widespread (Kho, 2000), hence the importance of N × P interaction. The effect of P deficiency on the N nutrition of crop can result from two processes: (i) a direct effect of P deficiency on plant growth that should lead to a decrease in crop mass and then, under an unchanged N supply condition, would lead to a diminution of the N dilution process, and hence to an increase in plant N concentration; and (ii) an indirect effect of plant P nutrition on soil N availability through mineralisation of soil organic matter and/or stimulation of root growth. As proposed by Sinclair and Park (1993), the concept of pseudo-substitution of inputs contributes to explaining nutrient co-limitation at the plant and population level. In soil with low N availability, plants may respond to P fertiliser application by increasing root growth and enhanced N uptake. So a part of the crop response to P application can be attributed to an indirect N nutrition effect.

Duru et al. (1997) used the NNI for analysing the interaction between N and P deficiency. Figure 12 shows that the application of P fertiliser on a P-deficient permanent grassland provoked two different effects: (i) an

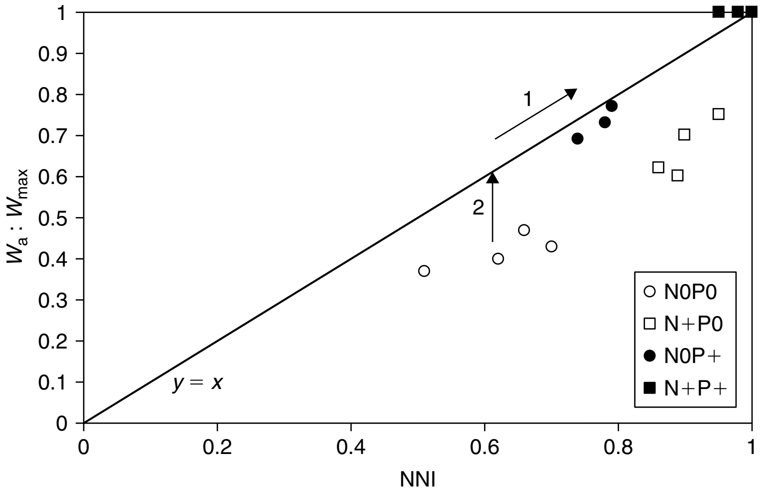

FIGURE 12

The ratio of actual crop mass (W_a) and maximum crop mass (W_{max}) as a function of nitrogen nutrition index (NNI) captures the interactions between N and P in natural grasslands. P deficiency can be decomposed in two effects: (1) an indirect effect through N availability and (2) a direct effect. (Source: Duru et al., 1997.)

increase in the NNI of the sward from about 0.6 to 0.75 for the non-fertilised N treatment and from 0.9 to 1.0 for the N-fertilised treatment; this increase in NNI was associated with a corresponding increase in sward biomass accumulation, that is an indirect effect of P application; and (ii) an increase in the sward biomass accumulation at similar NNI, that is a direct effect of P application. The NNI method therefore seems suitable for detecting and analysing interactions between nitrogen and phosphorus.

Sterner and Elser (2002) and Ågren (2004) revised the concept of ecological stoichiometry, with emphasis on C:N:P ratios and several authors proposed the use of plant N:P ratios as tools for diagnostic and fertiliser management in wetlands and other types of natural vegetation (Verhoeven et al., 1996; Koerselman and Meuleman, 1996; Güsewell and Koerselman, 2002; Güsewell et al., 2003; Drenovsky and Richards, 2004). In crop species, the large capacity of plants to store excess N or excess P in organic compounds (e.g. proteins and phytate) depending on the relative availability of soil nutrients, however, leads to large variability in N:P ratio limiting the value of this indicator for practical purposes (Sadras, 2006).

Plant nitrogen nutrition interacts greatly with S nutrition because some of the amino acids and proteins involved in plant metabolism have S bonds. Sulphur mineralisation in soil is also intimately coupled with N and P mineralisation through stoichiometric relationships. Recently Salvagiotti and Miralles (2008) reported the effect of the interaction of N and S fertilisation on biomass and grain yield of wheat showing that S deficiency may limit, under some conditions, the yield response to N supply.

4. NITROGEN USE EFFICIENCY

Improving NUE is a major goal in plant breeding for sustainable agriculture (Hirel et al., 2007). From an agronomic point of view, NUE is the increment of yield (ΔY) for each added unit of N fertiliser (ΔN_f), i.e.

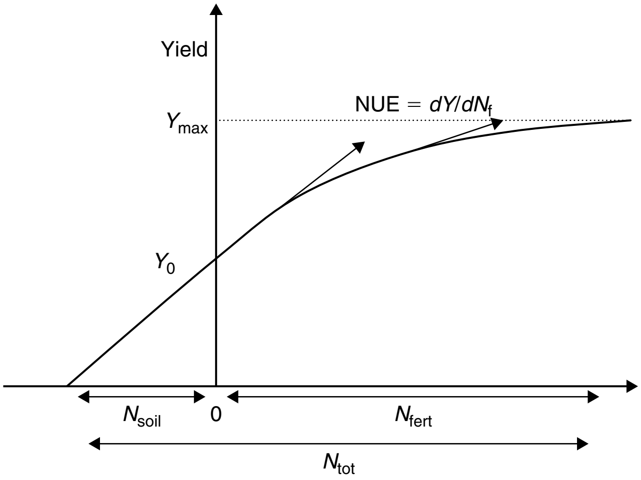

FIGURE 13
Schematic representation of crop response to N supply, and determination of nitrogen use efficiency. N_{soil} is the soil N supply through mineralisation of organic matter, N_{fert} is the fertiliser N supply and N_{tot} is the total N supply for the crop.

the slope of the crop yield response curve to the rate of N supply. As this response curve is asymptotic, NUE declines as the rate of N application increases (Figure 13).

From an ecophysiological and plant breeding perspective, such a global definition of NUE does not allow the identification of plant traits controlling NUE because plants respond to total N supply (N_{tot}) including fertiliser (N_{fert}) and soil N supply (N_{soil}) (Figure 13). So according to variation in N_{soil} due to both soil and climate, different N_{tot} can be obtained with the same N_{fert}, then leading to large differences in NUE not directly attributable to species or genotypes.

Moll et al. (1982) proposed to define NUE as the yield produced per unit of available N in the soil. Hence, the NUE can be divided into two components:

- **(i)** the N uptake efficiency (N_{upE}) as the increment in N uptake by the crop per unit of increment in N supply in the soil;
- **(ii)** the N utilisation efficiency (N_{utE}) as the capacity of the plant to produce a supplement of biomass per unit of N uptake.

According to crop species, yield represents either the above-ground biomass, as for forage crops, or the grain biomass as for cereals, grain legumes or oil seed crops. In grain crops, it is then necessary to take into account the harvest index HI. So NUE can be determined as follows:

$$\mathrm{NUE} = \frac{\Delta N_{\mathrm{upt}}}{\Delta N_{\mathrm{t}}} \times \frac{\Delta W}{\Delta N_{\mathrm{upt}}} \times \frac{\Delta Y}{\Delta W} \tag{21}$$

$$\mathrm{NUE} = N_{\mathrm{upE}} \times N_{\mathrm{utE}} \times \mathrm{HI} \tag{22}$$

Then NUE can be considered as resulting from three groups of processes: (i) the capacity of the crop to capture soil N; (ii) the capacity of the crop to use N for elaboration of biomass; and (iii) the ability of the plant to allocate C and N to grain.

4.1. N uptake efficiency

Genotypic variation in N uptake at different levels of N supply has been investigated in rice (Borell et al., 1998), wheat (Le Gouis et al., 2000) and maize (Bertin and Gallais, 2001). Some studies show that modern cultivars have a higher N uptake than older ones (Brancourt-Humel et al., 2003; Ortiz-Monasterio et al., 1997) because they have a higher N biomass production. This effect corresponds to a shift from points A to points B in Figure 3 and is quantitatively accounted for by Eq. 13. So the first way to improve N uptake capacity of a crop is to increase its growth rate. More interesting would be to increase the N uptake capacity of crop at similar crop biomass production. Figure 14 shows that a cocksfoot sward was more able to capture N than tall fescue when N supply was limited (60 kg N ha^{-1}), while the two species had similar N uptake capacities when rate of supply increased to 120 kg N ha^{-1}. Lemaire et al. (1996) also showed that grain sorghum had a higher N uptake capacity than maize when both crops were grown under low N supply, but the two species removed the same quantity of N from soil under conditions of high N supply. As for cocksfoot versus tall fescue, sorghum appears to have a greater root length density than maize. This would confer sorghum a better capacity of interception of mineral N before it is immobilised by soil microbes within the N mineralisation sites in soil. Soil N recovery by crops is the result of the nitrogen balance between crop uptake rate, immobilisation by soil microbial communities and losses by leaching, denitrification and volatilisation (Lemaire et al., 2004). Root architecture and perhaps root exudates could play an important role in this balance and hence on plant N uptake efficiency. So because of a permanent turnover of N in soil, plants having a dense root system are able to compete more efficiently against microbes for capturing mineral N when the principal source of N supply is mineralisation of organic matter. When there is ample mineral N in soil, the immobilisation capacity of microbial community is saturated and then the difference between species for N mineral capture greatly disappears. Nevertheless, Dybzinski and Tilman (2007) show that differences between species in N uptake capacity can persist even under high N.

Laperche et al. (2007) detected coincidences between quantitative trait locus (QTL) for root architecture and QTL for traits associated to N uptake efficiency on wheat. Moreover Camus-Kulandaivelu et al. (2006) identified a large genotypic variability across maize lines for the density and length of lateral roots. Hence, assuming no trade-offs (Chapter 9) it should be possible to breed maize for improved N uptake in low N

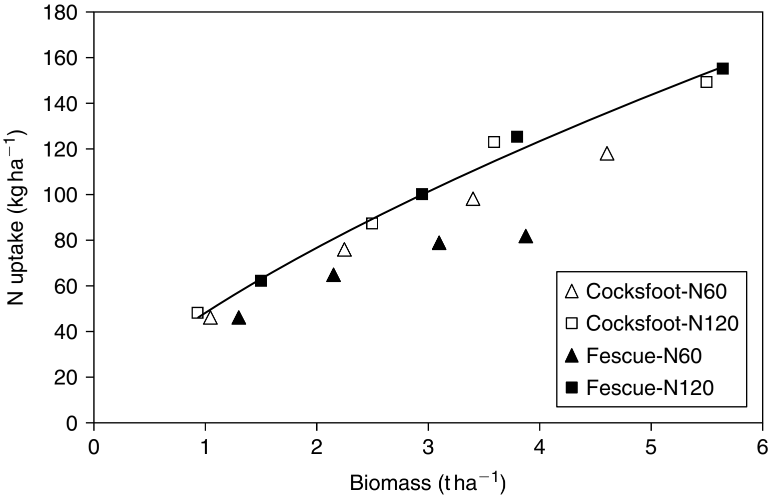

FIGURE 14

Comparison of N uptake of tall fescue and cocksfoot at two rates of N supply. The curve is the critical N uptake for temperate grass species with the parameters in Table 1. (Source: Lemaire and Meynard, 1997.)

supply conditions that would lead to a better use of soil N and then a reduction in the N fertiliser required for a target yield. Genetic studies showed that N uptake efficiency was the most important component of NUE in rice (Singh et al., 1998) and wheat (Le Gouis et al., 2000).

Improved ability of a plant to capture N in low N supply conditions could be related to several mechanisms:

- **(i)** denser root systems which would allow a more complete and rapid exhaustion of soil mineral N and a greater competition of plant against microbes or against neighbours (weeds or companion species in mixtures);
- **(ii)** a more efficient nitrate and ammonium transport system in roots which would also favour the plant in the competition with microbes for N released by gross mineralisation;
- **(iii)** a variation in the quantity and quality of C exudates which could change the gross N fluxes in the rhizosphere (Paterson, 2003).

All these mechanisms can operate simultaneously and all could involve significant trade-offs (Chapter 9). They provide however keys for interpreting genotype × environment interactions and relevant objectives for functional genomic and genetic approaches with the aim of improving N recovery by crops.

4.2. Nitrogen utilisation efficiency

Figure 3 shows that as the crop mass increases (from point A to B), the response to increased N uptake increases (dotted line). Hence the N utilisation efficiency ($N_{\mathrm{utE}} = \Delta W/\Delta N_{\mathrm{upt}}$) increases as crop mass increases. This approach allows the dynamic analysis of N_{utE} where time has to be implicitly taken into account through the crop growth rate: the higher the crop growth rate the higher the crop mass at a given time and then the higher the N_{utE}. So when comparisons of N_{utE} between crop species or genotypes are made, it is important to know that the less productive crop, that is having the lowest biomass, should have a lower N_{utE} than the more productive crop. This is a trivial effect. In consequence breeding for a high N_{utE} should lead to the selection of genotype having the higher crop mass potential. More interesting is detecting differences in N_{utE} among genotypes when comparisons are made at the same crop mass, that is by plotting the ratio of actual crop mass (W_{a}) and maximum crop mass ($W_{\max}$) versus NNI (Figure 12). To the best of our knowledge, such a comparison between crop species and genotypes has not been done and we have no clear indications if variation in N_{utE} persists when genotypes are compared at same growth potential except when we compare C_3 with C_4 crops.

4.3. Harvest index and protein concentration in grain

The effect of N deficiency on HI of grain crops has been analysed in Section 3.4. Equations 21 and 22 indicate that HI is an important source of variation in grain yield per unit of N uptake. In addition to agronomic NUE, the NHI is an important consideration for grain crops (Section 3.4). NHI reflects the grain protein content (Sinclair, 1998) and thus an important aspect of the grain nutritional quality. Desai and Bhatia (1978) showed that NHI among durum wheat cultivars was positively correlated with HI, thus indicating that the distribution of N between straw and grain, to a large extent, depends upon the partitioning of dry matter between these two compartments. These authors showed also that grain protein concentration was not correlated to NHI. Grain produced per unit of N uptake and grain N concentration are inversely related (Figure 15). A variable proportion of the variation in yield per unit N uptake is accounted for by grain protein concentration or by NHI according to the crop type (Figure 15).

5. CONCLUSIONS

The first conclusion of this chapter deals with the necessity to integrate all elementary processes and to scale them up to the level of whole plant and crop where they are agronomically relevant. The nitrogen metabolism

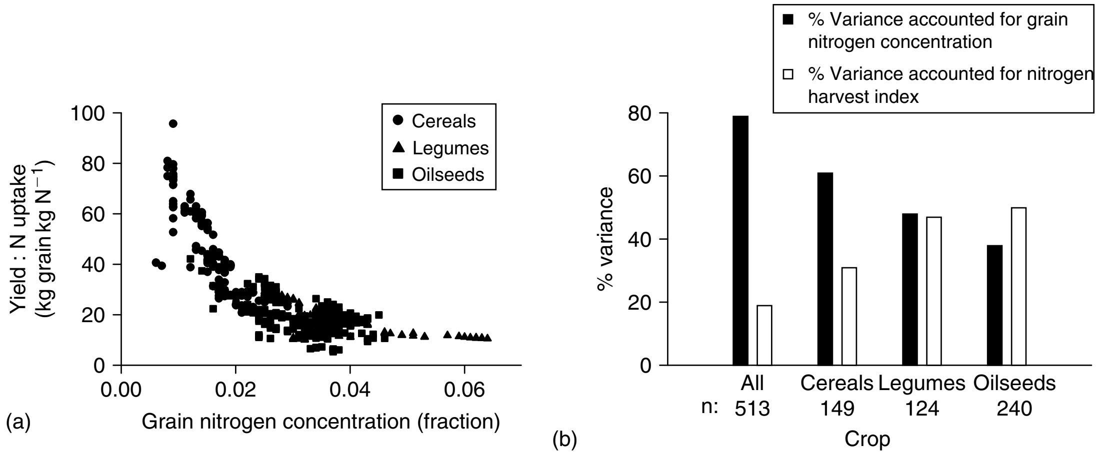

FIGURE 15

(a) Relationship between grain yield per unit nitrogen uptake and grain N concentration across different crop species. (b) Percentage of variance in grain yield per unit N uptake accounted for grain nitrogen concentration and nitrogen harvest. (Source: Sadras, 2006.)

of plants is controlled by physiological process such as nitrate or ammonium transport through cell membranes in root, nitrate reduction in root and leaf, N_2 fixation within nodules in legumes, and ammonium assimilation. Each of these metabolic processes is regulated at molecular levels with some degree of genetic variability. But when all these processes are integrated by scaling up to whole plant and plant population or community level the overall integrated regulation of N uptake and N use efficiency can be resumed by very general rules with very low inter-specific variability. For example, whatever the source of N, that is nitrate, ammonium or biological N_2 fixation, the feedback control of N acquisition by shoot growth appears to operate similarly and dominate the overall N uptake capacity of the plant despite different intrinsic capacity of N uptake per unit of root area or root mass. So the genetic variability in N uptake capacity potentially observed at cell or organ level seems to be 'buffered' at whole plant level where feedback mechanisms are operating (Chapter 1). Moreover when scaling up from individual plant-to-plant population competition for light and photomorphogenic responses leading to isometric growth impose a strong regulation of N uptake dynamics at crop level. Isometric growth of plants and N dilution curves are emerging properties at the plant population level and therefore they are poorly related to molecular and genetic controls. Hence, N acquisition and repartition within a crop in vegetative stage is dominated by the plant–plant interactions for light acquisition: sharing of N among individual plants parallels sharing of light.

The second conclusion deals with the possibilities of application of this integrated knowledge for improving N use efficiency of crops through crop breeding and agronomy. It appears that improving the ability of plants to absorb and accumulate N efficiently from soil (N uptake efficiency) is the first objective for high N use efficiency in cropping systems. This ability of plants to take up mineral soil N has to be investigated both under low and high N conditions. As demonstrated in this chapter, in both conditions N uptake efficiency of a plant is directly dependent upon its growth capacity depending on (i) its own genetic potential, (ii) external conditions such as soil and climate, (iii) cropping management techniques, and (iv) interactions between these three components. So any improvement in crop growth capacity by both breeding and crop management (e.g. irrigation, P, K and S fertilisation, and planting density) will increase N uptake efficiency. More important is to improve the N uptake capacity of a crop species at a similar crop mass. This would allow achieving a given yield with less N fertiliser. Such an objective requires a more efficient root system (root length density) to increase the competitive ability of the plant for using soil mineral N against soil microbes and weeds. Breeding for root architecture is not easy, but several studies demonstrated that it is possible (Section 5 in Chapter 13). Crop management techniques to enhance root development have to be more deeply tested through soil tillage and soil structure preservation and their quantitative effects on crop N uptake capacities must be investigated.

Timing of N fertiliser application is an important way for improving N fertiliser recovery by crops and hence N use efficiency. As crop N uptake capacity is largely determined by crop growth rate, application of N is ideally timed just before the acceleration of growth of the crop. Progress has to be made with non-invasive and operational tools for rapid diagnostics on crop N status, well calibrated with the NNI method (Section 2.2 in Chapter 19). These tools allow monitoring the evolution of plant N status all along its growth period. For most crops, studies on the effect of timing and intensity of short periods of N starvation along the growth cycle would allow the determination of periods of high responsiveness or low responsiveness in terms of grain yield and grain quality. Such information could be then included within decision-making tools to reduce fertiliser supply at the minimum to achieve target yield (Chapter 19).

Breeding plants to increase the N utilisation efficiency for dry matter production (forage or energy crops) is not easy because, apart from the difference between C_4 and C_3 species, no clear inter-specific differences are generally observed as attested by the similarity of the critical N dilution curves. However, the situation is likely to be different if we consider grain production and grain protein content owing to the great differences observed on HI and NHI among genotypes. The identification of the key elements responding to N deficiency in terms of grain development will provide us more information on the extent to which the whole plant N status has localised effects on grain formation, grain development and grain filling processes. Since the overall N status of a plant on its own does not allow for determining the N status of reproductive meristems, the development of more refined models describing both partitioning and translocation within plant will be necessary to take into account the intimate relation between N and C fluxes at the organ level. This will require, as reviewed by Hammer et al. (2004), a cooperative effort between plant molecular physiologists, geneticists, agronomists and specialists in bioinformatics.

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3
PART

Crop Physiology, Genetic Improvement, and Agronomy

CHAPTER 9

Darwinian Agriculture: Real, Imaginary and Complex Trade-offs as Constraints and Opportunities

R. Ford Denison

1. IGNORING TRADE-OFFS SLOWS PROGRESS

Despite continuing progress in plant physiology and molecular biology, the increases in yield potential achieved during the Green Revolution have not been repeated (Mann, 1999a). Yield potential is the yield of a crop that is not limited by water, nutrients, disease or pests (Evans and Fischer, 1999), so average yields can increase with wider adoption of improved cultivars and methods, approaching yield potential as a limit. For example, contest-winning yields for irrigated maize in Nebraska showed no increase from 1980 to 2000, even though average yields showed a steady increase over the same period (Duvick and Cassman, 1999). Cassman (1999) calculated a recent rate of 'genetic yield gain' of 0% per year for tropical rice and temperate maize under low-stress conditions. Trend analysis by Bell et al. (1995), for wheat in Mexico, concluded that 'improvement in yield through breeding was apparent only for cultivars released up to 1981'. Similarly, a comparison among cultivars released in France found that the yield potential of a cultivar released in 1992 was no greater than for one released in 1983 (Brancourt-Hulmel et al., 2003). Other data sets or analyses may lead to somewhat different conclusions, but it is clear that any recent genetic improvements in yield potential fall far short of those during the Green Revolution.

A better understanding of trade-offs is key to understanding past progress, remaining opportunities and the ultimate limits to crop genetic improvement. The success of the Green Revolution depended on trade-offs between the competitiveness of individual plants against each other, which was favoured by past natural selection, and the collective seed yield of crops (Donald, 1968). This chapter discusses these and other trade-offs, which can represent either constraints or opportunities.

For example, there can be a trade-off between the yield per crop and crops per year, because a higher-yield crop will often take longer to grow. Even if there is no increase in yield per crop, a rice crop that achieves the same yield in less time (Peng et al., 2008) can make it possible to grow three rather than two crops per year, increasing total grain production. However, this approach is not feasible where climate limits farmers to one crop per year, as is often the case with maize or wheat. There can also be trade-offs between yield potential and other breeding objectives, such as quality or stress tolerance. Limited progress in yield potential may partly reflect increasing emphasis on these other objectives.

Past natural selection, operating worldwide over millions of years, is unlikely to have missed simple opportunities to improve plant physiological traits, except for those that involve trade-offs (Denison et al., 2003b; Denison, 2007). This is not to say that every possible genotype has been tested by past natural selection.

The number of possible proteins the size of the rubisco large subunit is approximately 20^{489}, which is more than the number of atoms in the visible universe. But 'simple' is defined here as things like changing a few amino acids in an enzyme or two, or increasing the expression of a few genes. There are relatively few simple variants on a given protein sequence and even fewer distinct phenotypes. For example, there are only $489 \times 19 = 9291$ ways to change a single amino acid in rubisco, many of which would be interchangeable in their phenotypic effects. Generating and testing all these variants would be a major undertaking, for humans. But each single-amino-acid mutant (and especially each variant phenotype) must have arisen repeatedly, somewhere on earth, over the course of evolution.

The number of possibilities increases rapidly for multiple replacements, but natural selection has not been limited to changes that can occur in one step (Poelwijk et al., 2007). For example, evolution of antibiotic resistance requiring five mutations could occur by $5! = 120$ different evolutionary trajectories, each corresponding to a different sequential order of the mutations. Experimental testing of the fitness of all possible intermediates showed that 102 of these pathways are unlikely, because they include intermediate genotypes with reduced fitness, but that still leaves 18 plausible pathways (Weinreich et al., 2006). Thus, the variants that have arisen and competed with other alternatives over the course of evolution are a non-random subset of all possible genotypes, biased in favour of similarity to existing genotypes, but vastly in excess of the number of variants that humans will be able to generate and test any time soon. The winners of these past contests inherited the plant kingdom.

All else being equal, traits like efficient enzymes, high photosynthetic capacity and drought tolerance were beneficial throughout evolution, so trade-off-free opportunities to improve these traits are unlikely to have been missed by past natural selection. There remain, however, many opportunities for crop genetic improvement: those that do involve trade-offs. Not every trade-off represents an opportunity, but some of them do.

Some trade-offs that shaped past evolution still act as constraints on further crop improvement. For example, some molecular biologists have fantasised that we could improve the efficiency of rubisco by reducing photorespiration, citing the greater specificity of red algal rubisco for CO_2 (relative to O_2) as evidence that this is feasible (Mann, 1999b). But red algal rubisco also has a lower reaction rate than the rubisco in terrestrial plants (spinach), as shown in Table 1 of the paper by Uemura et al. (1997). The same table shows that rubisco from *Chromatium vinosum* has a higher reaction rate than spinach rubisco, but even worse specificity for CO_2. There appears to be a trade-off between specificity and reaction rate, with natural selection having balanced the two goals differently in terrestrial versus aquatic environments. A detailed mechanism for such a trade-off has been proposed (Tcherkez et al., 2006).

Similarly, a high-profile paper from scientists at Monsanto (Nelson et al., 2007) claimed that a new transgenic maize genotype had 'improved yield ($P < 0.1$)' under drought stress, apparently due to changes in expression of existing genes. Teosinte, the wild ancestor of maize, was repeatedly exposed to drought prior to domestication. Any mutations giving trade-off-free drought tolerance would have displaced drought-susceptible genotypes. Therefore, it seems likely that the reported increase in drought tolerance carries significant trade-offs, not yet discovered or not yet reported. The Monsanto group quickly offered the African Agricultural Technology Foundation a 'royalty-free agreement' to work with this material (Pennisi, 2008), which may prove valuable under some conditions. But they did not, for example, present any field comparisons with leading cultivars under favourable US conditions. Other drought-tolerant transgenic crops, where 'less-desirable developmental phenotypes, such as stunted growth, are often associated with high constitutive expression' (Nelson et al., 2007), have been disappointing. Molecular biologists who ignore trade-offs will continue to waste resources pursuing mirages.

However, some trade-offs can be acceptable, and represent unrecognised opportunities for improvement. Seed dormancy, for example, once acted as an expensive insurance policy for wild plants in risky environments – expensive because of the compound-interest benefit of germinating this year rather than next – but agricultural seed storage facilities can provide similar protection at lower cost. Additional examples are discussed below.

While emphasising the importance of trade-offs, I suggest that not all hypothesised trade-offs are real; some are imaginary. Some trade-offs are so complex that they may provide only limited guidance for crop improvement programs. Real trade-offs may represent constraints, which we would be foolish to ignore, but some trade-offs that shaped past natural selection in nature now offer opportunities worth pursuing. These points will be developed in the last two sections of the chapter, after presenting some background, including an attempt to classify trade-offs.

Yield potential will be an important goal as long as human population or per capita demand for farm products (including grain fed to animals or used for industrial processes, such as ethanol production) continues to grow. Wider adoption of improved cultivars or methods can increase average yields, as can genetic improvements in pest resistance (at least until new pests arrive or evolve), but increasing yield potential is essential to long-term progress (Section 1 in Chapter 15).

This point is illustrated by a comparison of the Green Revolution rice cultivar IR8, released in 1966, with more recent cultivars (Peng et al., 1999). When grown side-by-side, today, the recent cultivars have higher yield than IR8. But previously published data show that, when it was first introduced, IR8 had as high or higher yield as more recent cultivars do today (Peng et al., 1999). In other words, the apparent progress in yield potential over the last four decades was due to a decrease in the yield of IR8 since 1968, not increases over IR8's baseline yield.

Why has the yield of IR8 decreased? If the decrease is due to evolution of pests and pathogens that attack IR8 – pests have had less time to adapt to more recent cultivars – then much of the apparent progress since 1968 could be classified as Red Queen breeding (Denison et al., 2003b): running as fast as we can just to keep up with evolving pests and pathogens. Pest control in these tests was apparently good, but cryptic pathogens, pests attacking roots etc. might not have been detected. Adaptation to changing abiotic conditions, such as increasing temperatures (Peng et al., 2004) or changes in soil properties (Schmidt-Rohr et al., 2004), may also be important. Decreases in yield of a given cultivar over time are probably not universal, but they have also been reported in sunflower; de la Vega et al. (2007) attributed yield declines in individual sunflower cultivars after release to some combination of pest evolution and a soybean-driven shift to more marginal environments. In such cases, yields would decrease, rather than staying the same, were it not for the continuing efforts of plant breeders. To the extent that conditions continue to change – pests will certainly continue to evolve – some genetic improvements will be ephemeral, but they are nonetheless important.

Real increases in yield potential will require improvements in the physiological traits of crop plants. Crops resistant to insects or to herbicides can increase yields or lower costs, but only temporarily, until the insects or weeds themselves evolve resistance. A hypothetical trade-off-free increase in photosynthesis, on the other hand, could still be contributing to higher yields thousands of years from now. But the key word is 'hypothetical' (Box 1). Actual improvements have rarely, if ever, been trade-off-free.

Sinclair et al. (2004) attributed our lack of progress to problems with scaling up, for example from leaf photosynthesis to seed yield. I agree that scaling up can be a significant problem, but suggest that an evolutionary perspective and greater attention to trade-offs will be at least as useful as a focus on scale. Consider, for example, their most detailed example. They begin by assuming a 50% increase in rubisco gene expression. This is more realistic (in the sense of being feasible) than fantasising about an increase in the efficiency of rubisco. After all, natural selection has been working on rubisco efficiency for millions of years. Sinclair et al. (2004) estimated that this increased gene expression would increase canopy photosynthesis by only 18%, for plausible reasons that can reasonably be summarised as 'scaling up' issues. For example, only a fraction of leaf area is exposed to the high light needed to benefit from more rubisco. But then a new factor enters their analysis: the nitrogen requirements for seed protein. This is a legitimate constraint, but its quantitative consequences depend on the choice of soybean as the example crop. Of all crops that could have been used in this example, soybean requires the most nitrogen per gram of seed (Sinclair and de Wit, 1975). On the other hand, soybean, unlike rice, could use some of its 'extra' photosynthate to power N_2 fixation.

BOX 1 Yield and photosynthesis

Claims that major genetic improvements in photosynthesis are feasible or even imminent have attracted attention and resources for at least three decades (Mann, 1999b). For example, Zelitch (1975) claimed to have plants with '50% of the normal rate of respiration, and an increased net photosynthesis of about 40%'. Somerville and Ogren (1982) suggested that 'directed amino acid substitutions' in rubisco would soon increase photosynthesis. Ku et al. (2000) claimed that transgenic rice expressing some C4 enzymes from maize had 30–35% higher grain yield in preliminary field tests. None of these have led to cultivars that outperform those from conventional breeding. Such claims resemble 'vaporware' (Paris, 2001), exuberant descriptions of computer software that may actually never be released, intended mainly to suppress competitors. When natural selection does that, as when plants make taller stems to shade their neighbours, it typically results in lower overall productivity.

A more realistic view is to assume that all simple variations on extant photosynthetic systems have arisen repeatedly and competed with each other over the course of evolution. The enzyme structures and gene expression levels that our crop plants inherited from their wild ancestors must therefore be already at least as effective in promoting individual fitness as any simple alternative. This implies that further genetic improvement will require either radical changes to the photosynthetic machinery – at least as radical as the change from C3 to C4 – or exploiting trade-offs, such as those between individual fitness and the collective performance of plant communities (Box 2) or between past and present conditions.

Changing conditions provide new opportunities, but they may also undermine some proposed approaches to crop genetic improvement. For example, the yield benefits of a hypothetical CO_2-concentrating (C4) rice would decrease as atmospheric CO_2 increases (Sage, 2000).

Long et al. (2006) have suggested that 'the most widely promoted strategies – conversion of C3 crops to C4 and improved specificity of rubisco – may be the most difficult to achieve and, from a theoretical basis, might result in lower and not higher' efficiency. For example, if there is a trade-off between the CO_2-specificity of rubisco and photosynthesis rate (Tcherkez et al., 2006), then anticipating increases in atmospheric CO_2 might call for lower rather than higher specificity. Of the alternatives suggested by Long et al. (2006), engineering leaves to 'express a high catalytic rate form of rubisco initially . . . replaced with a high specificity form during shade acclimation' is an interesting but challenging approach, perhaps novel enough to be untested by natural selection. They also suggest that improvements in canopy architecture could increase radiation-use efficiency. This is consistent with the analysis of Trenbath and Angus (1975), who noted that 'the high proportion of crops having the theoretically least favourable pattern of leaf inclination . . . [maybe due to] earlier natural selection for aggressiveness . . . may also represent scope for improvement'. The likely trade-off with competitiveness may be acceptable. Combining the power of molecular methods with an appreciation of such trade-offs may someday lead to significant genetic improvement of crop photosynthesis.

Assuming for the sake of argument that genetic improvement in the efficiency of photosynthesis is possible, how might this affect yield?

One extreme view is that plants often produce excess photosynthate, so increasing photosynthesis could do more harm than good. It has even been suggested that leaf senescence is a way of disposing of excess carbon (Thomas and Sadras, 2001). My view is that senescing leaves represent a cost, but one outweighed by benefits like the recycling of nitrogen into seeds. During vegetative growth, nitrogen also moves from lower to upper leaves, with some of it lost in the process, but that nitrogen loss is apparently outweighed by the benefit of increased photosynthesis (Oikawa et al., 2008; Section 3.3.3 in Chapter 8). A plant consistently plagued by excess photosynthate could solve this hypothetical problem by moving nitrogen in the opposite direction, from upper to lower leaves. The fact that this never happens is an example of the evidence against a consistent surplus of photosynthate. Short-term surpluses may be common, however, and the relative importance of source and sink limitations may change over the growth cycle.

At the other extreme is the hypothesis that increasing photosynthesis would almost automatically lead to higher yield (Long et al., 2006). The key evidence comes from yield increases of up to 35% with elevated CO_2, under controlled conditions. Under field conditions, however, a meta-analysis concluded that 'only cotton, a woody crop, showed a significant yield enhancement with growth at elevated [CO_2]', whereas wheat and rice did not (Ainsworth and Long, 2005). There are also alternative explanations for even the non-significant apparent increases in yields of these crops, such as partial stomatal closure reducing water stress, although Long et al. (2006) do present some plausible arguments against this possibility.

(Continued)

BOX 1 Continued

Yield depends on multiple factors, so an increase in photosynthesis may be necessary but not sufficient to increase yield. The analysis by Sinclair et al. (2004), discussed Section 1, is a good example of how nitrogen supply and increased photosynthesis could interact to determine yield, depending on seed composition. A related point pertains to a suggested side-benefit of the proposed conversion of C3 crops to C4 photosynthesis. Because C4 crops concentrate CO_2 inside bundle sheath cells, their photosynthesis requires less rubisco, and therefore less nitrogen (Raven et al., 2005). Greater nitrogen-use efficiency for photosynthesis may have little effect on the overall need for nitrogen inputs, however, because nitrogen exported off-farm in grain or milk protein still needs to be replaced for long-term sustainability (Denison and Kiers, 2005).

This is where trade-offs come in. To the extent that soybean seed yield is limited by nitrogen, as assumed, we could increase seed yield simply by breeding for lower percent protein (and therefore lower nitrogen) in seeds. If nitrogen supply to seeds were the only factor limiting yield, then a 50% decrease in percent protein in seeds would double seed yield, while still giving a seed protein concentration greater than rice or maize. Nitrogen is unlikely to be the only limiting factor, but high-protein seeds also have a higher photosynthate cost (Penning de Vries et al., 1974). Whether lower-protein seeds would be a good idea or not depends on many factors. A higher-yielding cultivar with lower-protein seed might be appropriate for some uses but not others. Trade-offs imply choices. But first we need to identify and characterize the relevant trade-offs.

2. REAL, IMAGINARY AND COMPLEX TRADE-OFFS

Trade-offs can represent either constraints or opportunities. Some trade-offs limit our ability to achieve two conflicting goals simultaneously, such as maximising both seed yield and protein content. Identifying other trade-offs, however, can reveal new opportunities. In some cases, crops may have inherited limitations that are the result of past trade-offs that are no longer relevant. For example, seed shattering may have been favoured by natural selection among wild plants, but it is an undesirable crop trait in most systems. There are also various trade-offs between individual competitiveness and the collective productivity of the plant community (Donald, 1968). In such cases, natural selection continually favours individual competitiveness, but we can reverse the process and favour community-level crop performance instead (Denison et al., 2003b).

An important first step is to determine whether a hypothesised trade-off is real, imaginary or complex. Real trade-offs are those that are well-documented and well-understood, at least by the relevant experts. Physical linkage between two genes may represent a real short-term trade-off, if a beneficial allele is linked to one with negative effects. However, the problem of linkage can be solved. The emphasis here will be on trade-offs that are more fundamental. Simple examples include trade-offs inherent in conservation of matter (for each element) and energy. A given carbon atom can be used to make leaf or root, but not both at once. A given NADPH molecule in a leaf may be used to reduce CO_2 or nitrate, but not both. Conservation of matter has various implications, discussed previously in some detail (Denison and Kiers, 2005). For example, a farm that exports nitrogen and phosphorus to distant cities in grain or milk needs to replace those nutrients for long-term sustainability, no matter how efficient is within-farm nutrient cycling or crop nutrient use (see Box 2 in Chapter 1).

Imaginary trade-offs are those that have been proposed, but which lack a solid theoretical or empirical foundation, at least at present. For example, popular critiques of the Green Revolution sometimes claim that ‘high-yielding’ cultivars actually yield less than traditional varieties, when grown without fertiliser. However, the main reason that these cultivars have higher yield is their higher harvest index, that is greater allocation to grain rather than stem. Why should this trait lead to lower yields, relative to traditional varieties, when soil fertility is low? The available experimental evidence is inconsistent with the claimed trade-off. Austin et al. (1980) found that the wheat genotype with the highest yield at a high-fertility site also had the highest yield at a lower-fertility site, perhaps due to its harvest index of about 50%. Another wheat genotype, with a harvest index of about 35%, had the lowest yield at both sites; see also Figure 1 in Chapter 2. No trade-off there! Similarly, although the Green Revolution rice variety IR8 outyielded older varieties most at higher fertility, there was a slight yield benefit even without nitrogen fertiliser (Khush, 1999). This is not to deny the possibility of other trade-offs associated with Green Revolution cultivars. For example, greater allocation to grain at the expense of stem results in shorter plants, which are less competitive with weeds. Whether this trade-off is important depends on whether weeds can be controlled well even with less contribution from crop competitiveness. Chapter 18 discusses in detail the adaptations and trade-offs involved in the improvement of crop competitiveness with weeds.

The lack of a yield trade-off linked to nitrogen supply also does not exclude the possibility of trade-offs linked to other inputs, such as water. Araus et al. (2002) plotted grain yield against an 'environmental index' corresponding to a range of locations differing in water supply and other factors with higher index values corresponding to higher yields. They hypothesised (their Figure 3B) that cultivars selected by plant breeding programs in stressful environments could have higher yield, in those environments, relative to cultivars selected in more favourable environments. This is conceptually plausible. A cultivar with consistently deeper rooting might do better under drought, while paying a yield penalty for expensive root growth under well-watered conditions. Often, however, 'modern cultivars have consistently outyielded older cultivars, even in the lowest-yielding conditions' (Araus et al., 2002), as shown in their Figure 3C and D. Even if modern cultivars consistently yield better than traditional ones across a range of nitrogen and water supplies, there could still be particular traits that are beneficial under drought but harmful when water supplies are adequate.

Finlay and Wilkinson (1963) compared the yield of 277 barley varieties across a range of environments. Some pair-wise comparisons among varieties were consistent with trade-offs, but other varieties were superior in both favourable and unfavourable environments. Their most intriguing result, however, was that all of the varieties with the highest average yield across environments had similar, and intermediate, yield stability across environments. Apparently higher yield stability limited positive response to favourable environments, whereas lower yield stability mainly reflected decreasing yield under stress, rather than increasing yield under good conditions.

Weiner (2003) claimed that 'principles of engineering [not discussed in any detail] suggest that the relationship between short-term yield and sustainability will inevitably be negative'. This may be another imaginary trade-off. There are certainly some practices that would increase short-term yield at the expense of long-term sustainability. Solarisation, that is solar heating of soil beneath plastic films (Chase et al., 1999), may control weeds (Chatfield et al., 2000) and increase yields (Nair et al., 1990) in the short term. But if higher soil temperatures increase net mineralization of soil organic matter, that could have negative long-term effects. Similar arguments apply to tillage. However, other agricultural practices are probably beneficial from both a short- and long-term perspective. If applying fertiliser increases growth of non-harvested plant parts as well as grain, then soil organic matter should increase. So there is no universal trade-off between short-term yield and sustainability. On the other hand, a genetic increase in harvest index may be an example of such a trade-off, increasing grain yield but reducing the input of crop residues to soil organic matter.

Complex trade-offs are those for which there is good empirical or theoretical evidence but limited understanding. A complex trade-off may involve many interacting variables (Chapin et al., 1987), some of which are difficult or impossible to predict. These complications constrain our ability to improve crop management or crop genetics. Complex positive interactions are also possible, of course, but a trait that enhances seed production in two or more different ways is even more likely to have been optimised already by natural selection.

Plant chemical defences against herbivory are a good example of a complex trade-off. Cyanogenesis (cyanide production when wounded) benefits clover in warm climates but is harmful in cold ones (Daday, 1954). Benefits depend on the presence of cyanide-sensitive herbivores, whose prevalence may depend on cultural conditions as well as temperature. Costs (and therefore net benefits) are even more complex. Kakes (1989) found reduced flower production in cyanogenic plants, qualitatively consistent with a simple trade-off based on the metabolic cost of producing cyanogenic glycosides. But Kakes calculated that the carbon cost of producing cyanogenic glycosides was <5% of what would be needed to explain the decreased flower production. So there must be costs of cyanogenesis beyond the direct carbon costs. Agrawal and Karban (1999) identified some of the ways in which chemical defences can impose a fitness cost, in a discussion of the benefits of inducible, rather than constitutive defences. Of these, auto-toxicity (perhaps exacerbated by cold) seems most likely to apply to cyanogenesis, but there are others. Specialist herbivores may use defensive chemicals to which they are resistant as cues for finding their hosts. Spatial or temporal patchiness may increase herbivore movement, which can make them more apparent to predators like birds. Long-lived plants may benefit from slowing the evolution of resistance to their defences. Chemical defences may also have adverse effects on pollinators or other beneficials.

Inducible defences are an example of how plasticity in plant responses to their environment (discussed further below) can reduce the cost of trade-offs among environments (e.g. those with and without a particular pest). The complexity of inducible responses may make it difficult or impossible to predict whether they will provide a net benefit to the plant over a realistic range of environments, although having been favoured consistently by past natural selection hints at their value.

Once a trade-off is identified as real, imaginary or complex, how can we use this information? Real trade-offs must be recognised as important constraints on attempts to improve crop genetics or crop management. Imaginary trade-offs can be ignored for now, recognising that additional research may move some of them into the real or complex categories. Information about complex trade-offs will rarely provide simple and direct guidance. Without knowing how multiple factors interact over the range of environments to which our crops will be exposed, we may not be able to predict whether a given genetic change will be an improvement or not. Even without full understanding, however, recognition of complex trade-offs may at least keep us from making things worse. For example, we should hesitate before changing a chemical defence that natural selection has made inducible, to make it constitutive instead. If we were to ignore the complex trade-offs that have shaped plant defences, we might develop a crop that is more pest-resistant, but lower-yielding when pests are absent, for any of the reasons just discussed.

3. TRADE-OFFS AS CONSTRAINTS

Trade-offs based on conservation of matter (for each element) are unambiguously real, even if they are sometimes ignored. I remember seeing the suggestion that someone should breed much taller rice (to grow well in deep water) with the same high yield as short, Green Revolution varieties. The problem, of course, is that those varieties have higher yield mainly because they are short, so that they can allocate more resources to grain rather than stem. Similarly, the potential of perennial grain crops is also less than sometimes claimed (Cox et al., 2002), because of trade-offs discussed below.

Although compensation among yield components (e.g. seed number vs. seed size) as a consequence of conservation of matter has long been recognised (Adams, 1967), the importance of this constraint has sometimes been disputed or ignored. Spaeth and Sinclair (1984) suggested that 'the fact that the absolute magnitude of the negative correlations has been relatively low has implicitly offered the prospect that while the problem of compensation is a general phenomenon, it is not obligatory'. They, too, found only weak negative correlations, overall, between seed number per soybean plant and mass per seed. But they showed that variation in size among plants confounded what was fundamentally a strong underlying correlation. Within a given plant size range, they found strongly negative regressions (r up to -0.99) between seed size and seed number.

This shows a trade-off, at least for soybean, but the quantitative value of the trade-off is also important; for example a 10% decrease in seed size would be more than acceptable if seed number doubled. Henery and Westoby (2001), comparing wild species, found that the log-log slope of seed number (per square metre leaf canopy) as a function of mass per seed had a slope of -1, as expected from conservation of matter. Nitrogen or phosphorus per seed predicted seed number even better than seed size did, consistent with limitation by these two nutrients under natural conditions. Moles and Westoby (2006) have reviewed some of the complexities in seed-size trade-offs important in natural selection, including apparent effects on reproductive lifespan in perennials. Although increases in yield always involve increases in seed size or seed number, trade-offs mean that breeding for seed size or number will not automatically lead to higher yields (Spaeth and Sinclair, 1984).

Conservation of matter sets an ultimate limit on the product of seed size and number, as shown by Henery and Westoby (2001). The wild plants they studied had presumably evolved a fitness-enhancing balance between source and sink limitations. For crops, especially in new environments, there may still be room for improvement. Major crops appear to differ in the extent to which seed growth is source- versus sink-limited. In experiments manipulating source:sink ratios of individual plants (i.e. no evolution), soybean seed weight increases with increased photosynthate per seed, but this is less true of maize and especially wheat (Borrás et al., 2004). Increasing potential seed number or size may increase yield, but only to that extent that photosynthate and nutrient supply are sufficient to support more seed growth. The related issue of seed growth responses to variation in resource supply over years is discussed below.

The best solution for a given trade-off depends on the conditions where a crop will be grown. In the field, there is often more phosphorus available near the soil surface, but more water may be available deeper in the soil. Shallow roots are therefore most valuable when phosphorus is limiting, whereas deep roots are more valuable under drought. Plants typically adjust rooting patterns for soil conditions, but there are nonetheless genetic differences in rooting patterns. Ho et al. (2005) compared bean cultivars differing in rooting depth. Under field conditions, shallow-rooted cultivars produced more biomass than deep-rooted ones in the low-phosphorus, irrigated treatment, but the reverse was true in the high-phosphorus, non-irrigated treatment. Chapter 13 analyses root traits, their adaptive value and trade-offs in specific target environments.

Simple trade-offs based on conservation of matter usually lead to negative correlations between current reproduction and future survival and reproduction (Obeso, 2002). A perennial that needs to store resources for winter survival and spring regrowth is unlikely ever to match the yields of annuals, which can transfer all mobilizable resources into seeds. The argument that ‘perennials, which are larger overall than annuals, offer more potential for breeders to reallocate vegetative growth to seed production’ (Glover et al., 2007) is fallacious. It is not the size of the individual plant that matters, but rather the total crop biomass per hectare and how it is partitioned. To the extent that wild perennials have lower allocation to reproduction than wild annuals, there may be more room for improvement, but that does not mean that we can reach, or even approach, the harvest index of annuals. Perenniality can have advantages in some situations (e.g. reduced erosion), but ignoring or denying the trade-offs involved could lead to unrealistic expectations.

With enough data and enough quantitative analysis, even complex trade-offs may have the potential to guide crop improvement programs. The extent to which apical dominance is beneficial depends on conditions, for example, leading to complex interactions with herbivory (Aarsen, 1995). Miller et al. (2008) showed how interactions with herbivores can affect trade-offs. They found that, at least in *Opuntia*, increased flowering attracts more herbivores, leading to more floral abortion. Thus, plants that invest in more reproduction at the expense of vegetative growth (which would have increased photosynthesis and future reproduction) do not receive as much short-term benefit as expected. They showed that this explains a discrepancy between the actual allocation of reproductive effort in *Opuntia*, shaped by past natural selection, and that predicted from carbon balance alone. This illustrates how natural selection can solve complex optimisation problems involving multiple constraints. Perhaps, in some cases, we can learn to do the same.

4. TRADE-OFFS AS OPPORTUNITIES: CHANGED CONDITIONS

Some trade-offs that constrained past evolution may represent opportunities for present-day improvements. These fall into two major categories: (1) trade-offs that have changed with changing conditions and (2) trade-offs between individual competitiveness and the collective performance of plant communities.

Evolution always lags behind current conditions. Therefore, our crops may have inherited traits that are no longer beneficial. If crops over-invest in roots (Passioura, 1983), because of past natural selection in environments with unpredictable droughts, then breeding for reduced allocation to roots may increase yield, especially under irrigation. Consistent with this hypothesis, modern, higher-yielding wheat cultivars do have lower root:shoot ratios (Siddique et al., 1990).

Interactions among multiple trends complicate matters. Consider the simultaneous trends of increasing soil nitrogen supply, due to fertiliser use, and increasing atmospheric CO_2. If we assume that crops are still somewhat adapted to earlier conditions, what are the implications for crop genetic improvement? With higher atmospheric CO_2 concentrations than in the past, leaves need less rubisco to achieve the same photosynthetic rate. On the other hand, increased nitrogen in agricultural soils means that rubisco is cheaper, in the sense that nitrogen supply is less of a limitation for protein synthesis. Furthermore, amino acids 'stored' in rubisco can eventually be recycled into seed proteins, so the optimum amount of rubisco may exceed that needed for photosynthesis alone. A given amount of nitrogen could be stored either in fewer leaves with more rubisco per leaf or in more leaves with less rubisco per leaf. Thus, crops growing under current or future conditions might benefit from either higher or lower rubisco than in the past, but calculating the optimal amount might be difficult.

Acclimation or phenotypic plasticity is an additional complication. Without any genetic change, individual plants adjust resource allocation (e.g. root vs. shoot growth) and other phenotypic traits (e.g. stomatal opening) based on current conditions. For example, plants tend to produce less rubisco under elevated CO_2, especially if nitrogen supply is limited (Stitt and Krapp, 1999). The acclimation strategies of crop plants may not be optimum, however, having been shaped by natural selection under a range of conditions different from the present. Determining the optimum strategy and implementing it genetically is probably beyond our current abilities in many cases, but see below for a promising counter-example.

5. TRADE-OFFS AS OPPORTUNITIES: INDIVIDUAL VERSUS COMMUNITY

Trade-offs between past natural selection and present human goals may offer the most promising opportunities for crop improvement. The most important of these trade-offs is that between 'the competitive ability of cultivars, on the one hand, and their capacity for yield in pure culture, on the other' (Donald, 1968). Low competitiveness is necessary, but not sufficient, for high yield potential (Box 2). Donald discussed several specific traits that involve such trade-offs. For example, he advocated erect leaves, less branching, early flowering (so a longer grain-filling period) and shorter stems, a trait responsible for most of the yield advantage of Green Revolution cultivars; Table 3 in Chapter 18 compares cereal ideotypes for three situations, namely isolated plants, crop-weed mixture and dense monoculture. Varieties that put more resources into grain rather than stem have higher yield, in pure culture, but they are less competitive than taller, lower-yielding varieties. A review of published data supported several of the relationships claimed by Donald between yield and less-competitive crop traits (Denison et al., 2003b).

Additional data consistent with Donald's advocacy of erect leaves, in particular, were published by Pendleton et al. (1968) who used both genetic and mechanical manipulation of leaf angle in maize. They reported up to 40% higher yield with erect leaves than with horizontal leaves. With the sun roughly overhead – this is less common for temperate than for tropical crops – erect leaves spread the available light over a larger area. If photosynthesis tends to saturate at high light, then doubling the illuminated leaf area will increase canopy photosynthesis, even though the irradiance per unit leaf area is halved. The results of Pendleton et al. (1968) are interesting because, as a C4 plant, maize leaves should be less prone to light saturation than soybean leaves, for which Kokubun (1988) reported similar effects of leaf angle. Sinclair and Sheehy (1999) have noted the importance of leaves for storing nitrogen for grain filling, assuming that N uptake from soil during grain-fill is insufficient. They suggest that, if greater leaf area is required for this N storage, then leaves

BOX 2 Competitive ability of individual plants versus yield per land area

One requirement for a group of plants to have high yield is that each plant has little tendency to suppress the yield of its neighbours, which are presumably fellow crop plants. This assumes good weed control. Although poor competitors may not be high-yielding – they may be defective in some way – high-yielding cultivars will necessarily be poor competitors. For example, Jennings and de Jesus (1968) found that high-yielding dwarf rice was quickly displaced in competition with a lower-yielding traditional cultivar. Comparing different generations in a barley breeding program, Hamblin and Donald (1974) found that some traits that had a negative effect on individual plant performance in the F_3 generation were associated with higher F_5 whole-plot yields. In addition to decreased height, which sacrifices competitiveness to gain higher harvest index and lodging resistance, other 'communal' traits proposed by Donald (1968) can contribute to the collective performance of crop communities by sacrificing individual plant competitiveness, as discussed in Section 5. Achieving the benefits of less-competitive cultivars may require high seeding rates, good weed control and uniformity in both seeding and emergence.

Resistance to yield suppression by neighbours is also presumably desirable. Reynolds et al. (1994) compared wheat genotypes that had high versus low yield potential. When competing plants were removed midseason, genotypes that had low yield in monoculture had similar yield to those with high monoculture yield. The difference was that high-yield-potential genotypes maintained nearly this same yield in the presence of neighbouring plants, whereas competition reduced the yield of low-yield genotypes by half. Sadras et al. (2000) found a similar result for sunflower, after correcting for the effects of disease. The trick, then, is to breed crops that tolerate competition, but not by suppressing their neighbours. Chapter 18 (Section 9) discusses the trade-off between yield and competitive ability with emphasis on plant traits (e.g. early vigour, dry matter allocation, phenology) and crop-weed interactions.

must be more erect, in order for light to be adequately distributed throughout the canopy. Chapter 8 discusses in detail the links between canopy architecture, light distribution and vertical profiles of foliar N.

The value of erect leaves depends on close spacing of plants. Otherwise, the greater light interception by horizontal leaves can outweigh the greater radiation-use efficiency of erect leaves. Angus et al. (1972) found that closer plant spacing increased yield of an erect-leaf barley cultivar but decreased yield of a lax-leaf cultivar. The key trade-off here, as with plant height, is yield versus competitiveness. Erect-leaf cultivars are generally less competitive with weeds (Tanner et al., 1966). Furthermore, erect-leaf cultivars, like cultivars with less branching (another of Donald's suggestions), are less able to fill gaps resulting from uneven seeding and seedling mortality.

Crop performance during drought might seem to depend on the interaction of individual plants with their physical environment, rather than the individual-versus-community trade-offs discussed here. But Richards (2006), reviewing breeding for dry environments, noted that it is 'the community of plants that form a crop'. Some of the past successes he discusses are linked to more conservative water use by individual plants, due to increased resistance of roots or stomata. Much of the water that is thus saved for later use would, in nature, be used by competing plants. It is therefore not surprising that selection by humans was required, to reverse the effects of past natural selection. Other traits increase yield under drought (and perhaps also under favourable conditions) by increasing harvest index. For example, greater allocation to maize ears, at the expense of tassels and stems (Monneveux et al., 2005), increases the collective seed yield of groups of maize plants. But individual plants that invest less in stems may be less competitive for light, and those that allocate less to tassels will have lower male reproductive success. Under drought, plants sometimes increase allocation to pollen rather than seeds, perhaps because pollen is a less expensive way to increase individual fitness (Marris, 2008). Again, reversing the effects of past natural selection may increase seed yields.

There are likely to be additional trade-offs between competitiveness and yield, not discussed by Donald (1968). Crops whose upper leaves have less chlorophyll (Pettigrew et al., 1989) or less diaheliotropism would tend to make more light available to leaves lower in the canopy. Like crops with erect leaves, and for similar reasons, they would be less competitive but potentially higher yielding. As another example, past selection for competitiveness with neighbours may have favoured earlier spring leaf growth in perennials than is optimal for balancing the risk of losing leaves to frost (along with their nitrogen) versus the potential benefit of earlier photosynthesis (Denison et al., 2003b).

One way that plants manage risk, particularly that related to unpredictable environments, is through phenotypic plasticity. Although plasticity is often beneficial, DeWitt et al. (1998) have discussed some of its costs and limitations. For example, they mention the metabolic cost of ethylene receptor proteins, although that particular cost is presumably miniscule relative to the benefits that result from better regulation of various processes by ethylene. In terms of limits, they note that plasticity may not always lead to better phenotypes than fixed traits. In a relatively predictable environment, a plant that waits for surface soil to dry before growing roots into deeper soil may obtain less water than a neighbour with constitutively deeper rooting.

Like fixed traits, the DNA-programmed rules that control plasticity have been shaped by past natural selection. Here too, there may be opportunities for improvement, particularly when collective performance was limited by past trade-offs with individual competitiveness. For example, plants could respond to greater resource availability in good years by increasing either seed number or seed size. Sadras (2007) showed that wheat and soybean have much more variation in seed number than in seed size. He makes a plausible case that, although we have bred for seed-size uniformity, this only reinforces natural selection (before and after domestication) for greater plasticity in seed number than in seed size. He reasoned that, given diminishing returns on seed size (Smith and Fretwell, 1974) and the trade-off between size and number, plants with extra resources should increase seed number more than seed size. Of course, under natural selection there may be diminishing returns on seed number as well, if limited seed dispersal results in competition among a plant's own offspring. In agriculture, seed-size uniformity makes harvest and processing simpler, but there could nonetheless be an argument for maintaining plasticity in seed size. If extra resources are available towards the end of the growing season, it may be too late to increase seed number, but still possible to increase yield by extending seed growth and increasing seed size. If tons of wheat flour per hectare is our goal, it does not matter that doubling seed size would have resulted in less than a doubling in seedling survival.

Plant responses to the ratio of red to far-red light are another interesting example of how past natural selection may have left room for improvement, by human criteria, of phenotypic plasticity. *Portulaca* seedlings grow preferentially towards light that resembles sunlight (rather than shade) in its spectral composition, even where photosynthetically active radiation is lower (Novoplansky, 1991). It may be better to grow towards a rock, which will not get any bigger, rather than towards a neighbouring plant, which may grow. Elongation responses to neighbours, also based on light cues, may benefit individual plants (Schmitt et al., 1999), but are not necessarily optimum in terms of community productivity. For example, Boccalandro et al. (2003) increased tuber yield of potato by genetic alteration of light responses, so that plants wasted less resources in an 'arms race' to overtop their neighbours. As with some of the traits proposed by Donald (1968), closer spacing was needed for maximum benefit from plants that were less responsive to spectral cues from neighbouring plants. Furthermore, there were unexpected effects on stomatal conductance, so complex trade-offs may be involved.

Fixed traits and plastic responses that maximize individual plant fitness under water-limited conditions (Schwinning and Ehleringer, 2001) may not be optimal in terms of community productivity. Yield is maximised when a crop allocates no more resources to roots than needed to extract the available soil resources. However, Zhang et al. (1999) showed that natural selection favours genotypes that exceed this optimum, because individuals benefit from taking some of their neighbours' 'share' of soil resources. Unless this effect of past natural selection has been eliminated by plant breeding, we would expect crops to produce more roots than is optimal (Passioura, 1983).

Recent results suggest that the story is more complicated, with plastic responses to interactions among roots playing a leading role. For example, in a split-root experiment with beans, plants whose roots interacted with those from another plant produced more root biomass and (therefore?) less pod biomass, relative to when the same total soil volume per plant was divided so that roots did not interact (Maina et al., 2002). This appeared to be a tragedy of the commons (Hardin, 1968), consistent with the hypothesis that individual selection favours overly aggressive root behaviour that is wasteful from a community standpoint. However, Hess and de Kroon (2007) pointed out that roots in containers tend to proliferate to fill the available space. Therefore, independent of root interactions, one would expect more total root growth when the plants had access to two shared pots, relative to when each was in a single pot. They agree, however, that other experiments (Falik et al., 2003; Mahall and Callaway, 1991) do provide evidence for self/non-self recognition in roots. More recently, Dudley and File (2007) found that siblings sharing a pot allocated less to roots than did two unrelated plants of the same species, consistent with kin selection. This area merits further research, but it seems unlikely that the root responses favoured by past individual selection always maximise community-level productivity or water-use efficiency in an agricultural context. It is likely, therefore, that there may be significant room for genetic improvement in these traits, as discussed in Chapter 13.

Future cultivars that benefit from changes in aboveground or belowground responses of plants to their neighbours may require changes in crop production practices, just as shorter Green Revolution varieties require better weed control. Furthermore, if plastic responses depend on too many variables, the results of changing them may be difficult to predict in advance or to extrapolate from one environment to another.

6. TRADE-OFFS AS OPPORTUNITIES: CONFLICTS INVOLVING MICROBIAL MUTUALISTS

The interactions between crops and N_2-fixing rhizobium bacteria, mycorrhizal fungi and some other rhizosphere microbes (e.g. disease-suppressing pseudomonad bacteria) are generally beneficial, but there may be considerable room for improvement. This is because the traits that maximise microbe fitness are not necessarily those that maximise host-plant fitness (Denison, 2000; Denison et al., 2003a; Kiers and Denison, In Press). For example, rhizobia that fix more nitrogen may benefit from the resulting increase in their host plant's photosynthesis (Bethlenfalvay et al., 1978). But if this benefit is shared with competing rhizobium strains – there are usually several per individual host plant (Silva et al., 1999) – we have another potential tragedy of the commons. Natural selection will not favour costly individual investments that yield only a collective benefit.

With a realistic number of competing rhizobium strains per plant, mathematical modelling predicted that rhizobia investing mainly in their own reproduction would rapidly displace those that invest in N_2 fixation (West et al., 2002b). This model made two key assumptions. Our first assumption was that it is physically possible for rhizobia to divert resources from N_2 fixation to their own current or future reproduction. One simple way of doing so is to hoard energy-rich polyhydroxybutyrate (PHB). A mutant defective in PHB synthesis was found to have higher N_2 fixation (Cevallos et al., 1996), whereas a non-fixing mutant was found to accumulate more PHB per rhizobium cell (Hahn and Studer, 1986), at least when it shared a nodule with a fixing strain. So there is a trade-off between N_2 fixation and PHB synthesis, but does that imply a conflict of interest between rhizobia and plant? It does, if PHB enhances rhizobium fitness. We showed that this is the case, at least under resource-limited conditions. Under starvation, rhizobia with more PHB reproduced more and survived longer, relative to genetically identical rhizobia with less PHB (Ratcliff et al., In Press). If N_2 fixation has an individual cost to rhizobia (less PHB) and any benefits are shared with competitors on the same plant, then rhizobia that fix less N_2 should displace those that fix more, over only a few plant generations (West et al., 2002b).

This does not appear to have happened, however. Although some rhizobium strains provide essentially no benefit to their hosts (Abel and Erdman, 1964), and a few result in worse plant growth than an uninoculated control (Nutman, 1954), parasitic rhizobia are not as common as our model seems to predict. Erdman's (1950) results seem typical: about 25% of rhizobium strains are poor, 25% are good and the rest are mediocre. This still leaves considerable room for improvement, but it is not as bad as our simplest model predicted.

The discrepancy may be due to the assumption that the benefits of N_2 fixation are shared equally among all rhizobium strains on the same plant. When we modelled an alternative hypothesis, namely, that plants monitor actual N_2 fixation of individual nodules and impose fitness-reducing 'sanctions' (Denison, 2000) on those that fix less, we got very different predictions. With host sanctions, substantial investment in N_2 fixation was predicted, regardless of the number of strains per plant (West et al., 2002b).

But can plants actually detect and punish non-fixing nodules? To find out, we used tiny chambers around individual nodules to replace air (containing 80% N_2) with an $Ar{:}O_2$ atmosphere containing only enough N_2 to meet the nitrogen needs of the rhizobia themselves. These nodules grew less and the rhizobia inside reproduced less, relative to control nodules in chambers with air (Kiers et al., 2003). Non-fixing nodules also had lower O_2 permeability, although we have not yet shown whether that is what limited rhizobium reproduction. (Nodule interior O_2 levels were much too low for oxygen damage to nitrogenase to be a concern.) Subsequent work showed that intermediate rates of N_2 fixation trigger intermediate sanctions (Kiers et al., 2006), although nodules fixing at 50% of potential still contained about 77% as many rhizobia as control nodules.

What are the opportunities for genetic improvement of crop interactions with rhizobia? A comparison of old and new soybean cultivars showed that older cultivars benefited as much from a 50:50 mixture of N_2-fixing and non-fixing rhizobia (qualitatively similar to what we would expect in some locations) as they did from N_2-fixing rhizobia alone, whereas newer cultivars got much less benefit from such a mixture (Kiers et al., 2007). So genetic variation for plant interactions with diverse rhizobia exists, although it is not certain that sanctions were involved. Past natural selection among legumes should have favoured sanctions that waste fewer resources on ineffective rhizobia (West et al., 2002a). But the sanctions response favoured by individual selection is not necessarily optimal by human criteria. Suppose a plant is infected by a few rhizobia that are very active N_2 fixers and many rhizobia that fix less nitrogen. Even the less-beneficial strains might provide a net benefit to the plant, if soil nitrogen is limiting. So individual selection might favour continuing to support nodules containing mediocre strains, even though by doing so the plant increases the number of mediocre rhizobia released into the soil after nodule senescence. From the point of view of a farmer planning to grow the same legume crop again in future years, it might be better for the plant to support only the nodules that provide the most nitrogen, so that only the best rhizobium strains are later released alive back into the soil. We have calculated that rhizobia inside nodules can greatly outnumber those in the soil (West et al., 2002b), so crops that supported and released only the best local strains could significantly improve the composition of rhizobium populations in the soil, thereby benefiting future crops. To the extent that enhanced sanctions involved greater growth of nodules containing better rhizobia (Kiers et al., 2003; Singleton and Stockinger, 1983), high rates of N_2 fixation could still be achieved eventually, even within the first growing season. However, the delay in peak N_2 fixation, due to early abandonment of mediocre nodules, would presumably have some effect on first-year yields. Farmers could either accept this, as the price of future benefits, or perhaps apply supplemental nitrogen.

Our models are sufficiently general that they would also predict widespread 'cheating' by mycorrhizal fungi, where diverse strains or species also infect the same individual host plant. Because mycorrhizal fungi are mostly beneficial, at least when soil phosphorus is limiting (Johnson, 1993), we suspect that something analogous to sanctions is again limiting the spread of cheaters (Kiers and van der Heijden, 2006). But we know even less about the mechanism of these hypothetical sanctions against mycorrhizal fungi than we do for rhizobia. Similar tragedy-of-the-commons arguments apply to root-surface microbes that may benefit plants, but there it is harder to imagine how plants could impose sanctions that selectively favour one rhizosphere strain over another (Denison et al., 2003a; Kiers and Denison, In Press).

We could develop crops that only allow the best rhizobia to nodulate, based on arbitrary recognition signals. Rosas et al. (1998) have proposed a clever approach. In the short run, this 'partner choice' would save plant resources, relative to nodulating with all comers and then shutting down poor-performing nodules. But microbial evolution would soon generate less-beneficial microbes that mimic the signals of more-beneficial strains. Signal-based partner choice would therefore be a variant of Red Queen breeding: useful, but ephemeral. Legume sanctions against poorly performing nodules based on actual N_2-fixation would be more robust.

Given uncertainty about mechanisms, opportunities to improve sanctions or other crop interactions with potentially beneficial microbes might seem limited. But it may be possible to devise effective selection schemes even without a detailed understanding of mechanisms (Denison, 2007). One possible approach would start by growing a genetically diverse population of the crop, in pots containing soil with mixed microbial populations characteristic of field conditions. Next, one or more genetically uniform test crops would be grown in the same pots. For a maize-soybean rotation, for example, the uniform test crops (after a segregating soybean population) could be maize and then genetically uniform soybean. Any differences in maize growth could be due to differential effects of soybean genotypes on mycorrhizal fungi, for example (Johnson et al., 1992). Differences in the soybean test crop could be due to release of different rhizobium strains from nodules of the first crop. Seed from the first crop would be selected based, in part, on its effects on subsequent test crops.

This example illustrates how past natural selection may have left significant opportunities for improvement by humans. Natural selection should have optimised enzyme efficiency, in N_2 fixation as well as photosynthesis. But benefits to plants growing in subsequent years (perhaps a mixture of a plant's seedlings and their competitors) have presumably been ignored by natural selection. Humans have foresight, while natural selection is blind to future consequences. Human goals encompass the performance of the farm as a whole, not just the competitiveness of an individual plant. Such discrepancies between past natural selection and present human goals suggest that even millions of years of natural selection have left ample opportunities for genetic improvement of crops.

7. CONCLUDING REMARKS

The ideas presented here are only a subset of the potential applications of evolutionary biology to the genetic improvement of crop plants. Slowing the evolution, in agricultural pests, of resistance to our control methods (Tabashnik et al., 2008) and the overall design of agricultural ecosystems to minimize pest and disease problems, discussed briefly by Denison et al. (2003b), are among the important topics beyond the scope of this chapter.

The focus here has been on the implications of past natural selection for future genetic improvement of crops. It is probably fair, however, to say that '100% of the increase in grain yield is actually due to the interaction between genetics and agronomic practices' (Lee and Tollenaar, 2007). For example, the values of two traits noted by Lee and Tollenaar (2007), 'functional stay-green' (prolonged photosynthesis) and erect leaves, depend on increased nitrogen supply and increased plant population, respectively. Thus, these are examples of the trade-offs between past and current environments and between individual competitiveness and community performance, respectively.

Someday, people may learn to design crops, rather than only selecting from and tinkering with 'useful variations, given by the hand of Nature' (Darwin, 1859). But that day may be decades away. Could we design and implement C4 photosynthesis, a trait that natural selection has invented at least 31 times (Kellogg, 1999), from first principles, rather than by copying existing C4 plants? Could we genetically modify wild kale to resemble broccoli, a feat accomplished by traditional plant breeding, without using genes or gene sequences from broccoli? If not, then we are still in the age of genetic tinkering, not genetic engineering.

Until we can accurately predict the crop-level consequences of complex changes to crop genes, we should assume that it will be difficult to improve on past natural selection, except to the extent that our goals today are in conflict with individual fitness in past environments. Eliminating photorespiration is unlikely to meet this standard and we should not expect trade-off-free improvements in traits like drought resistance. But there are many traits, including some linked to crop performance under drought, for which trade-offs between past individual competitiveness and collective agronomic performance today are likely. Some of the resulting opportunities have already been exploited, to varying extents, but additional opportunities surely remain.

For those who accept these arguments (presumably, with some reservations!), what is the most promising way forward? Two potentially complementary approaches are (1) harnessing the power of selection to serve human goals and (2) the energetic application of human reason. The increasing power of computers may facilitate each of these approaches.

Engineers (Cogan, 2001) and molecular biologists (Paegel and Joyce, 2008; Santoro and Joyce, 1997) are increasingly using non-random selection from a randomly varying 'population' to solve problems that resist direct solution. Simply allowing 'natural' selection to continue by letting genetically diverse crops compete in an agricultural setting will favour some traits that are clearly beneficial (e.g. resistance to whatever pests are prevalent), but also undesirable traits. The latter include those that sacrifice community performance for individual fitness (e.g. increased height). So, could we modify computer-controlled seeding and harvesting equipment to select for yield (or other collective traits) of groups of genetically similar plants, as Muir (1996) has done successfully with laying hens?

Alternatively, we could continue Donald's (1968) trade-off-based 'ideotype' approach. Can we identify trade-offs that he overlooked? A combination of computer modelling and relatively simple experiments (Kokubun, 1988) may provide fairly inexpensive tests of the potential value of reversing past natural selection for particular traits, before committing to implementation in a breeding program. Chapter 10 outlines a modelling G × E × M framework via gene-trait-phenotype relationships.

An adequate test of either of these approaches could be expensive, consuming resources that could otherwise be dedicated either to futile attempts to eliminate photorespiration, for example, or to continuing successful and important efforts to maintain genetic resistance to pests and pathogens. This 'Red Queen breeding' is essential, but intrinsically ephemeral, given ongoing pest evolution. The useful lifetime of new trade-off-based physiological and morphological traits, on the other hand, may be measured in millennia.

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CHAPTER 10

Modelling Crop Improvement in a G×E×M Framework via Gene–Trait–Phenotype Relationships

Carlos Messina, Graeme Hammer, Zhanshan Dong, Dean Podlich and Mark Cooper

1. INTRODUCTION

Crop performance is determined by the combined effects of the genotype of the crop and the environmental conditions of the production system. Improving crop performance to satisfy an increasing demand for plant products is a constant challenge to plant scientists. Plant breeders approach this challenge by searching the genetic space for superior genotypes that have improved performance across the environments of the production system (Figure 1), while agronomists pursue the same goal by optimising management for the cohort of elite genotypes developed by plant breeding. Historically, plant breeding and agronomy have co-evolved, and both have contributed to improved crop performance. This iterative process has been extremely successful in creating superior crops as demonstrated by the steady increase in maize yields in the USA (Duvick et al., 2004; Duvick and Cassman, 1999; Castleberry et al., 1984), and the consistent but discontinuous progress in wheat yield in Australia (Chapter 2). Crop physiology and modelling, although useful to interpret and describe the physiological process underpinning such yield improvements (i.e. Gifford et al., 1984; Duncan et al., 1978; Duvick et al., 2004; Slafer, 1994; Otegui and Slafer, 2000), have provided little guidance for how to apply these concepts to improve the efficiency of the breeding process (Campos et al., 2004; Evans, 1976; Sinclair et al., 2004; Lee, 1995).

The current paradigm of creating improved crops by breeding new genotypes and then optimising their management at a later stage of the crop improvement process constrains breeders and agronomists to exploring a reduced set of the vast space defined by the full set of possible genotype (G) and management (M) combinations. In addition, variable environmental (E) conditions interacting with G and M (G×E×M) complicates the definition of the possible paths towards realised genetic gain in production environments and limits our ability to make inferences on the effects of alternative management practices. The size and complexity of the G×E×M system, and the difficulty of dealing with many interactions simultaneously, has traditionally being tackled by crop scientists through a discipline-centred approach that deals with components of the G×E×M interactions separately, most frequently as G×E by plant breeders and M×E by agronomists (Cooper and Hammer, 1996; Boote et al., 1996; Loomis and Connor, 1992). An open question is whether enhanced rates of crop improvement can be realised by a more integrated approach. The quantification of these interactions relies on the use of statistical methods (i.e. Cooper and Hammer, 1996), yet interpretation of these G×E×M interactions could be improved by means of crop modelling and simulation applied to understand their causes and their relevance to the target production system (Cooper and Hammer, 1996; Löffler et al., 2005).

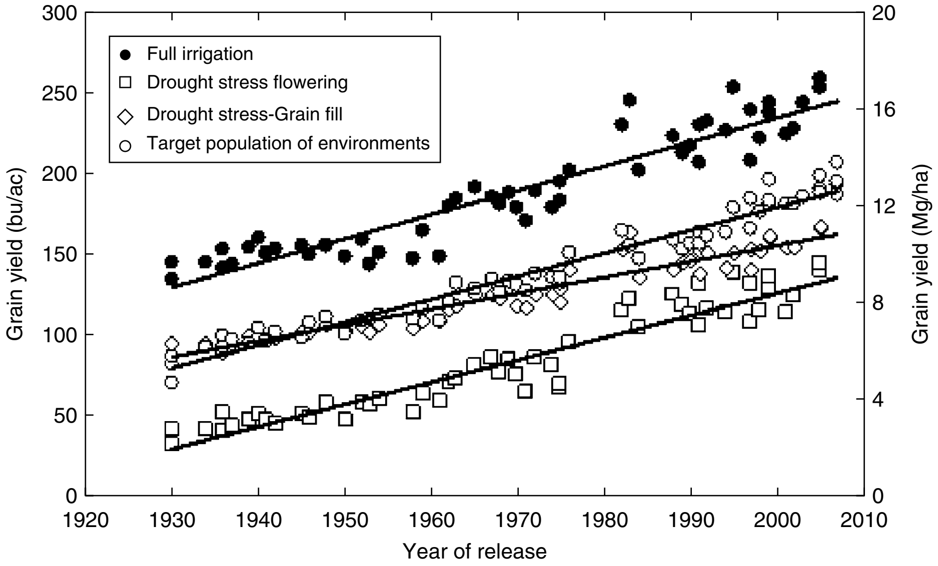

FIGURE 1

Maize yield improvement for a set of Pioneer hybrids released between 1920 and 2007 grown in the target population of environments ($y = 1.43x + 78.95$; $r^2 = 0.96$), full irrigation ($y = 1.51x + 129.4$; $r^2 = 0.88$) and drought stress imposed at flowering ($y = 1.39x + 28.6$; $r^2 = 0.90$), or grain filling ($y = 0.99x + 86$; $r^2 = 0.90$). Linear regressions estimate using 1930 as base year. Conversion factor between bu/a and Mg/ha is 0.06271.

The vast size and complexity of the G×E×M space that confronts breeders and agronomists present many challenges to the definition of practical approaches for developing improved crops and management practices as integrated and coordinated products since most of this space remains unobserved. The exhaustive empirical exploration of this space is not feasible. This led to the proposition that development of superior cultivars is limited by the ability to simultaneously identify favourable combinations of genomic regions and sustainable management systems that optimise resource capture in cropping systems operating in a target population of environment (TPE), given the resources available to plant breeders and agronomists to search among possible G×M combinations (Cooper and Hammer, 1996; Hammer and Jordan, 2007). In a context of rapid technological innovation in agronomy (Chapters 2 and 3), environmental change (Karl and Trenberth, 2003; Chapter 20) and increasing costs per unit yield gain (Duvick and Cassman, 1999), it is opportune to contemplate the following questions:

- Can we explore the G×E×M space more effectively?
- Can we leverage advances in knowledge of G×E×M interactions, and associated physiological concepts, to tackle this complexity in an integrated approach to develop improved crops?

It can be anticipated that positive answers to these two questions would lead to crop improvement methods that enable breeders and agronomists to project trajectories in the G×E×M space into the future and gain insights into the consequences of manipulating genomes to create improved crops for targeted management and environments. Central to these methods are the quantification of gene-to-phenotype (GP) relationships for key traits in the reference population of a breeding program and the capacity of the framework to identify genetic hypotheses that could be tested and utilised in the breeding program.

Significant efforts have been made to tackle the GP problem by seeking approaches that link information at the level of gene or genomic region to the expressed phenotype in a manner that is useful for selection

(Cooper et al., 2002, 2005; Hammer et al., 2006; Tardieu, 2003). An emergent synthesis of the promising approaches to the GP problem involves advancing mathematical models of crop growth and development to link genetic variation in adaptive traits to physiological determinants, developing advanced statistical methods that help relate genomic regions to parameters in the model control equations (van Eeuwijk et al., 2005) and modelling of the G×E×M systems as an extension of Kauffman's *NK* model (Box 1). The integration of these tools and their application in breeding has proven to be non-trivial. There is still debate about the level of details needed for crop growth models to be able to integrate processes across levels of organisation while predicting emergent functional consequences for the organism that arise from the interplay among gene networks, cell metabolism, plant organs, individuals in the crop and the environment (Hammer et al., 2006).

BOX 1 The *E*(*NK*) Model

The *E*(*NK*) model, and an informal extension to accommodate M, provides a framework to consider adaptation and fitness landscape. In this model *N* represent the number of genes involved in determining the performance of the genotype, *K* the average level of epistasis (interactions between a gene and any of the other $N-1$ genes for a given *E*) and *E* the number of environment types in the TPE (Cooper and Podlich, 2002). The parenthesis notation indicates that the number of genes and the level of epistasis can change with E, and by extension with M. The simplest form of the model assumes one environment and management to generate a fixed structure or potential surface, on which peaks are positions sought through breeding. The two-allele diploid $NK = N{:}0$ family of models, which corresponds to the additive finite locus genetic model used in quantitative genetics, has a landscape characterised by a single peak and a smooth surface, that is, the trait performance of genetically similar individuals are highly correlated. Landscapes become more rugged as *K* (level of epistasis) increases. In the limit where $K = N - 1$ ($N{:}N-1$ family of models), the landscape is fully random (Kauffman, 1993). For a given family of *NK* models, changes in environment types and their frequencies induce deformations to the adaptation landscapes; the magnitude of the deformation depends on the underlying trait physiology (Cooper and Podlich, 2002).

The aim of this chapter is to introduce fundamental concepts of modelling natural systems using a G×E×M framework and discuss prospects for an integrated approach for improving crop performance that tackles the G×E×M interactions holistically. First, we outline general principles of modelling biophysical systems, including a description of fundamental components of crop models. Second, we describe G×E×M systems and introduce GP models, the *E*(*NK*) framework and concepts of adaptation landscapes as applied to plant breeding. Finally, we demonstrate and discuss the application of the framework by studying genetic improvement of maize in the US Corn Belt.

2. MODELLING BIOPHYSICAL SYSTEMS

Crop models are implementations of theoretical frameworks in the form of a series of quantitative expressions. As such, crop models formalise and integrate concepts from disciplines such as physiology, micrometeorology, soil science and biophysics into an interrelated system of mathematical equations that describes the dynamic growth and development of a crop (de Wit, 1982; Thornley and Johnson, 2000). Crop models represent a simplified view of all or part of the natural system. The motivation for seeking a simplified quantitative representation of the target system is to help scientists approach complex problems by focusing on the important components and achieve their research objectives. The structure and complexity of a crop model (e.g. time step for integration) thus depends on the research or technology objective. In this context, crop modelling should be viewed as an iterative process in which model predictions become testable hypotheses, and the results of testing these hypotheses generate feedback to the model-building process to improve the representation of the biological and physical processes and the model structure whenever necessary. Simulation, which involves exercising the model in order to study system dynamics and properties, is a critical activity in this iterative model-building approach, as it provides a method to study the natural system through the properties captured in the quantitative model. With an acceptable model, such research can help understand emergent behaviour of the system and conceive new concepts that translate into new knowledge, sometimes expressed in the form of new equations and algorithms. The result of the systems modelling and simulation process is the assimilation of knowledge into an integrated theoretical framework from which quantitative predictions and testable hypotheses are proposed for experimental investigation (Hammer and Jordan, 2007; Thornley and Johnson, 2000).

The crop models in use today integrate physiological knowledge developed through more than 30 years of empirical research (Sinclair and Seligman, 1996). Since the first developments by de Wit in the 1960s (van Ittersum et al., 2003), many crop models have been built with different scope and objectives in mind. A recent symposium on Farming Systems Design listed more than 70 models (http://www.iemss.org/farmsys07/index.php). The review of all these models and their component processes is beyond the scope of this chapter. A description of the most common modelling platforms used in agricultural sciences and their 'pedigree' can be found elsewhere (Jones et al., 2003; Keating et al., 2003; van Ittersum et al., 2003; Stöckle et al., 2003). Reference publications provide detailed treatments and models for simulating energy balance and transpiration (Jones, 1992; Nobel, 2005), photosynthesis (Nobel, 2005; Boote and Loomis, 1991), different aspects of soil water and nutrient balance (Hanks and Ritchie, 1991; Ritchie, 1998; Loomis and Connor, 1992) and soil carbon dynamics (Parton et al., 1988, 1994). Chapter 20 (Section 4) outlines modelling approaches with emphasis on grain yield and climate change. With a narrower, more specific focus, other chapters discuss modelling approaches for capture and efficiency in the use of radiation (Chapter 7) and aspects of grain quality (Chapter 16). Here we outline common modelling approaches and fundamental components of crop models with emphasis on genetic, environmental, management and G×E×M drivers of grain yield.

Crop models of interest in crop physiology, and in particular those suitable to modelling G×E×M interactions, are continuous, dynamic (include a time dimension) and foremost explanatory (Thornley and Johnson, 2000; Hammer et al., 2006). This type of model can be viewed as a bridge across levels of biological organisation enabling the researcher to understand the behaviour of a system based on the knowledge gained by experimentation on its key component systems (de Wit, 1982). Experience has indicated that stable and credible models usually do not include components that simulate physiological determinants occurring at more than two levels of organisation away form the target level (Hammer et al., 2004; Sinclair and Seligman, 1996). Explanatory models thus focus on modelling processes that are formalised as rate variables (Figure 2; de Wit, 1982; Loomis et al., 1979). The separation of states of the system from underpinning determinant processes enables the identification of useful links among the environment, physiological processes and genetic determinants, and to formalise these links as metaprocesses that provide the backbone for GP modelling (Figure 2b; Tardieu, 2003; Hammer et al., 2006).

2.1. Anatomy of a crop model

Figure 3 highlights interactions between crop processes, and between crop processes and the environment, as captured in a generic simulation model. Algorithms associated with key aspects of plant growth and development are critical features of crop models. Plant development sets out the master control of the timing of events in the plant life cycle (i.e. transition between vegetative and reproductive growth; duration of reproductive growth). Plant growth is driven by organ development (e.g. canopy, roots), and the ability of the crop to capture resources (light, water and nitrogen) and convert them into vegetative and reproductive biomass.

2.1.1. Development

The prediction of the duration of the crop life cycle, and the timing of milestones that affect resource capture and partitioning, is the central component of any crop model; Chapter 12 summarises the environmental

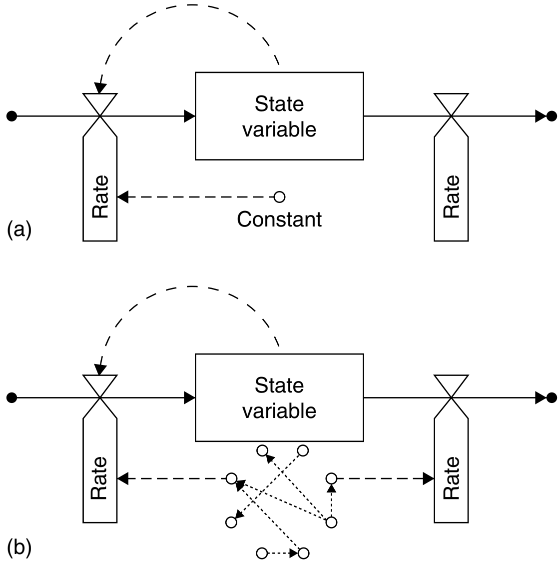

FIGURE 2
(a) Representation of a system model using a state-variable approach and drawn according to the convention of Forrester (1961). (b) Integration of the NK *model to predict systems state based on any genetic architecture via its effects on process rates.*

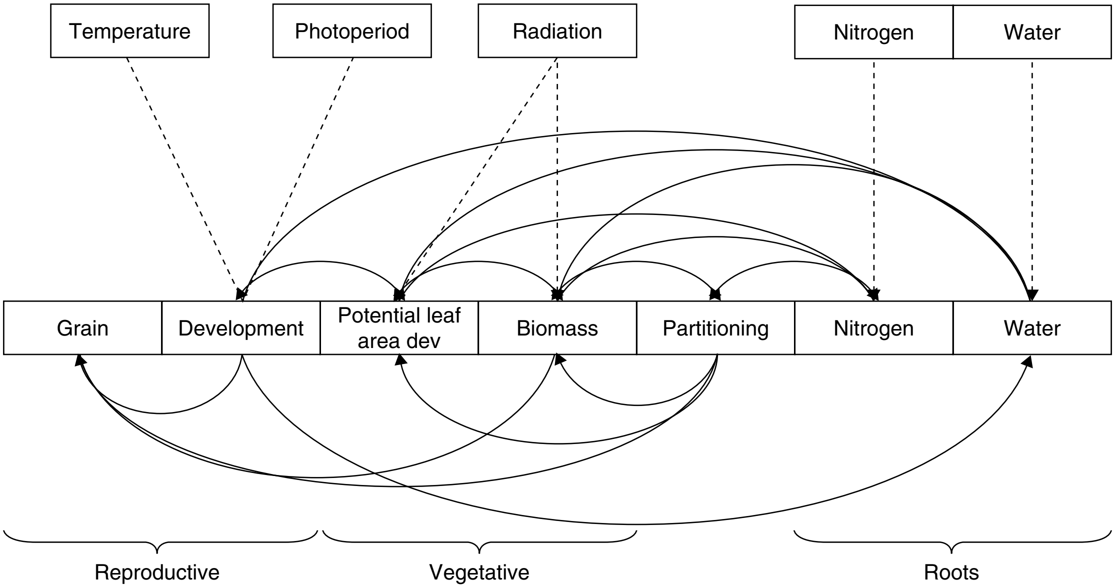

FIGURE 3
Schematic of major components of a crop model, their interactions among components and with the environment.

and genetic controls of crop development. There are many models of crop development through the various phases of the crop life cycle (Hammer et al., 1989; McMaster and Wilhelm, 1997; Ritchie and NeSmith, 1991; Grimm et al., 1994; Erskine et al, 1990; Sinclair, 1996). Because the genetic architecture of plant development is only incipient (Simpson et al., 1999; Koornneef et al., 1998; Corbesier et al., 2007; Tamaki et al., 2007), models of crop development remain empirical descriptions of the relationship between development rates and temperature and photoperiod. The metaphor of physiological day is an appealing and intuitive approach to model crop development. The concept proposes that under optimal temperature and photoperiod, the development rate is at its maximum and that the rate decreases as these conditions deviate from the optimum (Hammer et al., 1989). Then a development milestone (e.g. transition of a meristem from vegetative to reproductive) is reached after *n* physiological days, which is the inverse of the maximum development rate. The algorithm that implements this concept is represented by the following set of equations (Grimm et al., 1994; Soltani et al., 2006):

$$R(t) = F(N) \times F(T) \tag{1}$$

where $R(t)$ is the development rate (derivative of development with respect to time) on day t; $F(N)$ is the night length (or photoperiod) function; and $F(T)$ is the temperature function. $F(N)$ and $F(T)$ are computed each day and assume values between zero and one. A value of one represents the greatest development rate and occurs when one ‘physiological day’ is achieved in one calendar day. The generalised representation of these multiple linear response functions is illustrated for $F(T)$ as:

$$\begin{aligned}
F(T) &= 0 && \text{if} \quad T < T_b \\
F(T) &= \frac{T - T_b}{T_{opt1} - T_b} && \text{if} \quad T_b < T < T_{opt1} \\
F(T) &= 1 && \text{if} \quad T_{opt1} < T < T_{opt2} \\
F(T) &= \frac{T_{opt2} - T}{T_u - T_{opt2}} && \text{if} \quad T_{opt2} < T < T_u \\
F(T) &= 0 && \text{if} \quad T > T_u
\end{aligned} \tag{2}$$

where T_b is the base temperature below which no development occurs; $Topt_1$ and $Topt_2$ are the lower and upper bounds of the optimal temperature range for development; and T_u is the upper temperature limit for development. Similar equations could be used to model effects of abiotic stresses on development (Boote et al., 1998).

2.1.2. Capture of resources and crop growth

Crop growth depends on the ability of the crop to capture resources and convert them to biomass. Assuming no nutrients or pest limitations, radiation and water are the key drivers of growth, and crop biomass increments can be calculated by identifying whether the crop is primarily limited by radiation or water (Monteith, 1988; Chapman et al., 1993). Elsewhere, the book presents detailed accounts of capture and efficiency in the use of water (Chapter 6), radiation (Chapter 7) and nitrogen (Chapter 8). Here we deal briefly with radiation and water, from a modelling perspective.

2.1.2.1. Radiation-limited growth

In light-limited situations, above-ground crop growth rate depends on the radiation intercepted and radiation use efficiency (RUE). RUE has been studied widely and considered relatively stable for many given species (Sinclair and Muchow, 1999). However, recent studies have identified increases in RUE in modern elite maize hybrids (Lindquist et al., 2005). Although the cause of this increase remains unknown, other studies in wheat (Miralles and Slafer, 1997) have linked differences in RUE with root–shoot partitioning for lines varying in height. RUE can be derived from the photosynthetic response to light of leaf elements in the canopy and is dependent on the leaf nitrogen status of those leaf elements, via effects on maximum photosynthetic rate (Sinclair and Horie, 1989), and the amount and nature of the incident radiation (Hammer and Wright, 1994). Hence, RUE is a canopy-level measure of photosynthetic performance that sets limits on productivity under potential growth conditions.

The extent of radiation intercepted depends on the canopy leaf area and architecture. Light interception is commonly modelled via the Beer–Lambert Law of light extinction in a canopy (Monsi and Saeki, 2005), which quantifies the exponential decay of light with increasing leaf area. The extinction coefficient (*k*) is dependent on leaf angle (LA) in the canopy. Lower *k* is associated with more erect leaves (Monsi and Saeki, 2005), which can increase crop growth rate and RUE in canopies with high leaf area index by distributing light more effectively over the layers of leaf area within the canopy (Duncan et al., 1967). Hence, the development of the canopy leaf area is critical to the dynamics of radiation-limited crop growth through the crop cycle.

2.1.2.2. Water-limited growth

The demand for water in transpiration can be determined from the ratio of crop growth and transpiration efficiency (TE), with the latter adjusted for the effect of daytime vapour pressure deficit (Tanner and Sinclair, 1983; Sinclair et al., 1984). While this biophysical approach is robust for estimating transpiration demand, recent studies (Kemanian et al., 2005) have indicated it needs some adjustments under low-vapour-pressure-deficit conditions (Section 6.4 in Chapter 7).

Water-limited situations occur when the potential supply of water from root uptake cannot meet transpiration demand. In that situation, crop growth can be calculated as the product of the transpiration supply and TE (Monteith, 1988; Chapman et al., 1993). The supply of water from the soil can be modelled via predicting the depth of the root system and the amount of water that can be extracted from each occupied layer. The extraction potential follows an exponential decay equation (Passioura, 1983) that depends on the moisture content of the layer and a coefficient (*kl*) that quantifies the relevant soil–root system attributes that influence water extraction patterns. This approach, first outlined by Monteith (1986), has been applied successfully in a number of species (Meinke et al., 1993; Robertson et al., 1993; Thomas et al., 1995; Dardanelli et al., 1997, 2004).

In water-limited situations, given any specific soil condition, crop water uptake depends on the nature of the plant root system and its spatial arrangement. The extraction front velocity of sorghum and maize roots is about 3 cm day^{-1} up to flowering (Robertson et al., 1993; Dardanelli et al., 1997). In both crops, a rooting depth of around 2 m has been observed by early grain filling. The lateral spread of root systems is usually not incorporated in crop models, but it can also influence their occupancy of the soil and uptake capacity. Studies on root architecture in wheat (Manschadi et al., 2006) have noted a relationship among encompassing seminal root angle (RA), root system architecture and consequent water extraction from the soil. The variety with the narrower RA occupied a smaller soil volume but was able to extract more water, especially at depth. In maize, Campos et al. (2004) observed differences in water extraction between old and modern maize hybrids. During a period of water limitation, the old hybrid extracted more water from shallow soil depth, whereas the new hybrid appeared to be more effective at depth. A simulation study that included a two-dimensional root development model showed that such differences in rooting behaviour provide a plausible explanation for genetic improvement of drought tolerance as a component of the historical maize yield trends in the US Corn Belt (Hammer et al., 2008; Figure 1).

2.1.3. Canopy development

The potential for both light capture and water use are dependent on the canopy leaf area and the nature of its display. In cereal crops, potential leaf appearance and expansion are controlled by temperature and modelled as functions of thermal time that define the temperature-driven rates of leaf initiation, appearance and expansion rate (Tardieu et al., 1999; Hammer et al., 1993; Carberry et al., 1993; Birch et al., 1998b; Chenu et al., 2008; Ritchie and NeSmith, 1991). Potential rates of area growth are then reduced by water status, nitrogen or carbohydrate availability if any of these factors become limiting.

Approaches to predicting canopy leaf area growth have been developed at whole-plant and individual leaf levels. At the whole-plant level, functions describing the progression of potential leaf area with thermal time have been used to estimate potential leaf area growth (Amir and Sinclair, 1991; Hammer and Muchow, 1994; Sadras and Hall, 1988). At the individual leaf level, functions quantifying the potential size of individual leaves have been used in conjunction with estimates of leaf appearance rate (Birch et al., 1998a; Dwyer and Stewart, 1986; Jones and Kiniry, 1986). A number of studies (e.g. Birch et al., 1998b; Clerget et al., 2008) have shown that leaf initiation and appearance rates are stable when expressed in thermal time units.

Perhaps the least understood yet complex determinant of canopy development is the process of canopy senescence. Senescence is an emergent behaviour of the canopy that results from the dynamic interplay among resource capture, reproductive growth, the very own structure of the canopy and internal and external signals. Approaches to predicting canopy senescence have been developed for whole plants and canopies. In the absence of water and nitrogen stress, senescence is often modelled as a function of thermal time (Jones and Kiniry, 1986; Muchow and Carberry, 1989; Sadras and Hall, 1988), potential plant leaf area (Birch et al., 1998a) and the rate of green leaf area increase (Villalobos et al., 1996). Models that simulate water and nitrogen balances simulate leaf area senescence as a proportion of green leaf area and the severity of the abiotic stress (Jones and Kiniry, 1986) or as the result of the balance between nitrogen supply and demand. The latter suite of models enables nitrogen remobilisation and sink strength to drive leaf senescence (Sinclair, 1986; Villalobos et al., 1996; Boote et al., 1998; Borrell et al., 2001).

2.1.4. Reproductive growth

There are a number of approaches to simulating the growth of reproductive organs. The simplest models do not distinguish among yield components, fertile plants and tillers, fruit and seed number and weight; all components are lumped together in a coefficient (harvest index) that describes the fraction of total growth that corresponds to reproductive structures (Figure 4a; Sinclair, 1986; Muchow et al., 1990; Hammer et al., 1995). This approach is robust for the simulation of variation in yield across a range of environments but lacks sufficient detail to describe genotypic effects such as differences in maturity in sorghum (Hammer and Broad, 2003), as well as other genotypic effects underpinning yield improvement and tolerance to stresses.

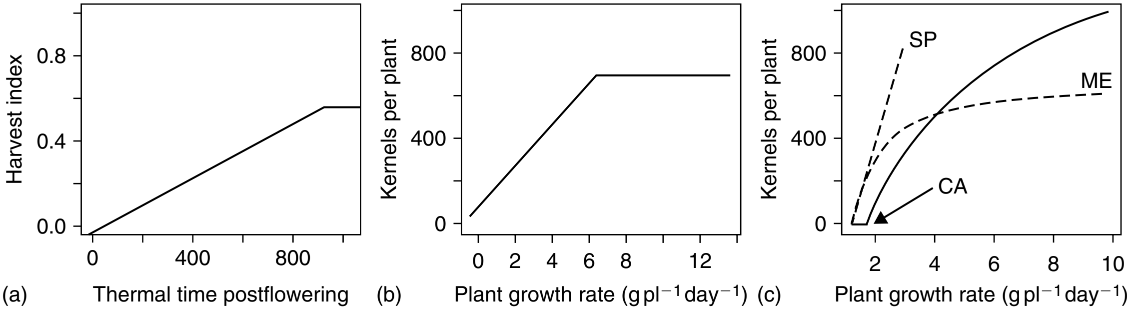

FIGURE 4

Models to simulate reproductive growth: (a) harvest index approach, and approach based on kernel number as a function of plant growth rate around flowering using (b) bilinear or (c) negative exponential or hyperbolic function. ME: maximum ear size representing kernel number at high plant growth rates; SP: initial slope and curvature integrate processes of silk exertion, synchronism in pollination, within-ear carbon allocation and kernel abortion; CA: carbon allocation to the ear and barrenness threshold.

More detailed models simulate barrenness, grain set and growth as separate processes. Grain growth is often simulated using a linear approximation of the commonly observed sigmoid growth pattern. The maximum grain growth rate is assumed characteristic of the genotype and independent of the kernel number (e.g. Duncan et al., 1978; Jones et al., 2003). Recent findings in maize questioned this assumption and suggested the need to model potential kernel growth rate as a function of plant growth per kernel around flowering time (Gambín et al., 2006). Once the potential is established, realised grain growth rate is determined by daily plant growth and the extent of carbon and nitrogen remobilisation (e.g. Jones et al., 2003; Keating et al., 2003; Boote et al., 1998).

Grain set is often modelled as a function of cumulative intercepted radiation (Ritchie and Alagarswamy, 2003; Andrade et al., 1993), crop growth rate (e.g. Andrade et al., 1999; Jones et al., 2003; Jiang and Egli, 1995; Vega et al, 2001; Tollenaar et al., 1992) or ear (panicle) growth rate (van Oosterom and Hammer, 2008) during a critical developmental period around flowering. The onset and duration of the critical window for grain set determination varies among crops (e.g. Otegui and Bonhomme, 1998; Fischer, 1985; Jiang and Egli, 1995). Critical windows for grain set are discussed in Chapters 12 (Section 5) and 15 (Section 3.2.2) from a breeding perspective and in Chapter 3 (Figure 4) from the viewpoint of integrating crops in cropping systems.

Figure 4b and 4c illustrate approaches to modelling kernel set in maize. Figure 4b is the function implemented in CERES-Maize (Jones and Kiniry, 1986) and could be considered the simplest approximation of the non-linear model in Figure 4c (Andrade et al., 1999; Tollenaar et al., 1992). Regardless of the mathematical formulation of the non-linear model, this form implicitly incorporates concepts of sink limitation due to maximum ear size (ME) and prolificacy (asymptote, ME; Figure 4c), silk exertion dynamics, synchronism in pollination, within-ear carbon allocation (CA) and kernel abortion (initial slope and curvature, SP; Figure 4c) and CA to the ear and barrenness (threshold, CA; Figure 4c). Ritchie and Alagarswamy (2003) extended the non-linear model shown in Figure 4c to simulate barrenness by modelling the fraction of ear-bearing plants as a function of cumulative intercepted radiation. An immediate advance on the framework, as proposed by Vega et al. (2001), is to explicitly simulate carbon partitioning to the ear and how this mass is converted into viable kernels. More mechanistic approaches to simulate fruit set, often applied to simulate pod number in legume crops, consider these fruits as populations of competing and interacting sinks for carbon and nitrogen. In this framework, fruit number at any time during the reproductive stage of the crop results from the balance between the addition of fruits as determined by crop development and the removal of fruits resulting from abortion due to insufficient resources (Wardlaw, 1990; Boote et al., 1998).

3. MODELLING GENOTYPE–ENVIRONMENT–MANAGEMENT SYSTEMS

A fundamental step in modelling is to define the purpose of the model or framework to be developed, the type of problems that the model should help investigate and solve and a concept map that relates the target natural system and the corresponding abstractions that become components of the framework (Peart and Curry, 1998; Thornley and Johnson, 2000). These principles were followed to design applications of crop growth models, and associated physiological concepts, to enhance plant breeding (Cooper et al., 2002; Chapman et al., 2003). More often, these applications have focused on valuing traits and attempts to design universal ideotypes (e.g. Boote and Tollenaar, 1994; Boote et al., 2001; Aggarwal et al., 1997; Yin et al., 2003; Sinclair and Muchow, 2001), and to understand genotype by environment interactions (Chapman et al., 2000, 2002a, b; Löffler et al., 2005). The development of these latter methods was dominated by typological thinking (e.g. Donald , 1968; Long et al., 2006; Century et al., 2008; Lee and Tollenaar, 2007) rather than population genetics concepts (e.g. frequency of favourable alleles, traits and phenotypes changing in a breeding population) as proposed in evolutionary (Nowak, 2006) and breeding studies (Cooper and Podlich, 2002). Approaches that sought to find universal ideotypes have imposed limitations on the successful integration of physiological knowledge into breeding programs by largely ignoring breeding objectives, germplasm context dependencies and genetic sources of unexplained phenotypic variation, and by often placing undue reliance on the ability of models to connect genetics and physiology to credibly predict subtle interactions and feedbacks associated with genetic variation for traits within the reference germplasm of a breeding program (Hammer et al., 2002).

3.1. Breeding objectives and purpose of framework

To define a relevant context for modelling the G×E×M system, it is convenient to distinguish between breeding objectives where:

(i) a genetic answer to the problem is known; for example, a target genotype has been identified, and the objective is to close the genetic gap between the current germplasm and the defined target to test the hypothesis, for example, to increase resistance to a biotic factor by introgressing alleles from exotic germplasm;

(ii) plausible genetic answers to the problem are currently unknown; for example, to increase grain yield or drought tolerance beyond those of the elite commercial products.

It is clear that the opportunity for modelling and physiology to contribute to plant breeding is closely tied to the second class of breeding objective, and that these should be components of a suite of methods to help breeders address questions about trade-offs between traits, the structure of adaptation landscapes, plausible selection trajectories towards interesting trait phenotypes and genotypes, the likelihood of finding improved genotypes in the adjacent possible genetic space and outcomes of competing selection and breeding strategies (Hammer et al., 2006).

3.2. Concept map

Figure 5 shows a simplified yet extended concept map to build a G×E×M system (Cooper and Hammer, 1996). Cooper et al. (2002) formalised the concept that was later demonstrated in a theoretical study for sorghum by Chapman et al. (2003). The testing of the hypotheses proposed in the theoretical study is currently underway (Hammer et al., 2005). In this dynamic and iterative framework, empirical data are continually analysed and used to encode knowledge for model building and enhancement (Podlich et al., 2004). Model-based predictions and concepts become genetic, physiological and agronomic hypotheses to test through experimentation in the real world of the target G×E×M system. A central concept to the quantitative framework is that of adaptation landscapes to represent the complexity of the G×E×M system to be explored, equivalent to the concept of fitness landscapes discussed in evolutionary studies (Wright, 1932; Kauffman, 1993; Fontana et al., 1989). Applying this framework, plant breeding can be viewed as a set of search strategies applied to that landscape or search space and constrained by the germplasm available to the breeder, the prescribed agronomic management and the environments sampled in the field trials. In this framework, a breeding population can be thought of as a cluster of individuals located at neighbouring positions that flow through regions of the adaptation landscape in response to selection (Kauffman, 1993; Cooper et al., 2002).

3.3. Definition and consideration of the search space and adaptation landscapes

The search space could be defined by the outcome of all possible combinations of genomic regions, environments and management practices. A narrow-sense definition of this space, perhaps a practical one, assumes limits imposed by the germplasm available to the breeder, the target agronomic management and the composition of the TPE. A broad-sense definition can extend the search space to include novel cropping systems (Section 5 in Chapter 3), alternative environment scenarios (Chapter 20; Ainsworth et al., 2008; Karl and

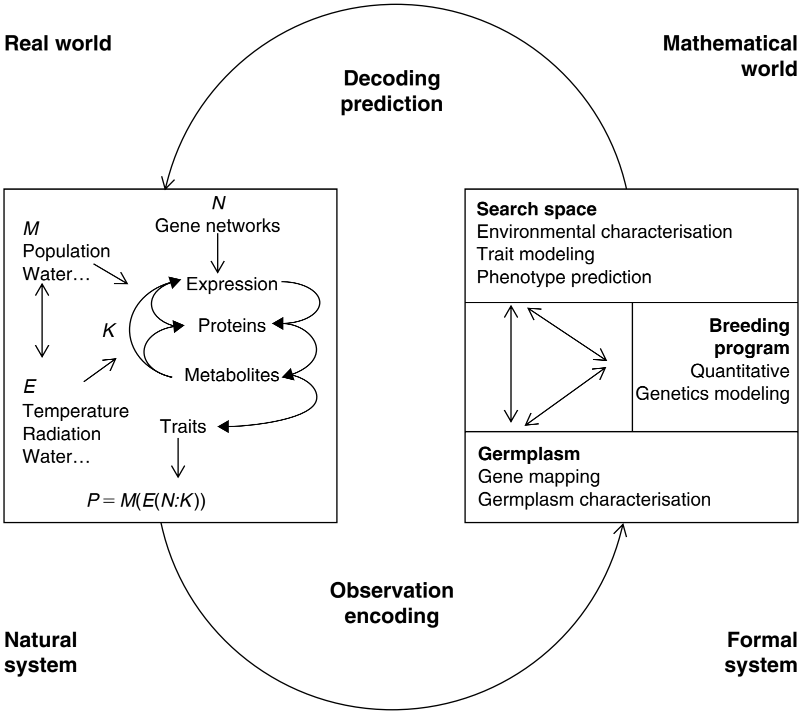

FIGURE 5

Concept map, main system components and model-building framework for modelling genotype–environment–management systems in the context of plant breeding. G: genotype; M: management; N: number of genes involved; E: environment; K: average level of epistatic interactions; P: phenotype.

Trenberth, 2003) and novel sources of germplasm and engineered genetic elements (e.g. Century et al., 2008). The G×E×M search space has an associated adaptation landscape. The $E(NK)$ model (Box 1), and an informal extension to accommodate M, provides a framework to consider this landscape.

A number of approaches were proposed to parameterise the $E(NK)$ model and assign a fitness value to a given genotype:

1. constructing Boolean networks and assigning fitness contributions to each gene from a statistical distribution (Kauffman et al., 2004; Kauffman, 1993);
2. defining inheritance models using empirical evidence from quantitative genetics parameters (Wang et al., 2003; Cooper et al., 2005);
3. specifying gene networks to represent attributes of known genetic networks and biochemical pathways (e.g. Ravasz et al., 2002; Bhalla and Iyengar, 1999; Peccoud et al., 2004);
4. directly parameterising, using results from mapping studies (Cooper et al., 2005);
5. considering the $E(NK)$ model as the consequence of N genes that control variation for physiological traits, the number of E identified for the TPE and the physiological relations encoded in a crop model that determine the patterns of crop growth and development (Cooper et al., 2002; Chapman et al., 2003; Hammer et al., 2005).

Approach 5 can be considered as partitioning the predictable component of the GP relationship continuum into gene-to-trait (physiological process) and trait-to-phenotype relationships; crop models predict crop performance phenotypes associated with trait performance (e.g. yield), based on the interplay among traits, environment cues and resources and management (Figure 5).

3.4. Crop modelling as a component in gene-to-phenotype mapping

The links between genes and phenotypes can be approached using top-down or bottom-up methods. Top-down methods use physiological dissection and integration via crop modelling to work from whole-plant phenotypes to the molecular genomic level (Hammer et al., 2004). This is also the classical forward genetics approach used to study the genetic architecture of traits; observe phenotypic variation and attempt to determine an appropriate genetic model to explain the phenotypic variation. When applying crop models to enhance genetic discovery, the central paradigm of this method is the focus on understanding and modelling processes at or around the level of organisation at which phenotypic predictions are being targeted and use a level of abstraction necessary to model processes and functional controls following the philosophy pioneered by de Wit and Penning de Vries (1983) of 'modelling plant hormone action without modelling the hormones'. The bottom-up approach integrates knowledge at the molecular level, across levels of organisation, to explain trait phenotypic variation (Minorsky, 2003; Yuan et al., 2008). This method is aligned with the reverse genetics approach to gene discovery (Section 2 in Chapter 14). It has been argued that the application of such bottom-up approaches to understand the genetic architecture of complex traits would face several challenges common to the study of other complex systems and in particular the challenge of integration of genetic information to capture emergent behaviour at the whole-plant level, with limited scientific understanding (Hammer et al., 2004). Simulation and propagation of errors across spatial and temporal scales that could vary by orders of magnitude would complicate making accurate predictions (Thornley and Johnson, 2000).

3.4.1. From the top-down

Top-down approaches have been tried with variable success. Yin et al. (2003) described the use of a crop model for barley based on the SUCROS crop model (Goudriaan and Van Laar, 1994) with quantitative trait loci (QTL) mapping to predict yields from QTL allele information. The model used as inputs the specific leaf area, the leaf N concentration, the fraction of biomass partitioned to leaves and to spikes and the separation of the life cycle into vegetative and reproductive stages. Using 94 recombinant inbred lines, these parameters were mapped, allele values for each QTL and trait calculated and yield predictions made using the ecophysiological model. Predictions for yield were clustered in two meaningful groups, based on two- and six-row types of virtually constant yield within each group. A similar study that used a crop model to link information for known loci and model parameters led to the Genegro model (White and Hoogenboom, 1996). This model incorporated effects of seven genes affecting phenology, growth habit and seed size of common bean (*Phaseolus vulgaris* L.). The parameters in the Genegro model were derived from the states of alleles at each of the seven loci, using a set of linear functions. These linear functions were estimated by regressing allele values (alleles were coded as either 1 or 0) against model parameters calibrated ('reverse engineered') using a set of field trials. Genegro accurately predicted dry bean phenological development but poorly explained yield variations between sites (Hoogenboom et al., 1997). These two examples demonstrate the limitations of using reverse engineering approaches to GP modelling and the importance of understanding the genetic architecture that controls the trait of interest. The ability of Genegro to predict bean phenology is due to a fundamental understanding of the genetic controls and genotypic variability on the response of beans to temperature and photoperiod (Coyne, 1970; Kornegay et al., 1993; White and Laing, 1989).

GP models developed for individual physiological components showed promising results for both plant development (Messina et al., 2006; Yin et al., 2005) and leaf growth (Reymond et al., 2003). Yin et al. (2005) combined ecophysiological modelling for phenology (of the form presented in Eq. 1) and QTL composite mapping to predict barley response to temperature and photoperiod. Parameters for the ecophysiological model were first estimated for genotypes, and QTL mapping was conducted on the population variation for these parameters. Using the allele values for each QTL and consequent model parameters, predictions were made for a set of recombinant inbred line genotypes in eight environments. The QTL-based model accounted for 72% of the observed variation among the recombinant inbred lines. Messina et al. (2006) used a photothermal model (Eq. 1) to determine allele values at six QTL loci for soybean model parameters. The model accounted for 75% of the time-to-maturity variance when tested in multi-environment trials (MET). Reymond et al. (2003) mapped QTL for the parameters of an ecophysiological model of leaf elongation rate (LER) for maize (Ben Haj Salah and Tardieu, 1997),

$$LER = (T - T_0)\,(a + bVPD + c\psi) \tag{3}$$

where T is meristem temperature, VPD vapour pressure deficit and ψ soil water potential; b and c are constants coding for the response of LER to VPD and soil water potential after correction for T effects; a and T_0 are the slope and *x-intercept* of the LER response to meristem temperature. Under optimal soil water and VPD conditions, LER becomes a function of temperature alone and the model becomes equivalent to Eq. 1. Upon parameterisation of 11 recombinant inbred lines at marker loci, the model accounted for 74% of the variability of LER. Further evaluation demonstrated the model useful for describing genetic variation in LER for a large number of recombinant inbred lines (Sadok et al., 2007).

3.4.2. Genes, traits, phenotypes and adaptation

The LER model is a useful example to illustrate the concept of partitioning the GP continuum into gene-to-trait and trait-to-phenotype relationships and to connect the biophysical and the *NK* models. The state model in Eq. 3 can be reformulated to formally incorporate QTL effects as

$$\frac{dL}{dt} = (T - \sum w_{ij}\mathrm{QTL}_i)(\sum w_{ij}\mathrm{QTL}_i + \sum w_{ij}\ \mathrm{QTL}_i\mathrm{VPD} + \sum w_{ij}\mathrm{QTL}_i\psi) \tag{4}$$

where w_{ij} are allele values of each QTL_i for the parameter j. Further generalisation suggests specifying Eq. 4 in terms of the *NK* model as

$$\frac{dL}{dt} = (T - NK_j)(NK_j + NK_j\mathrm{VPD} + NK_j\psi) \tag{5}$$

where the *NK* model is allowed to vary among parameters *j*. That is, the genetic networks associated with each of the model parameters could have common components; pleiotropic effects are formally incorporated via shared nodes among networks; epistasis is implemented as described earlier (Box 1). This formulation based on the *NK* model can be extended to the *E*(*NK*) model where network topology is allowed to vary in response to environment cues. Error terms could be included in the model to account for components of the unexplained variation in the GP relation continuum (Cooper et al., 2005).

The model in Eq. 5 fully describes the gene-to-trait relation. However, Eq. 5 applies only to single leaf and scaling of some sort from the organ to the whole plant is necessary to map the G×E×M space into the phenotype space (e.g. plant leaf area). Chenu et al. (2008) developed a model that coordinates the growth of all leaves of a plant and uses the single-leaf LER model to drive growth. The framework was implemented as a component of APSIM (Keating et al., 2003), which provided the dynamic feedback effects on leaf growth via transpiration and soil water uptake. Because the LER model is integrated within a crop growth-modelling framework, the likely impact of genetic variation for QTL affecting LER on adaptation (e.g. grain yield) could be assessed as demonstrated in previous studies for sorghum (Chapman et al., 2003) and soybeans

(Messina et al., 2006). In summary, crop models have the potential to map the G×E×M space into phenotype and adaptation landscapes. To enable these connections, however, thorough basic physiological and genetic studies are necessary to support the model architecture and provide validated evidence for the physiological determinants of genetic variation in adaptive traits.

3.5. Breeding programs as search strategies in genetic space

Plant breeders create new genotypes with improved crop performance and adaptation to a TPE by observing, understanding, predicting and creating new trajectories in genotype and phenotype space. Three fundamental processes under the breeders' control support the creation of these trajectories: (i) development of genotypic novelty through strategic sampling of germplasm, recombination and segregation; (ii) design of testing systems that adequately sample the TPE for evaluation of cultivars and expose genetic variation for traits of interest; and (iii) selection as a means to change gene frequencies in the germplasm to improve adaptation relative to the current set of cultivars. Breeders' decisions on these three components define the breeding strategy, and therefore the regions of the adaptation landscape that the breeding program would explore in search of peaks of adaptation and crop performance.

Breeding simulation provides a means to predict trajectories in GP space. QU-GENE (Podlich and Cooper, 1998) is a computer simulation platform to specify genetic models in the context of the *E*(*NK*) framework and G×E×M systems in order to evaluate alternative breeding strategies. The stochastic components in QU-GENE implement the simulation of genetic recombination and segregation, within the search for genotypes with higher fitness in the adaptation landscape; note the analogy between this component in QU-GENE and global optimisation algorithms (Mitchell, 1996). Specific modules in QU-GENE simulate the processes involved in the creation, evaluation and selection of genotypes within the breeding program and implement the simulation of breeding strategies such as mass selection, pedigree and single-seed descent, double haploid, S1 recurrent selection and half-sib reciprocal recurrent selection.

4. CASE STUDY: MAIZE BREEDING IN THE USA

Despite the complexity of the mechanisms underpinning yield determination, conventional breeding has effectively increased maize yield in well-watered and water-limited environments of the US Corn Belt (Figure 1; Duvick and Cassman, 1999; Duvick et al., 2004; Campos et al., 2006). Trajectories from over 50 years of maize breeding in the US Corn Belt show that many traits have changed markedly, even when there was no direct selection for these traits. These include decreases in tassel size, protein concentration in kernels, rate of leaf senescence during grain filling, root and stalk lodging, rows of kernels per ear, and anthesis-silking interval, and increases in LA (more erect leaves), ears per plant, kernel weight and harvest index (Duvick and Cassman, 1999; Duvick et al., 2004; Lee and Tollenaar, 2007). The future direction of these trajectories is a subject of debate (Lee and Tollenaar, 2007; Century et al., 2008; Tuberosa et al., 2007; Pennisi, 2008) and opens the opportunity to apply the framework described in the previous section to address questions of relevance to breeding. This section illustrates the use of a coupled crop system – breeding model to study past trajectories in GP space and outline plausible future trajectories in maize breeding.

4.1. Genotype–environment–management system

This study used the GP framework described in Section 3 to build a G×E×M system representative of past and present maize production in the US Corn Belt. The breeding objective is to improve yield in the TPE beyond that of current germplasm. The purpose of the framework is to study past trajectories in maize breeding and to provide insights on future trait trajectories, given representative environment types and plausible changes in management. Components of this framework were constructed by modelling adaptive traits of interest to breeders based on their physiological determinants (Section 2); linking genetic variation to those determinants in the context of the *NK* model (Box 1); simulating maize phenotypes for relevant genotypes, managements and environments; classifying production environments (Section 4.1.3); and simulating trait trajectories in genetic space for breeding programs conditioned to defined environments and management (Figure 5).

4.1.1. Trait modelling

A Pioneer proprietary module of APSIM-Maize was developed to incorporate adaptive traits of interest for trait variation relevant to Pioneer elite hybrids. The module includes algorithms that implement concepts that link RA with spatial and dynamics aspects of root exploration and occupancy of soil layers; thus RA controls time of access and intensity of resource capture (Hammer et al., 2008). LA and RUE are connected by implementing a series of equations to model canopy photosynthesis (Duncan et al., 1967; Hammer and Wright, 1994; Loomis and Connor, 1992). The module includes algorithms to model aspects of maize reproductive biology relevant to yield, including the connections between kernel set and CA to the ear and within the ear (Vega et al., 2001; Cárcova and Otegui, 2007), silking dynamics and synchronism in pollination (SP) (Cárcova et al., 2003; Borrás et al., 2007) and ME (Tollenaar et al., 1992). The model accounted for the connection between growth and development (Borrás et al., 2007), the co-regulation of kernel set and kernel size (Gambín et al., 2006) and their response to timing of drought stress during reproductive stages. Figure 6 compares simulated and observed yields for Pioneer hybrid P90-1 grown in a rain-free environment under six irrigation regimes. These regimes covered full irrigation control (FI) and five treatments where water was withdrawn for 500 °C d for overlapping periods separated by 100–200 °C d (S1–S5) at the commencement of the treatment.

4.1.2. Linking genotypes and traits

To demonstrate an application of the framework, genetic variation for five adaptive traits was defined using an additive genetic model based on three genes (equal effects) and two alleles per locus ($NK = 3{:}0$). It was assumed that there were unique sets of genes for each trait and that genes were unlinked. Thus, for the purpose of demonstration here, the genetic model does not include epistasis and pleiotropic effects at the level of the genetic architecture of the five traits. For a single trait, this genetic model results in 27 unique genotypes but only 7 unique expression states, given the additive effects model. For each locus, one allele was considered to increase expression relative to the alternative allele. For example, at a given gene *A*, it is defined that allele *A* increases trait expression (+) relative to the allele *a* (−). Then the expression state for the genotype is defined by the sum across genes of the effects of the + alleles. For example, given the additive model, the genotypes *AAbbcc*, *aaBBcc*, *aabbCC* and *AaBbcc* all have the same expression state of two (e.g. two positive alleles each). For this simulation experiment, which was based on five adaptive traits, the genetic model defines 14×10^6 genotypes but only 1.6×10^4 expression states. This first approximation of the genetic architecture of the component traits is substantiated by multiple QTL mapping studies. It is the simplest representation suggested by the data that would enable the simulation and representation of the full adaptation landscape. Other genetic models could be considered and implemented in the framework, and would have generated different relations among genotypes, expression states and phenotypes.

This simulation experiment included genetic models for five adaptive traits: RA, LA, CA to reproductive growth, synchronous pollination (SP) and potential ear size (ME). Model parameters for the latter three traits could be interpreted as determinants of CA, SP and ME in the current models of kernel set outlined in Figure 4c. Herein, we refer to these traits and interpret the results in the context of the kernel set response to plant growth rates.

4.1.3. Environmental classification

Maize phenotypes were simulated for a range of plant densities (8 and 12 pl m^{-2}), soil types (high and low soil water holding capacity; Löffler et al., 2005), 4 soil water contents at sowing and 50 years of weather in central Iowa, using APSIM-Maize (Keating et al., 2003) and Pioneer proprietary modules. Soil water content

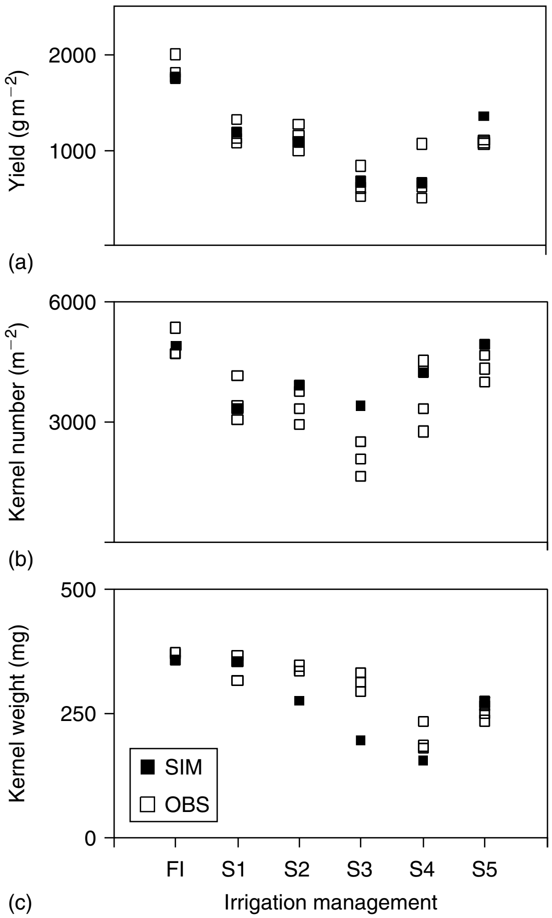

FIGURE 6

Assessing model capacity to predict (a) yield and yield components, (b) kernel number and (c) kernel weight under six regimes of water supply. FI: full irrigation; S1–S5, water was withdrawn for 500°C d over overlapping periods of 100–200°C d. Experiment details are provided in Campos et al. (2006).

at sowing was estimated by simulating long-term soybean–maize rotations and clustering results to form groups of water content distribution in the soil profile at sowing. Each combination of plant density, soil type and soil water content at sowing defines a unique environment and could thus be considered as one of many possible outcomes in a multi-environment trial.

Each of the 800 (2 × 2 × 4 × 50) simulated production environments was classified based on water supply and demand patterns (Hammer et al., 2005; Chapman et al., 2000) for a reference genotype. APSIM-Maize was parameterised and run for the Pioneer hybrid 3394 as the reference genotype; see Hammer et al. (2008) for model parameterisation. Daily outputs of the ratio of water supply to demand were averaged every 100°C d from emergence. Cluster analysis, using the *k*-means algorithm, revealed four major environment types depicted in Figure 7. The frequency of occurrence was 18% for severe terminal stress (ET1), 20% for early grain fill stress (ET4), 25% for moderate terminal stress (ET2) and 37% for no stress (ET3).

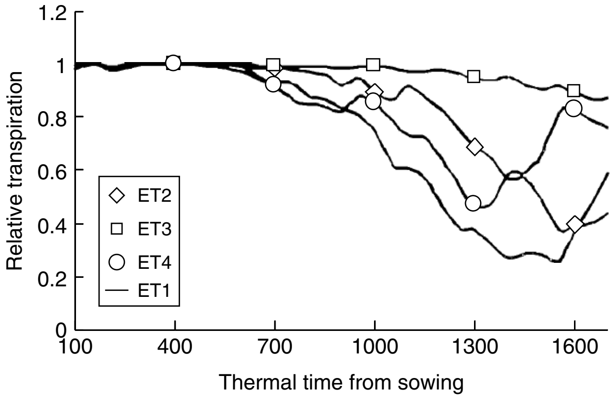

FIGURE 7

Drought stress patterns for environment types (ET) that define the Target Population of Environments. Relative transpiration simulated for a reference hybrid.

4.1.4. Adaptation landscape

The adaptation landscape was generated with yield as the measure of fitness. APSIM-Maize was run for each of the 16×10^4 expression states corresponding to unique combinations of adaptive traits, and each of the 1.6×10^3 environments and management combinations. Model parameters not determined by a genetic model, thus by any expression state, were set to the values determined for the hybrid 3394. This is a realistic representation of the execution of the framework in a real breeding program where genetic improvement is sought relative to a reference germplasm. For the purpose of this example, all conclusions about genetic improvement are drawn in reference to the hybrid 3394.

4.1.5. Breeding simulation

For each environment type and management, reciprocal recurrent selection with pedigree selection within two heterotic groups was simulated using QU-GENE (Podlich and Cooper, 1998; Podlich et al., 2004). The QU-GENE software managed the creation, evaluation and selection of genotypes within the breeding program. Reference breeding populations were created by specifying allele frequencies to 0.5 in two heterotic groups; any other starting point could have been considered. The evaluation system was set to a single breeding program and 10 testing sites. Each testing site sampled the TPE (Figure 7) in proportion to the frequency of occurrence of each environment type. Trait trajectories in G space conditioned to E and M emerge from breeding simulations that are similar to the trajectories reported for the sequence of hybrids in Figure 1. Selection experiments were conducted under a unique environment and management (e.g. ET1 and 8 pl m^{-2}), and for a sample of environments and plant populations.

4.2. Structure of simulated adaptation landscapes

Adaptation landscapes could be characterised by different metrics and graphical representations (Kauffman, 1993; Cooper and Podlich, 2002; Wright, 1932; Nowak, 2006; Fontana, 2002). In this example, the adaptation landscape was represented as a set of conditional cross sections for grain yield in the G and P dimensions (herein referred to as a GP plot). The grain yield distributions are conditional on the expression states for a defined trait. For example, for LA, there are seven expression states and therefore seven yield distributions. The yield distribution is generated by the yield variation created by all other traits conditional on the defined expression level for the selected trait of interest. The GP dimension views can be constructed for specific environments or a combination of environments. Genotype relative frequencies at regular intervals for yield are shown as a heat map to visualise the distributions (Figure 8). This graphical representation of landscapes allows the identification of features such as position of global maxima, trends in central tendency and local optima for yield with respect to G and expression states, presence of saddles and plateau regions. The global maximum is identified as the maximum in the *y-axis* across all frequency distributions. In the example presented for drought stress environments, this maximum corresponds to genotype *AABBCC* for RA and *ddeeff* for LA (Figure 8). Local optima correspond to the maximum yield conditioned to G. Both global and local optima provide information about opportunities and paths to yield improvement in the adjacent genetic space, given the reference populations of the breeding program.

Trends could be identified in local optima and central tendencies. In environment ET3, trends in yield with respect to the expression state of LA are evident in both central tendency and local optima (Figure 8). In contrast, in ET1, the landscape is rather flat for genotype bins 1–4 (genotype *ddeeff* corresponds to bin 1), but there is a marked non-linear trend in the local optima. This trend reveals a point of instability due to the presence of a saddle and has implications for breeding. Yield increase is feasible by either increasing or decreasing LA. The resulting changes in allele frequencies, and LA phenotypes, in a breeding population selected for yield increase, will depend on the initial frequencies of alleles. At this point in G space, the behaviour of the breeding system and the potential for genetic improvement become dependent on initial conditions. The global maximum in ET1 can only be reached by increasing the frequency of + alleles. The alternative trajectory leads to a higher peak in the adaptation landscape but compromises the potential for continuous genetic gains due to variations in LA.

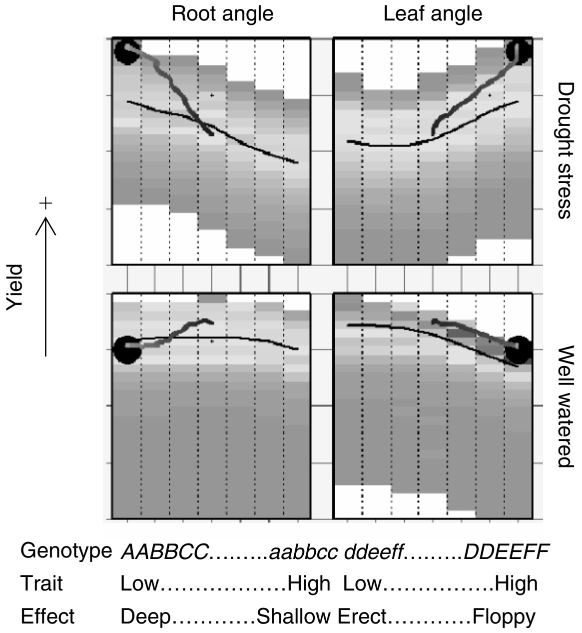

FIGURE 8

Breeding trajectories (thick lines) in a gene-to-phenotype adaptation landscape. Black dots represent individuals in the breeding population; dot size is proportional to the number of individuals. The thin line represents central tendency across genotypic bins. Landscapes correspond to environment type severe terminal stress (ET1) and no stress (ET3). Breeding simulation conducted for drought stress environments. Genotype frequency is colour coded in Plate 1.

Changes in environment types can induce deformations to the adaptation landscapes. The magnitude of any such deformation depends on the underlying trait physiology. Figure 8 illustrates this effect for RA and LA. Yield increased with increasing frequencies of + alleles conditioning the expression states for RA. Greater water capture associated with deeper root systems had a positive effect on simulated yields under ET1. In contrast, there were no marked effects on yield in ET3, which is manifested as a smooth and flat landscape (Figure 8). The comparison of landscapes for LA in ET1 and ET3 reveals a trade-off between light capture and RUE and water use. Yield increased with the increasing frequency of + alleles (erect-leaf-type phenotypes) under no-stress environments where light capture and its distribution within the canopy limits carbon assimilation and yield. The opposite pattern is evident in drought stress conditions where improved RUE generates higher water use, which intensifies the severity of stress during reproductive stages. Water conservation strategies that improve the partitioning of water use between vegetative and reproductive stages are discussed in Chapter 6 (Section 3).

The landscape structure generated for this small G×E×M system has complex features as viewed through the GP plots. The complexity of the landscape is assessed by the analysis of all GP cross sections. The presence of weak trends in a given cross section indicates that a given trait is not a strong determinant of yield response in the context of all other traits (Figure 8). But the absence of any trends across all cross sections indicates a rugged landscape, where peaks in grain yield performance are dependent on the expression states for multiple traits. The example presented in Figure 8 illustrates this contrast. While the adaptation landscape view for ET3 is determined to a large extent by the frequency of + alleles for erect-leaf-type phenotypes, landscapes for ET1 are rather flat, with trends for both RA and LA and the presence of saddles. Adaptation landscapes under drought stress are more complex than in the absence of stress, and the GP plots indicate multiple paths are plausible for crops to cope with stress. The characterisation and understanding of adaptation landscapes and how these respond to E help to study, interpret and anticipate response to selection. The approach allows assessment of the relevance of traits in the context of all other traits under consideration in a specific environment, and aids in strategically selecting germplasm for breeding objectives that target specific sections of GP space.

4.3. Exploring trajectories in GP space: what traits can improve adaptation?

Breeding simulation is a step beyond the study of the structure of adaptation landscapes and has been used to assess breeding strategies (Podlich et al., 1999; Chapman et al., 2003; Wang et al., 2003; Cooper et al., 2005) and the integration of molecular technologies into breeding methods (Podlich et al., 2004; Cooper et al., 2005; Hammer et al., 2005). In the example presented here, breeding simulation was used to study plausible trait phenotype trajectories in GP space under contrasting management and drought stress environments (Figures 8 and 9). Each trajectory represents the average of an ensemble of 20 QU-GENE runs (i.e. 20 replications of the breeding program starting from the same reference breeding population). The common pattern across environment types and management in the allele frequency dynamics is the uniqueness in the relevance of traits and their interdependence. The relevance of a given trait could be judged by the onset and the rate of change in allele frequencies conditioning the expression states of the trait, and the effects of traits on yield at other loci. When the MET was simulated at commercial plant densities, LA was the first trait to change allele frequencies towards the + alleles, reaching fixation upon 20 cycles of selection. The direction of change, however, was opposite in the two environment types. LA decreased (shift towards erect leaf type) with increasing cycles of selection in ET3 (no stress) and increased (shift towards floppy leaf type) at about the same rate in ET1 (severe terminal stress). Similar patterns were simulated for high-density stands, but the rate of change was not as pronounced as under commercial density, and a delay in the onset of change was evident in ET3.

The frequency of the + alleles for RA increased in successive cycles of breeding when selecting for yield in drought environment type ET1. Conservative water use and enhanced water capture in deep soil layers dominated the trajectories, particularly during the first cycles (Figure 9). The value of this yield improvement

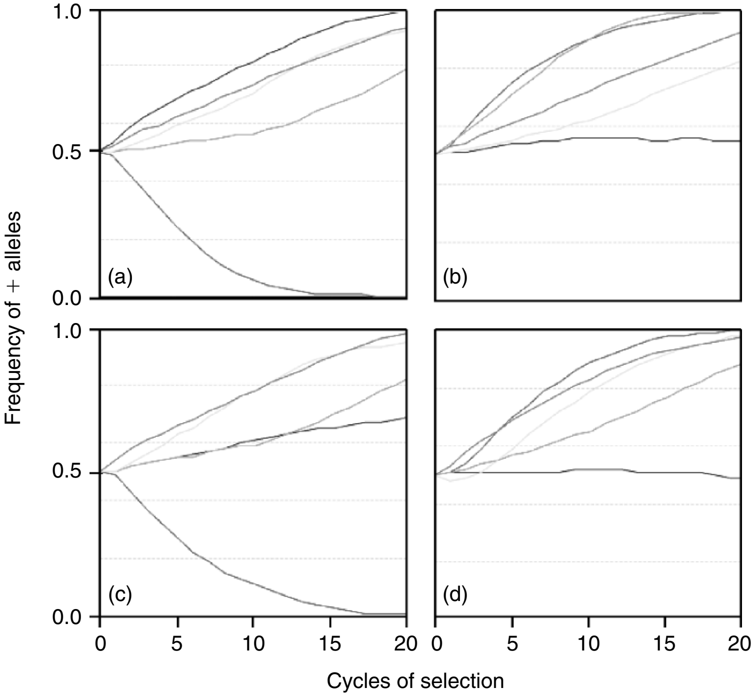

FIGURE 9

Mean changes in gene frequencies for alleles associated with root angle (RA), leaf angle (LA), potential ear size (ME), threshold carbon allocation to the ear and barrenness (CA) and synchronous pollination (SP) with cycle of selection. Selection simulated for specific management: 8 pl m^{-2} (a, b) and 12 pl m^{-2} (c, d); and two contrasting environment types: severe terminal drought stress (ET1) (a, c) and no stress (ET3) (b, d). Traits are colour coded in Plate 2.

strategy was demonstrated in maize populations selected for increased osmotic adjustment (Chimenti et al., 2006). Although this physiological mechanism underpinning the enhanced ability to access water stored in deep soil layers may not be valuable in some germplasm (Bolaños and Edmeades, 1991), the effectiveness of the strategy to improve the maintenance of leaf area, growth and yield in the simulation experiments provides the basis for a testable hypothesis. The reduction in RA, resulting in a deep root system, implies a redistribution of root mass among soil layers. The feasibility of this alternative path towards accessing additional water in deep soil layers is supported by evidence of genetic variation in root architecture (Tuberosa et al., 2002; Tuberosa and Salvi, 2006), variations in patterns of soil water uptake between modern and old hybrids (Campos et al., 2004) and root architecture response to selection (Edmeades et al., 2000). It is apparent from the breeding simulations that this strategy is not universal (Figure 9) and its contribution to yield improvement is constrained to defined domains in the G×E×M space. Water use increased with increasing plant population, thus limiting some of the benefits of enhanced water capture as indicated by a lower rate of change in + alleles for RA. Chapter 13 discusses in detail root attributes for improved capture of resources.

In high-stress environments, ET1 and 12 pl m^{-2}, the breeding simulations showed that selection for yield favoured mechanisms to cope with stress. The frequency of + alleles for CA and SP rapidly increased in successive cycles of selection. The interpretation of these changes is that selection for yield results in lower thresholds to biomass allocation to the ear, to kernel set, and vigorous and synchronous silking (Figures 4c and 9). In contrast, when METs were simulated for low-stress environments and commercial plant populations, selection favoured the main mechanism to realise the environmental potential by increasing + alleles' contribution to augment light interception and RUE (as discussed above) and to increase ME. There was a concurrent increase in + alleles for both traits ME and LA. Empirical evidence supporting this trait trajectory was documented for mid-maturity maize selected in Argentina (Luque et al., 2006). The frequency of + alleles for CA to the ear changed slowly from cycle 0 to 15. A break point becomes apparent following the realisation of improvements in resource capture and use efficiency, and alleles for LA are close to fixation in cycle 15 of the simulation; thus allocation to the ear becomes a limitation to yield improvement.

4.4. Breeding opportunities for broad and specific adaptation

Plant breeders often face the dilemma of designing breeding strategies with the right balance of efforts directed towards breeding for broad versus specific adaptation. Necessary conditions for breeding for specific adaptation are the occurrence of repeatable environment types, and the existence of genetic variation in traits that generate positive, sizable and repeatable G×E×M interactions. Breeding simulations in Figure 9 could be studied as the outcome of a breeding strategy to evaluate opportunities for specific adaptation. Trait phenotype trajectories in Figure 9 suggest opportunities for improvements in both broad and specific adaptation to drought stress within the context of the simulated reference population of the breeding program. The increase in frequencies of + alleles contributing to higher CA and SP, regardless of the environment type and crop management, suggests a breeding strategy that favours selection for + alleles for these traits as a means to improve broad adaptation. Although change in root architecture contributed to yield improvement only in ET1 (Figure 9), the absence of crossover G×E×M interactions (Figures 8 and 9) suggests that selection for + alleles for RA could be one component of a breeding strategy seeking improvement for broad adaptation. Successful improvement for this trait can create genotypes with enhanced yield stability (i.e. less susceptibility to drought stress) and thus extend their domain of adaptation in the G×E×M space. It is also feasible to conceive selection for + alleles for RA as a component of a breeding strategy designed to improve specific adaptation to drought stress. Because changes in allele frequencies for LA generated crossover G×E interactions (Figure 8), this physiological trade-off forces plant breeders to accommodate selection for specific adaptation in the breeding program. To this end, it is necessary to formally define the TPE based on the classification of environments by type (Figure 7). The application of weights to the data from the multi-environment trials to match the environment-type expectations of the TPE, weighted selection strategy, was shown to increase response to selection (Podlich et al., 1999).

This study simulated genetic gains for yield when breeding for specific conditions (Figure 9) relative to those attained if selection samples the TPE. Simulated genetic gains differed little for selection performed in only ET3 environments, compared with the entire TPE. In contrast, genetic gains for selection in ET1, regardless of the management, were double those attained when selection was conducted in the entire TPE (data not shown). Management contributions to the rate of genetic gains were evident but of lower magnitude than those due to environment variation. These results lead to the proposition that incorporating knowledge on G×E×M into breeding can increase genetic gain and hasten crop improvement.

4.5. Opportunities to enhance molecular breeding

Since the discovery of molecular markers and their application to the construction of molecular maps and to the mapping and dissection of quantitative traits (Lander and Botstein, 1989; Lander and Schork, 1994; Paterson et al., 1991), molecular marker technologies have been successfully integrated into many aspects of plant breeding. Opportunities for molecular breeding and use of marker-assisted selection were the motivations for in silico studies and reviews (Chapter 14; Cooper et al., 2005, 2006; Lee, 1995). But the realisation of the potential use of DNA markers to improve methods for predicting expected phenotypes of progeny from parental information as suggested by Paterson et al. (1991), and its utilisation in breeding programs, came about after significant developments in analyses and prediction methods, often based on a mixed-model framework (i.e. Malosetti et al., 2007; van Eeuwijk et al., 2005; Boer et al., 2007), and improvements in and the deployment of information management technologies (Cooper et al., 2006; Graham, 2008).

Many of the activities within molecular breeding rely on statistical models that summarise associations between genotypic and phenotypic variations. These statistical models often provide a static view of traits and their association with genomic regions (QTL). The treatment and analysis on a trait-by-trait basis limits these methods to effectively capture the dynamic relationships between traits, leaving to the breeder the subjective interpretation of the interplay and emerging trade-offs among traits. As evidence accumulates towards the need for considering epistasis and pleiotropy for the deployment of enhanced methods for molecular breeding, it is opportune to contemplate the utility of the G×E×M modelling approach outlined in this chapter as a framework for considering the biological and physiological interplay of QTL, traits and environments in a way that adds value to the well-established and effective statistical framework for molecular breeding. In the G×E×M framework, epistasis and pleiotropic effects are emergent properties of the physiological framework (Hammer et al., 2006). The trait trajectories depicted in Figure 9 illustrate the conditional dependencies among traits to contribute to yield improvement. While the genetic models defined for all traits in this study were additive at the individual trait level, the grain yield value of the different alleles for a given trait is conditional to the state of other loci as demonstrated by the non-linear structure of the trait trajectories in genotype space. These simulations suggest that physiological dissection and modelling can help assign biological function to QTLs, and explain and resolve G×E×M interactions, thus providing a foundation to improve molecular breeding strategies in maize. This argument could be extended to the application of the framework to known genes for the assessment of their function at the whole-plant level, that is, to assess the extent to which the effects of gene expression at the molecular level propagate across levels of organisation. The framework could be used for designing in silico breeding strategies that make use of transgenics as a step prior to the initiation of experimentation that would require significant management and investment. Hammer et al. (2005) demonstrated in a theoretical study of sorghum that marker-assisted selection could be improved (enhanced rate of yield increase over cycles of selection) by considering knowledge from trait physiology and modelling.

4.6. How consistent are simulated trajectories with changes in traits due to genetic improvement for yield?

To interpret the results of the breeding simulation in the context of observed trait trajectories, we must define the environment types, changes in management and selection objectives that prevail during the selection process. Major breeding objectives are to increase yield and yield stability across years and geographies. Selection decisions in the past were mostly driven by data collected in the TPE; that is, a large fraction of the data driving selection decisions were obtained in environments that exposed maize crops to low drought stress (Löffler et al., 2005). However, as the TPE is by definition a mixture of environments, in certain years, drought stress could have contributed to the pool of data and germplasm improvement. Crop management also changed through time, with plant population, irrigation and N use increasing since 1960 (Cassman and Liska, 2007).

In the context outlined above for dominant environment types, management practices and breeding objectives, the expectation set by outcomes of breeding simulation (Figures 8 and 9) is to observe a rapid decrease in LA (towards hybrids with an erect leaf type) associated with improved RUE in high-density stands, to some degree deeper root systems selected in drought-prone environments and dry years and increased kernel set due to higher resource allocation to the ear. Observed trait trajectories for selection in the north-central USA compare well with the expectations from the breeding simulation (Duvick et al., 2004; Figure 10). After the onset of the era of intensive agriculture in the early 1960s, LA scores increased linearly, reaching a plateau denoted for hybrids released since the late 1980s. Breeding simulation indicated this trajectory in the absence of nitrogen limitations and in ET3 (Figures 7 and 9), which together with ET2 (low stress around flowering) accounts for 65% of environment types in the TPE. Both simulated and observed leaf scores (Figures 9 and 10) indicated that breeding for yield had moved the breeding populations towards a region in the G space that optimises light capture and use efficiency under E×M typical of intensive agriculture, with apparent little room for further contributions to yield improvement.

Changes in root architecture in response to selection have not been documented. However, there is evidence for a reduction in biomass allocation to roots in the topsoil (Bruce et al., 2002). This observation is

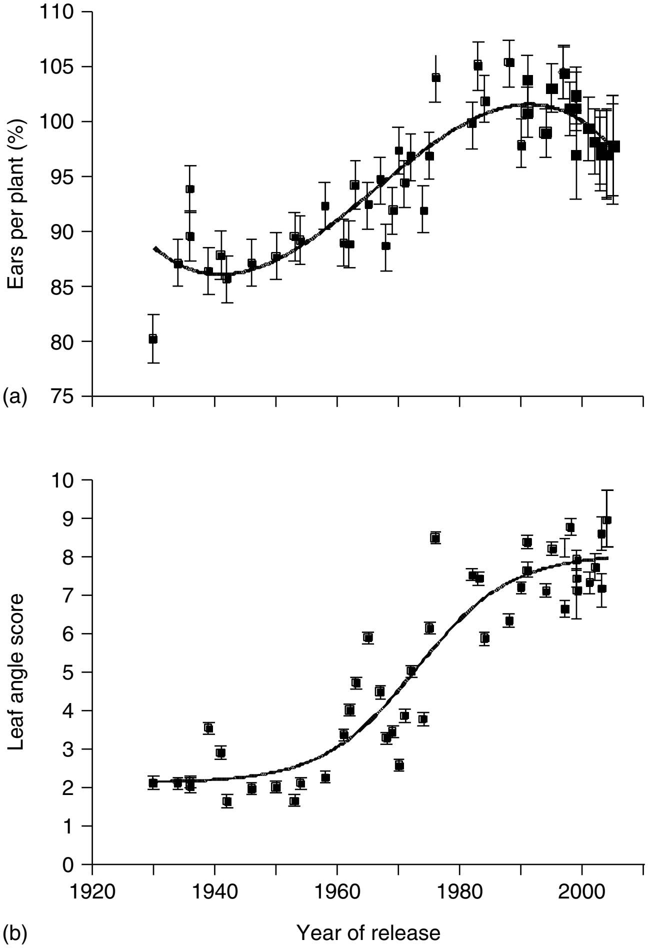

FIGURE 10

Observed trajectories in non-barren plants (a) leaf angle score (b) in a series of Pioneer hybrids released between 1930 and 2007. Leaf angle scores range from 0 to 10 assigned to floppy-type and erect-type hybrids.

consistent with a predicted trajectory towards deeper root systems and lower root density in upper soil layers (Figure 9). Lower RAs predict a more uniform water use pattern in depth and time as well as a more uniform biomass distribution in the profile. Campos et al. (2004) showed that older hybrids use more (less) water from the top (bottom) soil layers than modern hybrids. As suggested by breeding simulation, these observed patterns of increased water capture and conservative water use may have resulted as a consequence of selecting hybrids with yield stability across locations and years. Based on simulated trait trajectories for ET1 environments, it is suggested that there is unrealised potential to progress further yield stability in main production areas in the maize belt and yield under drought stress.

Reproductive traits ME, CA and SP increased in successive cycles of breeding (Figure 9), leading to the creation of hybrids with increased CA to the ear and increased kernel set for a given E and M (Figure 4c).

Empirical evidence and theoretical predictions agree well in that selection for yield increased the kernel number per plant, per ear and per unit area (Chapman and Edmeades, 1999; Echarte et al., 2004; Campos et al., 2006; Luque et al., 2006; Tollenaar et al., 1992; Duvick et al., 2004; Edmeades et al., 2000), and fertile ears per plant largely contributed to this increase (Duvick et al., 2004; Chapman and Edmeades, 1999; Tollenaar et al., 1992). Increased partitioning and reduced barrenness in the context of the modelling framework are related to the reduction in CA (Figures 4c and 9). Simulated trait trajectories are consistent with measurements by Echarte et al. (2004) but not by Luque et al. (2006) and Tollenaar et al. (1992). In the latter two studies, model parameters linked to ME and CA to the ear were correlated. Because of such correlation, it is difficult to contrast model predictions with empirical evidence. The framework used in this study captures some aspects of the underpinning mechanisms causal of barrenness but further advancement on the model, perhaps through incorporating theoretical aspects of interplant competition (Pagano et al., 2007; Pagano and Maddonni, 2007), will be necessary to better connect genetic variation and physiological determinants of barrenness. Luque et al. (2006) observed increases in ME only under high-yield environments, in agreement with predicted trait trajectories in this study (Figure 9, environment type ET3).

5. CONCLUDING REMARKS

This chapter reviewed and summarised theoretical developments towards a framework that integrates quantitative genetics, breeding simulation and modelling of physiological traits and dynamic GP relations. Such a framework is intended to enable breeders and agronomists to project trajectories in the G×E×M space into the future and gain insights on the consequences of manipulating genomes to the creation of improved crops for target management and environments.

A central concept emphasised throughout this study and applied to the different aspects of modelling and simulation is the iterative nature of the process, and thus the need to integrate modelling and simulations as one component of the breeding program. The execution of this framework is feasible only through such integration that forces individuals to align breeding objectives, physiological questions and genetic hypotheses, which ultimately have to be tested in the breeding program.

This study demonstrated in silico the validity of a method to effectively explore the G×E×M state space, to integrate and apply physiological concepts to plant breeding and the value of leveraging this knowledge to develop improved crops. Nevertheless, executing this framework poses a number of grand challenges, and a significant scientific and technological ground has yet to be covered. There is a clear need to advance the scientific debate about the detail and complexity needed for crop growth models to be able to integrate processes across levels of organisation while predicting emergent functional consequences for the organism. Related to this issue is the need for a considerable effort and investment in creating knowledge and developing robust links between genetic variation for adaptive traits relevant to breeders and the underlying physiological determinants. Despite the agreement between observed and simulated trait trajectories for the past 50 years of breeding in the US Corn Belt, there is a clear need for a theoretical and empirical demonstration that these technologies can be used to improve future rates of genetic gain in elite breeding populations.

We are optimistic that breeding simulation will help understand observed breeding trajectories for traits contributing to yield improvement; identify emergent, in some cases counterintuitive, behaviour of the breeding system; and quantify trait and environmental context dependencies. This understanding, along with quantitative knowledge of QTL function, via trait dissection and integration using physiological modelling and a G×E×M framework, will enable predictions to be evaluated in the target breeding program. This emerging breeding technology can help manage and adapt germplasm to effectively navigate through the G×E×M space, producing improved hybrids that meet the needs of changing farming systems and environments.

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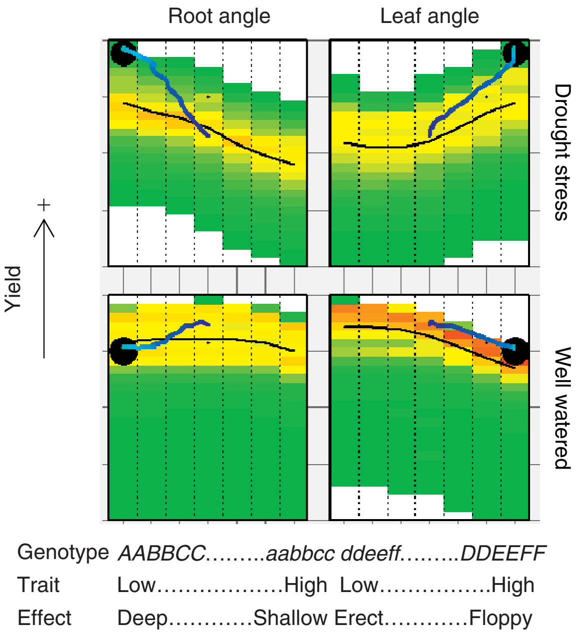

PLATE 1

Breeding trajectories (thick lines) in a gene-to-phenotype adaptation landscape. Black dots represent individuals in the breeding population; dot size is proportional to the number of individuals. The thin line represents central tendency across genotypic bins. Landscapes correspond to environment type severe terminal stress (ET1) and no stress (ET3). Breeding simulation conducted for drought stress environments. (see Fig. 8 of Chapter 10).

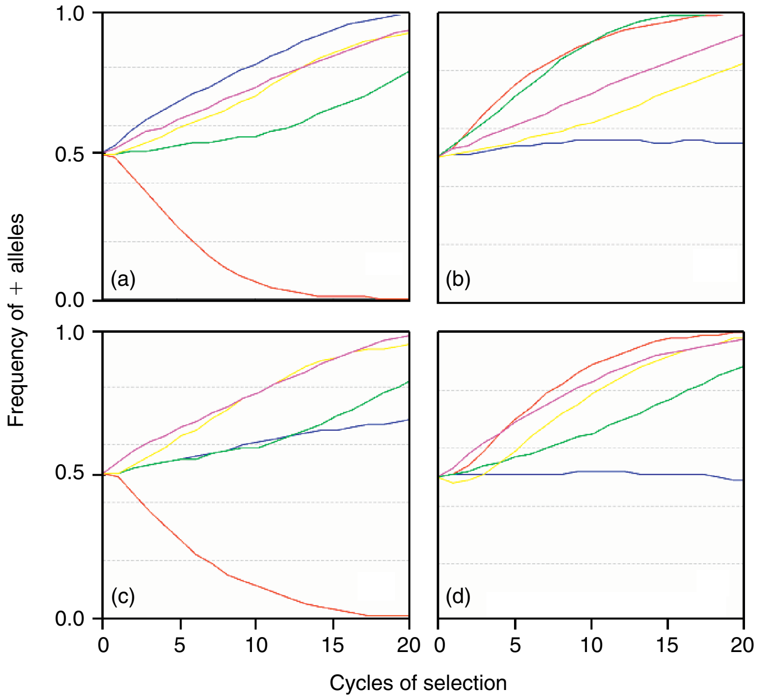

PLATE 2

Mean changes in gene frequencies for alleles associated with RA (--), LA (--), ME (--), CA (--) and SP (--) with cycle of selection. Selection simulated for specific management: 8 pl m^{-2} (a, b) and 12 pl m^{-2} (c, d); and two contrasting environment types: severe terminal drought stress (ET1) (a, c) and no stress (ET3) (b, d). (see Fig. 9 of Chapter 10).

Integration of Biotechnology, Plant Breeding and Crop Physiology: Dealing with Complex Interactions from a Physiological Perspective

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… The beauty of nature lies in details; the message, in generality…

Stephen Jay Gould

1. INTRODUCTION

The goal of plant breeding is to produce cultivars with high yield potential and stability under most of the environments where they are grown (Hallauer, 2007). This is challenging, partially because complex traits such as yield depend strongly on environmental efects (E) and genotype by environment (G × E) interactions. The prevalence of these interactions has been a source of frustration for breeders (Blum, 2005) despite their success in yield improvement during the twentieth century (Section 3.2 and Figure 1 in Chapter 15).

Crop physiology can provide conceptual and practical tools to improve breeding efficiency aimed at high yield potential, stress adaptation (Sections 5–6 in Chapter 15) and quality attributes of grain (Section 4 in Chapter 16). During the past 50 years, substantial progress has been made in understanding the physiological basis of yield and quality determination as driven by genotype, environment and the G × E interactions (Boote and Sinclair, 2006). Despite this progress and a handful of successful examples (e.g. Bolaños and Edmeades, 1993; Rebetzke et al., 2002), in many cases crop physiology has failed to lead to improved crop performance (Jackson et al., 1996; Sinclair et al., 2004; Sinclair and Purcell, 2005). A number of reasons underlie this apparent underperformance including poorly developed links between disciplines (Miflin, 2000) and the limited availability of rapid, accurate and affordable phenotyping methods applicable to large populations. Although biotechnology has produced an impressive amount of scientific and technological knowledge (Chapter 14), its contribution to increase yield potential in breeding programmes has been so far very limited. Causes of this could be neglect or superficial understanding of trade-offs (Section 1 in Chapter 9), scale issues in the definition of traits (Chapter 1), the complexity of polygenic traits (Mackay, 2001; Holland, 2007) and G × E interactions (Austin and Lee, 1998). Considering the vast knowledge gained in crop physiology, breeding and biotechnology, a framework integrating these complementary disciplines could be important to achieve steeper gains in plant breeding programmes (Section 3.4 in Chapter 10). In this context, this chapter discusses the potential contributions of biotechnology to facilitate the use of physiological traits in plant breeding and to crop physiology studies. Particularly, we focus on how these techniques could help to bridge the gap and stimulate creative interactions between both disciplines. Reciprocally, we focus on the contribution of crop physiology to plant breeding and biotechnology. The physiological principles with applications in crop improvement are discussed in other sections of this book (i.e. capture and efficiency in the use of resources in Part 2; phenological development in Chapter 12). Therefore, our aim is not to abound in these concepts but to highlight the value of crop physiology to the understanding and interpretation of complex genetic and physiological mechanisms with strong interaction with the environment.

2. CONTRIBUTIONS OF BIOTECHNOLOGY

Biotechnology has proved valuable to agriculture in three main aspects: (a) improved tolerance to biotic stresses, such as plagues and diseases, which lead to a reduction in the use of agrochemicals; (b) resistance to herbicides that favoured soil conservation practices and opened opportunities for novel farming systems (Section 5 in Chapter 3) and (c) improved and diversified quality of agricultural products (Section 4.3 in Chapter 14). These achievements are a reality now, partly because the relevant traits have a relatively simple inheritance and involve few genes, which are integrated in linear cascades or small networks, the G × E interaction is small, there are no major scaling-up issues and trade-offs, if any, are minor (Benedict et al., 1996; Creus et al., 2007; Elmore et al., 2001; Dunwell, 1998; Struik et al., 2007). In contrast, the contribution of biotechnology to the increment in crop yield potential and yield stability is much more relegated because it has to deal with more complex genetic and physiological mechanisms, trade-offs and strong G × E interaction (Edmeades et al., 2004; Campos et al., 2004; see Section 3.1).

A particular trait is generally attenuated when scaling up across levels of organisation because many factors interact and complexity increases (Section 5.3 in Chapter 1). This buffering response reduces the relevance of many traits to the crop level or farming system. Moreover, traits can be controlled by gene networks, so single gene action in a biochemical pathway is commonly of limited use in understanding yield potential or crop adaptation to the environment (Chapman et al., 2002; Sinclair and Purcell, 2005).

Relevant examples of the complex interactions that take place at the trait or quantitative trait locus (QTL) level are presented in Section 3.1 to indicate that caution must be taken when interpreting and analysing the potential of the new available information derived from crop physiology or molecular studies. The new available biotechnologies, however, could play an important role in the integration between crop physiologists, breeders and molecular biologists. In the next section, we emphasise how biotechnology could facilitate crop physiology studies as well as the use of physiological traits in plant breeding.

2.1. Biotechnology facilitates the use of key traits in plant breeding

Decades ago, it was indicated that four main conditions must be met for a trait to be successfully employed in crop breeding: (i) it must be relevant for growth and crop productivity; (ii) it should have intra-specific variability; (iii) it should have medium to high heritability; and (iv) it should be easily monitored (Donald, 1968; Schrader, 1985; Bruce et al., 2002). An additional consideration for traits associated with improvement of crops (e.g. secondary traits) is that they do not have to affect negatively crop performance under G × E interaction. For example, for stress tolerance the trait must not be associated with yield losses under optimal growing conditions (Bruce et al., 2002). Biotechnology could notably facilitate two of these criteria, because of its potential to generate genetic variability by mutagenesis or transgenesis, and to easily screen the desired traits in large segregant populations by means of molecular markers, without the need of further phenotypic evaluations (Jones et al., 1997). The use of molecular markers can also accelerate the selection process, by fixing a trait in early generations or by speeding up backcrossed trait introgression.

A major challenge and a limiting factor for the success of the interdisciplinary approach is the identification of the main traits that confer yield potential and yield stability in different environments, an area in which crop physiology could contribute considerably.

2.2. Contributions of biotechnology to crop physiology

Ascertaining the association between traits by comparing their respective phenotypic expressions is not always a reliable approach. QTL analysis constitutes a powerful tool for dissecting complex traits, by finding

QTL related to traits at different levels (e.g. crop growth and enzyme activity), or by linking primary and secondary traits, enzymes and their substrates or products, and structural genes with enzyme activity or their products. Some examples are the studies of Causse et al. (1995) and Prioul et al. (1997) who used QTL analysis to identify key control factors in carbohydrate metabolism; Reymond et al. (2003) who found that QTL of abscisic acid concentration in the xylem sap colocalised with QTL of leaf growth response to soil water deficit, and Sala (2007) who used QTL analysis to study field grain drying rate and its discriminant factors in maize. Molecular markers and trait dissection could allow to identify key genes and to 'design' superior genotypes with optimal complementation among different traits (Peleman and van der Voort, 2003). Many examples of how QTL analysis could further benefit the integration among disciplines are available in the literature (Simko et al., 1997; Tuberosa et al., 2002; Quarrie et al., 1997; Salvi et al., 2002) and Section 3 in Chapter 14.

The noise arising from different genetic backgrounds in many traditional crop physiological studies has often been disregarded. The development and use of near-isogenic lines that differ only in the trait of interest (Tanksley and Nelson, 1996; Guo et al., 2007) provides a useful tool for studying the effects of a particular trait on plant behaviour. For instance, Creus et al. (2007) evaluated several pairs of sunflower isohybrids with (R) and without (S) QTLs associated with resistance to *Verticillium dahliae* in five locations. They found that (i) disease incidence and severity for all R isohybrids were negligible, (ii) grain and oil yield of S isohybrids was nearly 30% less than those of their R counterparts in the most severe disease conditions and (iii) R and S isohybrids presented similar yields under low disease severity. In another study, Fonts et al. (2008) used molecular markers and backcrosses to develop and study sunflower near-isogenic lines for the two most important QTL (A and B) associated with growing degree-days to flowering (DTF). Results of this study are presented in Section 3.1.2. The use of such genetic materials allowed determining QTL effects for different isohybrids or isolines removing the 'noise' from the genetic background.

Another alternative to reduce the background effect is to pool all the results from QTL analysis into a consensus map. In such manner, Sala (2007) was able to identify hot-spot regions that were consistently associated with maize grain moisture at harvest across a range of genetic backgrounds or to identify new putative regions associated with field grain drying rate. This approach would theoretically reduce the need to map individual crosses over and over for a given trait (Tuberosa et al., 2002; Edmeades et al., 2004) and it would increase the power of QTL detection.

Technologies from functional genomics (microarrays, ESTs, proteome analyses) to structural genomics (mapping, genome sequencing, synteny and colinearity with related species) can allow identifying candidate genes that are putatively involved in the expression of diverse traits (Ishitani et al., 2004). The most promising genes could then be assessed for associations with existing genetic information, such as from QTL. After selecting a reasonable number of candidate genes, their expression and phenotypic effect could finally be examined using a number of tools available today, such as TILLING mutants, RNA interference and gene overexpression/silencing (Salvi and Tuberosa, 2005).

Crop physiologists should exploit the numerous tools and pieces of information that are continuously generated by genomics-oriented studies. Molecularly characterised populations and isogenic lines derived from such studies should constitute the main source of genetic material for investigating physiological traits. Along with the use of available information on molecular markers, candidate genes and associated secondary traits in the target crop and related species, this approach constitutes an avenue in the investigation of those mechanisms responsible for crop behaviour that remain unknown or poorly understood.

3. CONTRIBUTIONS OF CROP PHYSIOLOGY TO PLANT BREEDING AND BIOTECHNOLOGY

The identification of relevant traits or genes associated with crop performance constitutes a huge challenge because of trade-offs, trait attenuation and strong interactions resulting from scaling up across levels and from complex and redundant regulation of plant systems (Section 2). The role of crop physiologists is essential since they should contribute to (i) characterise target environments, (ii) assess the potential traits to improve yield potential or crop adaptation in those environments, (iii) identify relevant secondary traits easy to measure, with high heritability and high correlation with crop performance, (iv) understand complex interactions among traits and with the environment. Crop physiology can then contribute to not only the identification of relevant traits for yield potential and crop adaptation following a top-down approach (Chapman et al., 2002), but also the interpretation of the potential of the new available information derived from molecular studies (from gene to phenotype; Ishitani et al., 2004).

Other sections of the book deal with the identification of relevant traits for crop growth, development, yield and quality determination and crop adaptation to the target environment (Chapters 6, 7, 8, 12 and 16) and easy-to-measure secondary traits for breeding programmes (Chapters 14, 15 and 16). The next section presents examples of the complex interactions that take place at the trait or QTL level that support our view on the synergy that can arise at the interface between crop physiology, plant breeding and biotechnology.

3.1. Disentangling complex interactions

3.1.1. Interactions at the trait level

Effects of water deficit on crop productivity are not easy to predict since they vary with the timing, duration and intensity of stress, and factors including crop previous history and other environmental aspects. Traits with putative benefits for adaptation to dry environments are not universal and strongly interact with other traits and the environment.

For example, deep roots would be a desirable trait for areas where substantial amounts of water are left in the soil at physiological maturity and soil stored water can be replenished in the subsequent fallow period (Passioura, 1983; Sadras and Rodriguez, 2007; Schwinning and Ehleringer, 2001). Also, induction of a large resistance to water flow in the plant through drying topsoil is a way to save water for later, more critical growth stages, in areas where drought is progressive and become more severe towards the end of the growing season (Passioura, 1983). If water is mostly absorbed from a pulse-dominated shallow soil layer, adaptations that maximise growth per unit water use are small root:shoot ratio, shallow root system, high leaf conductance and high stomatal sensitivity to plant water status; contrarily, if the crop relies mostly on deeper soil water, favourable traits are large root:shoot ratio, predominantly deep root system, lower leaf conductance and low stomatal sensitivity (Schwinning and Ehleringer, 2001).

Moreover, early flowering would be a favourable trait where crops are exposed to severe terminal water stress, so that the plants can complete their growing cycle without severe stress at the critical stages for grain yield determination (Richards, 1991; Chapman et al., 2003; Debaeke and Aboudrare, 2004). In environments or seasons with mild or no terminal water stress, however, full season cultivars and consequently later flowering would be preferred because of the greater yield potential associated with late maturity (Capristo et al., 2007).

Finally, leaf expansion responses to dehydration, a trait that shows genetic variability (Reymond et al., 2003; Pereyra-Irujo et al., 2008) could have variable value according to the target environment. In environments where crops depend on stored soil water, reduction in leaf area would be desirable to save water for later, more critical reproductive stages. Maintaining high rates of leaf expansion under stress, however, would be appropriate for short periods of drought during vegetative growth since this strategy would enable the crop to use the incoming radiation and resources more efficiently upon stress relief. Moreover, if the crop relies on in-season rainfall, early vigour would reduce soil evaporation (Agüera et al., 1997; Rebetzke and Richards, 1999; Richards and Lukacs, 2002).

3.1.2. Interactions at the QTL or gene level

The following two case studies illustrate physiological interpretations of complex information derived from molecular studies. The first example refers to a genetic linkage analysis of two traits, namely growing degree days to flowering (DTF) and photoperiodic response in sunflower families derived from the cross between lines HA89 and ZENB8 (León et al., 2000, 2001). Two QTLs A and B were highly associated with the photoperiod response that controls thermal time to flowering. Near-isogenic families for those QTLs were developed through backcrosses with the aid of molecular markers. This genetic material was used to study the effects of both QTLs on sunflower photoperiod response, considering the moment of apex change, that is Stage 1.3 in the scale of Marc and Palmer (1981), and its subsequent rate of development (Fonts et al., 2008). The longest crop periods to floral induction and to end of floral differentiation were observed when QTL A was selected homozygous as HA89 parental line and QTL B homozygous as ZENB8 parental line (Figure 1). This previously unnoticed gene x gene interaction is compatible with the web-cascade reaction system proposed for the control of time to flowering and for the transition from vegetative to reproductive stages (Valverde et al., 2004; Blázquez, 2000; Imaizumi and Key, 2006). Additionally, QTL B significantly interacted with photoperiod for both traits (Fonts et al., 2008). Under extended photoperiod the additive

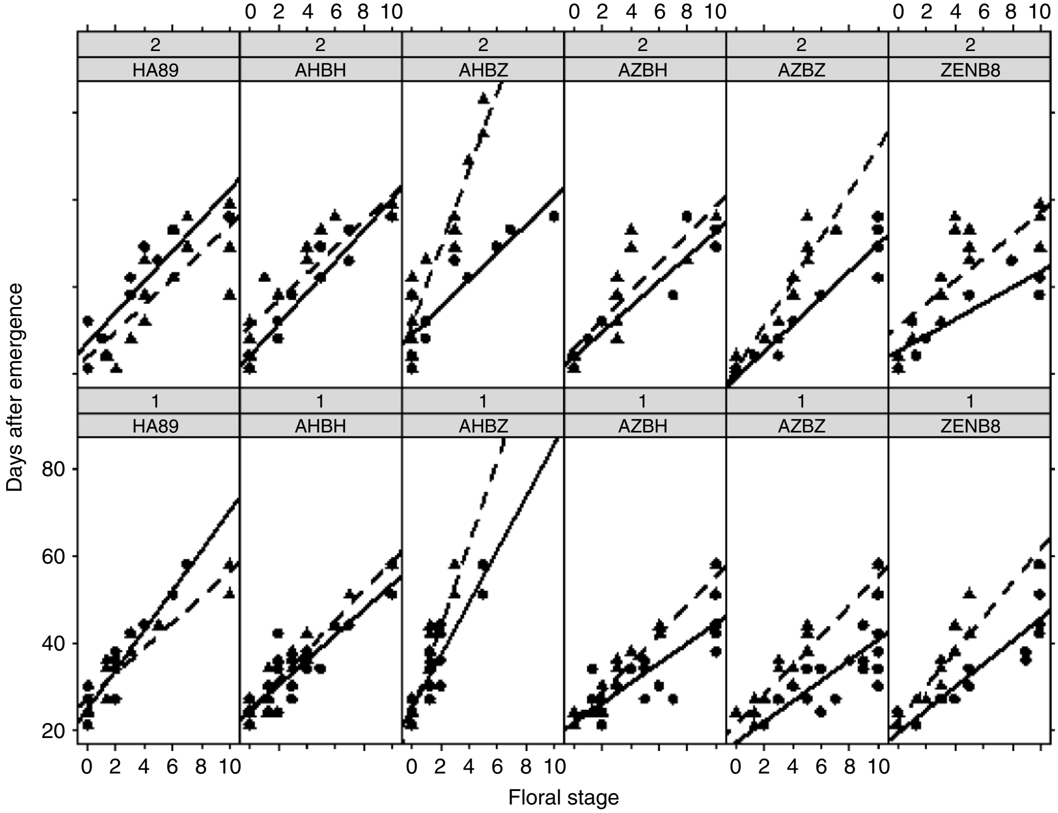

FIGURE 1

Relationship between days after emergence and floral stage for the near-isogenic families AHBH, AHBZ, AZBH and AZBZ, and for parental lines HA89 and ZENB8 grown under extended (triangles) and short (circles) photoperiods. Each point indicates an individual observation. Floral stages correspond to the scale of Marc and Palmer (1981). Continuous (short photoperiod) and dashed (extended photoperiod) lines are fitted linear regressions. Upper and lower panels are from replicate experiments (1 and 2). In the near-isogenic families, alleles from HA89 (H) or ZENB8 (Z) in each of two QTLs (A and B) are indicated.

effect of QTL B for phase duration increased, denoting a short day response. The presence of ZENB8 alleles in QTL B and HA89 alleles in QTL A produced a much stronger delay in development up to the end of floral differentiation under long than under short photoperiods (Figure 1). Thus, a second-degree interaction between QTL A, QTL B and photoperiod was found for rate of development. This higher-order interaction effect is also compatible with the complex web of processes controlling flowering responses to photoperiod, in which a clock regulated transcription factor is stabilised by light (long days) and activates or suppresses key flowering genes (Turner et al., 2005; Imaizumi and Key, 2006).

A second example deals with the use of molecular markers to locate QTLs associated with oil concentration and DTF in the same sunflower population grown in a range of latitudes from Fargo (46.8°N) to Venado Tuerto (33.2°S) (León et al., 1995, 2001, 2003). A QTL on linkage group B was associated with both grain oil concentration and DTF. Consistent with the phenotypic correlations, additive effects for higher DTF and lower grain oil concentration in linkage group B were derived from ZENB8 (Table 1). Also, these additive effects were largest at high latitudes. The highest LOD scores for this QTL in association with DTF were observed under long photoperiods at crop emergence (For example, Fargo; Table 1). Moreover, the highest LOD score for this QTL in association with grain oil percentage was also observed at Fargo (Table 1), the environment with the highest rate of decline in temperature and radiation during the grain filling period. This environment also showed the most significant phenotypic correlation coefficients between DTF and grain oil concentration (-0.29; $P < 0.001$). Especially in areas with short growing seasons, such as Fargo, late flowering genotypes (alleles from Zen B8 in QTL on linkage B) were exposed to poor environmental conditions during grain filling and produced less grain oil than early flowering genotypes. This is because low temperature and radiation have negative effects on grain growth rate and grain oil concentration (Andrade and Ferreiro, 1996; Connor and Hall, 1997; Hall, 2000; Dosio et al., 2000; Section 2 in Chapter 16). Genetic linkage between grain oil concentration and DTF could not be discarded. However, the similarities in QTL position, parental effects, gene action and QTL × E interaction would be indicating that the oil concentration effect promoted by QTL B was a consequence of altered phenology (Table 1). The modified oil concentration was not a direct effect of the QTL; it was a consequence of trait interaction derived from the phenological changes induced in the plants by that QTL, which in turn strongly interacted with the environment.

Table 1 Linkage Group, Position, Flanking Markers, LOD Scores and Additive Effects of QTL B Associated with Growing Degree-Days to Flowering and Grain Oil Concentration in Sunflower

Trait	Linkage Group	Position (cM)	Left–Right Locus	Average Additive Effect	LOD Score			
					Long Photoperiod	Short Photoperiod	High Latitude	Low Latitude
Growing degree-days to flowering	B	64	C1735–C0741	35.2	24.5	1.3		
Grain oil concentration	B	66	C1735–C0741	−1.0			6.1	0.9

Data obtained from a genetic linkage analysis in families derived from the cross between lines HA89 and ZENB8 (León et al., 2001, 2003). A negative sign for the additive effect means an increase in the mean value of the trait due to HA89 alleles. A positive sign for the additive effect means an increase in the mean value of the trait due to ZENB8 alleles. HA89 allele in this QTL decreases the growing degree-days to flowering and increases grain oil percentage. LOD scores and additive effects of this QTL strongly interact with the environment. Crops were grown in two contrasting locations: Fargo (46.8°N) and Venado Tuerto (33.2°S). Photoperiod was measured at crop emergence.

These interactions are magnified and become more difficult to understand when considering more complex traits such as yield potential or yield under restricted water supply (Mackay 2001; Holland, 2007). For example, QTLs associated with yield under water deficit are generally cross specific, with strong interaction with the environment and with small individual effects (Campos et al., 2004; Beavis and Keim, 1996). These QTLs could increase, decrease, or be irrelevant to grain yield depending on the environment. Accordingly, a considerable difference was observed in gene expression profiles between water-stressed plants in a limited rooting volume versus those stressed in the field (Habben et al., 2001, Zinselmeier et al., 2002). As discussed earlier, confounded conclusions could be reached if interactions between traits and with the environment are omitted. Therefore, applying molecular technologies in breeding such as marker-assisted selection (MAS) may not be completely straightforward and constitutes a continuous challenge (Young, 1999; Xu and Crouch, 2008). Undoubtfully, conventional breeding, MAS and genetic engineering for higher yield potential and crop adaptation to the target environment can proceed faster if the physiological mechanisms of grain yield determination and their interaction with the environment are better understood.

4. CONCLUSIONS

Crop physiology, as stated by Evans (1994) has two main areas of research: one oriented to agronomy, the other oriented to plant breeding. The integration between breeding and agronomy explained the consistent rise in yields during the last decades (Duvick and Cassman, 1999; Passioura, 2002, Box 1 in Chapter 2). In this context, the interaction with biotechnology could provide novel and powerful tools that can help to increase the depth and accuracy of crop physiological studies for breeding purposes. Crop physiology can establish key links between phenotypic traits and crop performance, since it seeks to explain and predict the complex interactions between relevant traits and/or between traits and the environment. Thus, this discipline is crucial for understanding and extrapolating processes and mechanisms occurring at different levels of organisation. Breeders have questioned the early concept of ideotype, sometimes by its simplicity, sometimes by its technical difficulties. After many years of research, physiologists have learned from their failures and few successes, and as such, have highlighted the importance of interactions within plants and between plants and dynamic environments (Sinclair and Purcell, 2005); this experience may help to capture the potential benefits of biotechnology in plant breeding. The key lies in integration. The most notable examples of connection of transgenic approaches with field performance come from initiatives which allocate enormous amounts of human and economic resources in multidisciplinary actions integrating agronomists, crop physiologists, breeders and molecular biologists (Passioura, 2007). This and other authors (e.g. Wollenweber et al., 2005) claim for dialogue across disciplines for effective scaling up of yield potential and yield stability traits. We are starting to see evidence that this type of integrated multidisciplinary framework will reinforce and contribute to higher and more stable yields in the future.

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Crop Development: Genetic Control, Environmental Modulation and Relevance for Genetic Improvement of Crop Yield

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1. INTRODUCTION

Crop development is a sequence of phenological events controlled by the genetic background and influenced by external factors, which determines changes in the morphology and/or function of organs (Landsberg, 1977). Although development is a continuous process, the ontogeny of a crop is frequently divided into discrete periods, for instance 'vegetative', 'reproductive' and 'grain filling' phases.

Patterns of phenological development largely determine the adaptation of a crop to a certain range of environments. For example, genetic improvement in grain yield of wheat has been associated with shorter time from sowing to anthesis in Mediterranean environments of Western Australia (Siddique et al., 1989), whereas no consistent trends in phenology were found where drought is present but not necessarily terminal, including environments of Argentina, Canada and the United States (Slafer et al., 1994a; Slafer and Andrade, 1989, 1993) (Figure 1).

This chapter focuses on two major morphologically and physiologically contrasting grain crops: wheat and soybean. For both species, we have an advanced understanding of development and physiology in general. Wheat is a determinate, long-day grass of temperate origin, which is responsive to vernalisation. Soybean is a typically indeterminate (but with determinate intermediate variants), short-day grain legume of tropical origin, which is insensitive to vernalisation. Comparisons with other species are used to highlight the similarities and differences. The aims of this chapter are to outline the developmental characteristics of grain crops and the links between phenology and yield, to revise the mechanisms of environmental and genetic control of development and to explore the possibilities of improving crop adaptation and yield potential through the fine-tuning of developmental patterns.

2. CROP DEVELOPMENT

In this section, we briefly describe major developmental stages or phases of wheat and soybean separately (as developmental features are in many cases unique), and then discuss the relationships between crop phenology and yield determination.

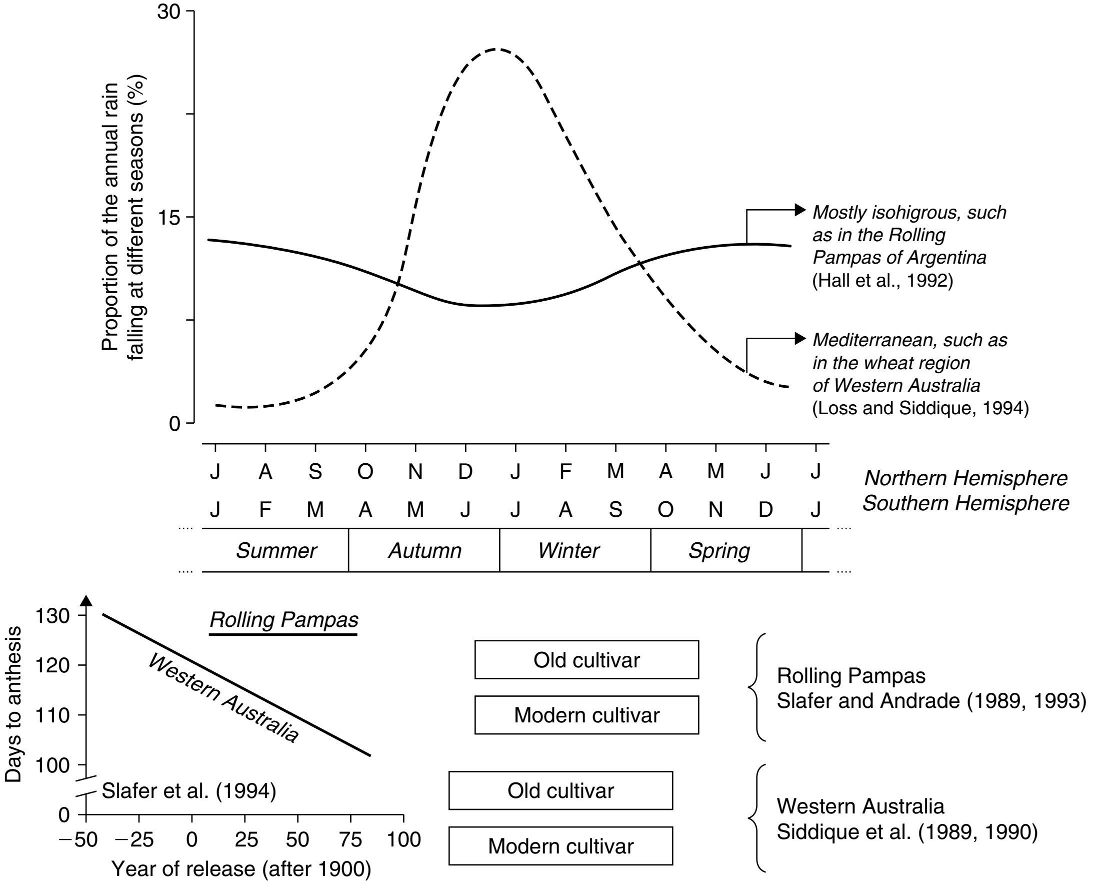


FIGURE 1

Retrospective studies comparing the seasonal pattern of rainfall and the changes in earliness of wheat cultivars released in Western Australia and the Rolling Pampas. The bars cover, for each type of cultivar, region and common periods from sowing to anthesis derived from the studies quoted. Source: Araus et al. (2002).

2.1. Major developmental stages or phases

2.1.1. Wheat

The development of the wheat plant comprises phases defined in terms of microscopic and macroscopic changes that have been integrated into several phenological scales (Miralles and Slafer, 1999). Figure 2 shows developmental progress of wheat based on easily recognisable events including microscopic (e.g. double ridges, terminal spikelet initiation) and macroscopic (e.g. crop emergence, heading, anthesis, maturity, harvest) delimiters of phases. In this simple scheme, development involves three major phases:

(i) the vegetative phase, when the leaves are initiated;

(ii) the reproductive phase, when first spikelet and then floret development (including floret mortality) occurs, until the number of fertile florets is determined;

(iii) the grain-filling phase, when the grain first develops endosperm cells, and then grows to its final weight.

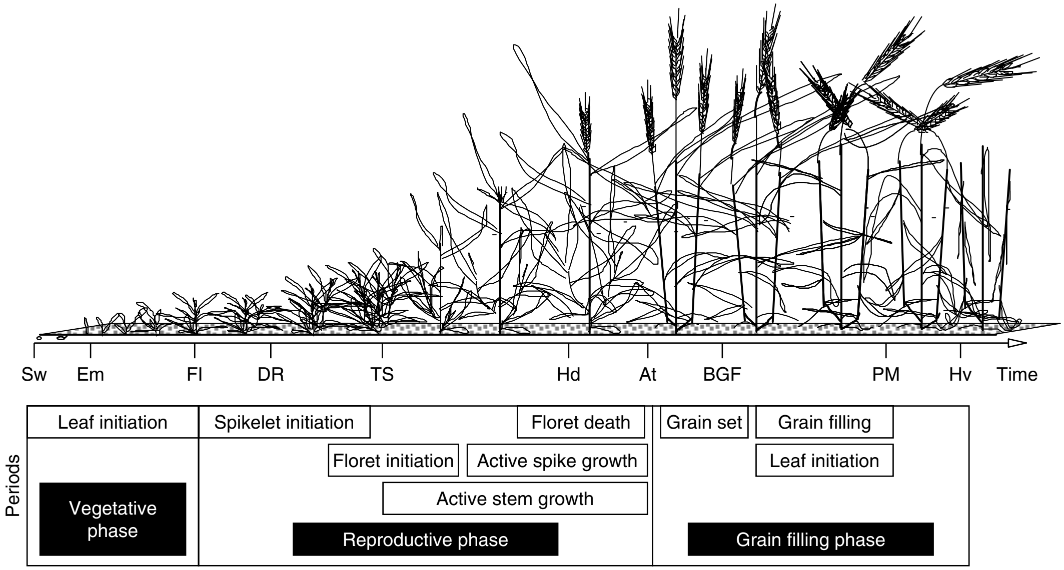


FIGURE 2

Diagram of wheat growth and development showing the stage of sowing (Sw), seedling emergence (Em), floral initiation (FI), initiation of the first double ridge (DR), terminal spikelet initiation (TS), heading (Hd), anthesis (At), beginning of the grain filling period (BGF), physiological maturity (PM) and harvest (Hv). Boxes indicate the periods of differentiation or growth of some organs within the vegetative, reproductive and grain-filling phases. Source: Slafer and Rawson (1994a).

These phases are delimited by sowing-floral initiation, floral initiation-anthesis and anthesis-maturity (Figure 2). Although they do not delimit major developmental phases, the initiation of both the first double ridge and the terminal spikelet are important early reproductive markers. The former is the first (microscopically) visible sign that the plant is reproductive, while the latter marks the end of the spikelet initiation phase, when the final number of spikelets per spike is determined, which under most field conditions coincides with the onset of stem elongation.

A mature wheat seed normally contains four leaf primordia (Kirby and Appleyard, 1987; Hay and Kirby, 1991). After sowing, seed imbibition and initiation of leaf primordia is reassumed; a typical seedling has six differentiated leaves at emergence under non-stressful field conditions. Leaf initiation continues until the onset of floral initiation, when the maximum number of leaves in the main shoot is determined. Measured in thermal time, the rate of leaf initiation (or its reciprocal, the plastochron) is relatively constant between different leaf primordia (Kirby et al., 1987; Delécolle et al., 1989), but genetic variation has been reported (e.g. Evans and Blundell, 1994). The timing of floral initiation is therefore a major driver of the length of the crop cycle to anthesis, as all leaf primordia appear at a certain rate (the reciprocal of phyllochron) before the last internode elongates to produce heading. Phyllochron is approximately constant, although under circumstances of slow development inducing the initiation of a large number of leaf primordia in the main shoot (>10), the phyllochron of later leaves tends to be longer than that of early leaves (Miralles and Slafer, 1999). Although it is frequently assumed that phyllochron is approximately 100°Cd (base temperature 0°C, representing about one leaf per week), it is affected by both genetic and environmental factors (e.g. Halloran, 1977; Rawson et al., 1983; Rawson, 1986; Stapper and Fischer, 1990; Kirby, 1992; Rawson, 1993; Slafer et al., 1994a, 1994b; Slafer and Rawson, 1997).

Cereals develop the capacity to produce a tiller in each phytomer. The process of emergence and growth of tillers, termed tillering, starts when the first tiller bud is mature to grow. The onset of tillering is approximately three phyllochrons after seedling emergence; from then on, the emergence of tillers is closely related to leaf emergence (Masle, 1985; Porter, 1985). Under favourable conditions, the pattern of potential tiller emergence is exponential (Miralles and Slafer, 1999) for a short period. When growth resources become limiting to maintain all tillers, some die in the reverse order of their emergence, thus contributing to the synchrony and convergence of development in a crop (Hay and Kirby, 1991). This process stabilises during the period immediately before anthesis, when the number of spikes per unit land area is defined.

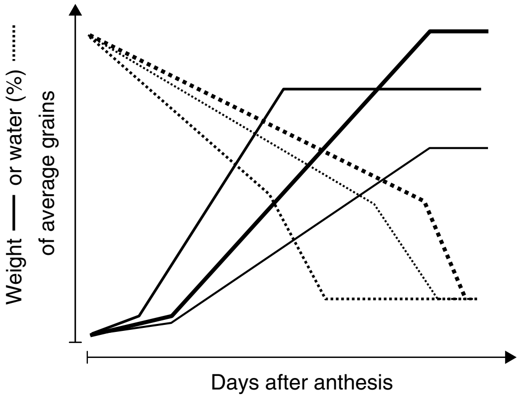
In each shoot after floral initiation, the apex starts initiating spikelet primordia; later on, floral initiation starts in the earliest initiated spikelets. Although the double ridge stage has been used as a morphological indication of floral initiation, the first spikelet primordium is normally initiated before double ridge (e.g. Delécolle et al., 1989; Kirby, 1990), so that floral initiation can only be dated a posteriori by relating total number of primordia with time (or thermal time), considering the final leaf number (Miralles and Slafer, 1999). The phase of spikelet initiation finishes with the initiation of the terminal spikelet in the apical meristem, when the maximum number of spikelets is fixed. Floral initiation, which had been started in the earliest developed spikelets (in the middle third of the spike) before this 'terminal spikelet initiation' stage, continues in all spikelets. Floret development starts in the proximal (to the rachis) positions of each spikelet, and progresses towards the distal positions (e.g. Sibony and Pinthus, 1988). This is why the carpels (at anthesis) and the grains (at maturity) of proximal florets are larger than those in more distal positions (e.g. Rawson and Evans, 1970; Calderini et al., 2001). Floret initiation within each spikelet continues approximately until booting (Kirby, 1988; González et al., 2003b, 2005b), reaching a maximum number of floret primordia per spikelet ranging between 6 and 12 (Sibony and Pinthus, 1988; Youssefian et al., 1992; Miralles et al., 1998), mostly depending on the spikelet position. The development is then arrested in a huge proportion (normally 70–80%) of florets, leading to a large rate of floret mortality coincidently with the onset of rapid growth of stems and spikes shortly before anthesis (Kirby, 1988; González et al., 2003b, 2005b). This suggests that competition for assimilates would determine the rate of floret mortality (González et al., 2005b). Thus, the more the spike can grow at these critical stages, the more florets can reach the stage of fertile florets (and grains afterwards), irrespective of whether this growth is dependent on crop growth or partitioning, or whether it is due to agronomy or genetic improvement. [See Slafer (2003) and Slafer et al. (2005) for an extended discussion and other specific references.] Just before anthesis, pollination and fertilisation occur in fertile florets. Grain set-the proportion of fertile florets producing 'normal' grains-is often less than 100%, more likely due to competition for assimilates (Savin and Slafer, 1991). The period of grain set is characterised by substantial grain development with virtually no grain growth, and is therefore described as the 'lag phase' (Stone and Savin, 1999).

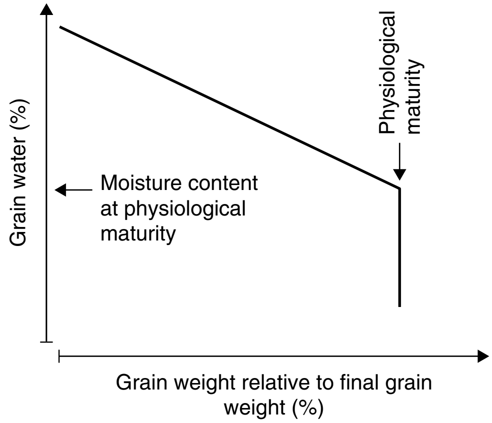
Grain growth and development are normally partitioned into three phases: the above-mentioned lag phase, the effective grain-filling period and the maturation and drying phase (e.g. Bewley and Black, 1985; Savin and Molina-Cano, 2002). Most of the endosperm cells are developed during the lag phase, when grains rapidly accumulate water but almost no dry matter (Evers, 1970; Nicolas et al., 1984). The effective grain-filling period involves rapid accumulation of the dry matter in the form of seed reserves; water content continues to increase rapidly, and eventually establishes the maximum volume of the seed. During the maturation and drying phase, seeds lose water, reach 'physiological maturity' (maximum dry matter accumulation) and enter a quiescent state (Bewley and Black, 1985). Thus, physiological maturity is the phenological stage that indicates the end of the grain growth period. Although the most precise method to determine the timing of physiological maturity is establishing when grain growth ceases (Egli, 1998), this method is laborious and only serves to indicate achievement of physiological maturity several days after the event has actually occurred (because a group of consecutive observations are needed to determine that constant grain weight has been reached; Rondanini et al., 2007). The apparent consistency between the dynamics of water and dry matter in grains of all major crops has led to a reliable, simple method to estimate grain development towards maturity based on the water content of the grains (Box 1).

BOX 1 Quantifying grain development through its moisture content

The most common characterisation of post-flowering development progress towards maturity has been qualitative, dividing the development into loosely defined stages, such as ‘aqueous’, ‘milky’, ‘dough’ and ‘hard’ grain. As this characterisation is based on the water proportion of growing grains, it could be possible to put forward a quantitative developmental scale based on the actual grain water content, reflecting the proportion of the time to maturity already elapsed at any particular time. Realism and universality are required for such a scale to be useful, which in turn depend on (i) a steady change in grain water content during the whole post-flowering period and (ii) patterns of change in moisture that apply to most genotypes of a particular species irrespective of environment and management.

On a common time scale, the dynamics of grain growth and grain water content are loosely related and strongly influenced by genotype and environment (right, upper panel). However, the relationship between grain growth and its water content is much more stable, as there is a positive relationship between the rate of grain growth and the rate of water loss. If grain weight is normalised as a percentage of the final grain weight (right, lower panel), there seems to be a universal sharp negative relationship between grain water content and grain weight. So, disregarding profound differences in final grain weight, in the dynamics of grain growth, all crops within a particular species reached physiological maturity at a similar water content in the grain. Studies in maize (Saini and Westgate, 2000; Borrás et al., 2003; Borrás and Wesgate, 2006), wheat (Schnyder and Baum, 1992; Calderini et al., 2000), sorghum (Gambín and Borrás, 2005), soybean (Swank et al., 1987) and sunflower (Rondanini et al., 2007) have shown that final grain weight is achieved at, or near to, a particular moisture content irrespective of the actual size of the grains (affected by genetic or environmental factors),[1] revealing that dry matter accumulation in developing grains and the concurrent loss of water are closely related phenomena.





Thus, it seems that duration of grain filling is determined by the interaction between reserve depositions and declining cellular water content, where deposition of reserves such as starch or oil replaces water until critical minimum water content is reached. For each crop, (i) water percentage of final grain weights at flowering and at maturity is rather constant for a wide range of grain-growing conditions, and (ii) it decreases linearly from flowering to physiological maturity. Hence, it can be proposed that the progress of grain development towards maturity may be trustworthily based on the water content of the grains. For instance, if for wheat the limits are ca. 80% water content just after anthesis and ca. 40% at physiological maturity (Calderini et al., 2000), it can be directly established what proportion of the grain-filling period has elapsed at any time we measure grain moisture content in the field. This quantitative assessment, which allows determining how much of the grain filling has been already completed, may be instrumental in management decisions such as when to apply a desiccant to the crop to advance harvest without losing yield (Section 3.2.2. in Chapter 3; e.g. Calviño et al., 2002).

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[1] In some extreme conditions, moisture content at maturity may also be affected within a crop, but a constant value for a particular crop seems an agronomically realistic assumption.

2.1.2. Soybean

External development in soybean is described in terms of the number of leaves or nodes on the main stem (V-stages) or the presence or growth of reproductive organs in the upper nodes on the main stem (R-stages) (Figure 3). After seedling emergence (VE), the cotyledons open and the two unifoliate leaves unroll (VC); then trifoliate leaves appear and expand at a rate that depends mainly on temperature (Hesketh et al., 1973; Thomas and Raper, 1976; Sinclair, 1984a), defining the successive V-stages (V1, V2, Vn), with a phyllochron of approximately 50 °C d (base temperature 11 °C, Sinclair et al., 2005). Under many field conditions, approximately one leaf expands every three to four days (Fehr and Caviness, 1977; Bastidas et al., 2008). The opening of the first flower (usually in an axillary raceme on the main stem) defines the flowering stage R1. When flowers open at one of the two uppermost nodes on the main stem, the full bloom stage R2 is defined. Subsequent stages are defined by the presence and size of reproductive organs on one of the four uppermost nodes on the main stem with a fully developed leaf, irrespective of the organs present in other positions of the plant: a pod of 5 mm (R3: beginning pod) or 2 cm (R4: full pod), a seed 3 mm long within the pod (R5: beginning seed) or seeds filling the pod cavity (R6: full seed). Maturity begins when one normal pod on the main stem reaches its mature pod colour (R7), and full maturity (R8) is attained when 95% of the pods have reached their mature pod colour.

The dormant plumule in the soybean seed has two unifoliate leaves, the first trifoliate leaf primordia initiated during seed development in the mother plant (Lersten and Carlson, 2004). After germination, the pre-formed leaves resume their growth and new foliar primordia are differentiated from the shoot apex; shortly afterwards, branches are differentiated from axillary meristems (Borthwick and Parker, 1938; Sun, 1957; Thomas and Kanchanapoom, 1991). Flower initiation is determined by the appearance of a knob-like primordium in the axil of a bract that precedes the differentiation of floral cycles (Guard, 1931; Carlson and Lersten, 2004). From axillary buds, floral primordia are produced in racemes, while the terminal meristems

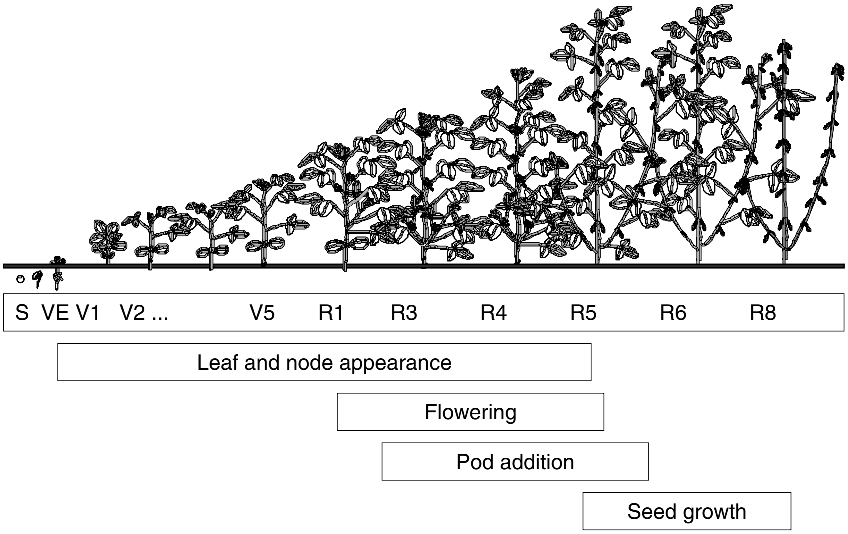


FIGURE 3

Diagram of soybean growth and development showing the stages of sowing (S), seedling emergence (VE), appearance of different leaves (V1-Vn), until the appearance of the first open flower (R1), followed by different reproductive phases in which flowers become pods and seeds start to grow inside pods (R3 to R7) until maturity (R8).

of the main stem continue differentiating foliar primordia (Borthwick and Parker, 1938). In determinate type plants, the terminal apex ceases to differentiate leaf primordia soon after flower initiation and forms a pronounced terminal raceme (Thomas and Kanchanapoom, 1991). In indeterminate type plants, the terminal meristem remains vegetative for a longer time and differentiates new foliar primordia, while floral differentiation progresses from the lower to the upper nodes (Saitoh et al., 1999). Eventually, the terminal meristem of indeterminate plants forms a floral primordium and ceases the differentiation of leaves (Caffaro et al., 1988), but does not develop a terminal raceme like determinate genotypes. After floral initiation, the flower primordia progress into complete flowers. Soybean flowers typically are self-pollinated on the day when the corolla opens (Fehr, 1980). From anthesis to pod set, pistil length and weight increase and fertilised ovules develop into embryos (Peterson et al., 1992; Carlson and Lersten, 2004). After a fairly long lag-phase, the seeds begin to accumulate reserves in the cotyledons while water concentration progressively decreases to 55–60%, when physiological maturity is achieved (Swank et al., 1987; Egli, 1998). There are positive correlations between pistil length during early stages of pod development, ovule size and embryo cell numbers, suggesting that changes in external characteristics of flower or pod are correlated with seed development (Peterson et al., 1992). Moreover, seed growth rate during grain filling is highly correlated with the number of cells differentiated in the cotyledons (Egli et al., 1981, 1989; Munier-Jolain and Ney, 1998).

A large proportion of soybean reproductive structures aborts and abscises. Abortion can occur at several stages of reproductive development, including flowers (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986), immature pods (Hansen and Shibles, 1978; McBlain and Hume, 1981; Egli and Bruening, 2005) or young seeds (Duthion and Pigeaire, 1991; Westgate and Peterson, 1993); when seeds enter the linear phase of growth, the chance of pod abortion decreases (Egli, 1998). Combined flower and pod abscission may range from 32 to 82% (van Schaik and Probst, 1958; Hansen and Shibles, 1978; Wiebold et al., 1981). Reductions in crop photosynthesis increase abortion (Hardman and Brun, 1971; Schou et al., 1978; Egli and Zhen-wen, 1991; Jiang and Egli, 1995); pod age, position and timing of development modify the chances of surviving (Egli, 2005). Abortion and abscission are higher in nodes at the top and the bottom of the canopy than in those in the middle of the canopy (Heindl and Brun, 1984). Within a node, secondary inflorescences (Piegaire et al., 1988) and distal flowers in the raceme (Peterson et al., 1992) are more likely to abort than primary racemes or proximal flowers, while late developing pods have less chance of surviving than early pods (Huff and Dybing, 1980; Brun and Betts, 1984; Heitholt et al., 1986; Egli and Bruening, 2002, 2006b).

There are two characteristics in soybean development that highly contrast with wheat: (i) the period of leaf appearance and node elongation partially overlaps with the phases of flowering and pod-addition, and (ii) reproductive development is highly asynchronous. Both characteristics are related to the difference in growth habit. In determinate soybean, leaf appearance in the main stem ceases soon after R1 (Bernard, 1972). In contrast, indeterminate plants may produce more than two-thirds of main stem nodes after flowering (Heatherly and Smith, 2004); leaf appearance cessation roughly coincides with R5 (Sinclair, 1984b; Bastidas et al., 2008). In intermediate semi-determinate types, stem growth terminates fairly abruptly after a flowering period almost as long as that of indeterminate plants (Bernard, 1972). Besides these differences, overlapping still exists in determinate soybeans at the plant level, as the production of nodes on the branches is maximum between R1 and R5 in both extreme types (Board and Settimi, 1986; Egli et al., 1985). The degree of overlap and the differences between extreme growth habits are also dependent on environmental conditions. Short photoperiods or very adverse growing conditions reduce the number of nodes appearing on the branches after R1 in indeterminate (Bernard, 1972; Caffaro and Nakayama, 1988) and determinate cultivars (Settimi and Board, 1988; Frederick et al., 2001).

Asynchronous development at the plant level includes inter-nodal and intra-nodal variations. Continued node production on the main stem of the indeterminate cultivars highly delays flowering of the upper nodes (Saitoh, et al., 1999), leading to high inter-nodal differences in post-flowering development (Munier-Jolain et al., 1993, 1994; Kantolic, 2006; Egli and Bruening, 2006a). In determinate plants, most main stem nodes and the basal nodes of the branches begin to flower near simultaneously (Bernard, 1972; Gai et al., 1984), but flowering at a node level is longer than in indeterminate plants (Gai et al., 1984). At a whole-plant level, flowering (defined as the time from R1 until the opening of the last flower) and pod-addition (defined as the period when new pods are formed) phases are generally longer in indeterminate than in determinate plants (Egli and Leggett, 1973; Foley et al., 1986; Egli and Bruening, 2006a). Under normal field conditions, asynchronism declines as the plant approaches maturity (Munier-Jolain et al., 1993; Kantolic, 2006). Seeds developing from flowers opening at later growth stages tend to have shorter seed-fill durations (Egli et al., 1987), and reach maturity only a few days after the first pods lose their green colour (Spaeth and Sinclair, 1984).

3. DEVELOPMENTAL RESPONSES TO ENVIRONMENTAL FACTORS

The processes regulating crop development are complex due to interactions between genetic and environmental factors. Water deficit delays phenological development in some species such as sorghum (*Sorghum bicolor*) and quinoa (*Chenopodium quinoa*) (Donatelli et al., 1992; Geerts et al., 2008). Availability of resources, that is water, nutrients, radiation and CO_2, may affect the rate of development (Rawson, 1992, 1993; Evans, 1987; Rodriguez et al., 1994), but these factors have only small effects on development of wheat and soybean (Slafer, 1995). In this section, the analysis of environmental control of development will therefore be restricted to the main environmental drivers of crop development: temperature (both temperature per se and vernalisation) and photoperiod.

3.1. Temperature per se

Of the three major environmental factors, temperature per se is the only one that has a universal impact on the rates of development (Aitken, 1974). This means that all crops and all phases of development are sensitive to temperature (Miralles and Slafer, 1999). In general, the higher the temperature, the faster is the rate of development and consequently the shorter is the time to complete a particular developmental phase (Slafer and Rawson, 1994a). In all species, developmental responses to temperature start as soon as the seed imbibes (Roberts, 1988), and continue until maturity (Hesketh et al., 1973; Angus et al., 1981; Del Pozzo et al., 1987; Porter et al., 1987; Jones et al., 1991; Slafer and Savin, 1991; Cober et al., 2001; Setiyono et al., 2007). From the various models that have been proposed to predict the timing of development as affected by temperature, the most widely accepted is the thermal time (with units of degree days, °Cd; Monteith, 1984). The thermal time model is the calendar time weighted by the thermal conditions; it assumes that the rate of development increases linearly with temperature between the cardinal thresholds of base and optimum temperatures. At temperatures higher than the optimum, there may or may not be a plateau followed by a sharp decrease in rate of development until it becomes zero at the theoretical maximum temperature at which development ceases. Although the general model is universal, the actual cardinal temperatures are generally higher for crops of tropical origin (e.g. soybean, rice, maize, sorghum) than for their temperate counterparts (e.g. wheat, barley, canola). Intra-specific, stage-dependent variation in cardinal temperatures has also been reported (e.g. Angus et al., 1981; Del Pozzo et al., 1987; Porter et al., 1987; Slafer and Savin, 1991; Rawson and Richards, 1993; Slafer and Rawson, 1994b, 1995a; Boote et al., 1998; Cober et al., 2001; Grimm et al., 1993; Setiyono et al., 2007). During the growing cycle, cardinal temperatures increase for wheat (e.g. Slafer and Savin, 1991) but decrease for soybean (Grimm et al., 1994, Setiyono et al., 2007). This reflects the adaptation of wheat to increasing temperatures during its reproductive development, while the opposite occurs in soybeans. Consistent with this proposition, cardinal temperatures decrease with ontogeny in sunflower (Goyne and Hammer, 1982).

3.2. Photoperiod

In comparison to temperature, photoperiod responses are more complex. The degree of variation within species and across stages of development also includes complete insensitivity. Although photoperiodic stimulus is perceived by leaves and transmitted to the apex since the emergence of the crop, many species exhibit a juvenile phase of insensitivity to photoperiod immediately after seedling emergence that imposes a lower limit for the length of the vegetative phase and thus for the final number of leaves. A juvenile phase has been demonstrated for at least some cultivars of soybean (Collinson et al., 1993), maize (Kiniry et al., 1983), barley (Roberts et al., 1988) and sunflower (Villalobos et al., 1996). Other crops such as wheat do not appear to possess a juvenile phase before it becomes sensitive to photoperiod (Hay and Kirby, 1991; Slafer and Rawson, 1995c). These plants perceive the photoperiod stimulus immediately after seedling emergence, and therefore the minimum number of leaves may coincide with the number of leaf primordia initiated by seedling emergence. For example, if photoperiod is sufficiently long after emergence, spring wheat may only have six leaves in the main shoot from seedling emergence to anthesis, which include the four leaves already present in the embryo plus a couple of leaves initiated from sowing to seedling emergence, when the photoperiod can be perceived (Section 2.1.1). Most soybean cultivars have a juvenile phase of variable duration, from 8 to 33 days under optimum temperature (Shanmugasundaram and Tsou, 1978; Board and Settimi, 1988; Ellis et al., 1992; Collinson et al., 1993) but some genotypes have no juvenile phase (Wilkerson et al., 1989; Wang et al., 1998).

Sensitivity to photoperiod is generally quantitative rather than qualitative; that is development is delayed rather than prevented when photoperiod is not optimum (Major et al., 1980; Summerfield et al., 1993; Slafer and Rawson, 1994a). Most plants are classified by their quantitative photoperiodic response according to the changes in the rate of development and thereby in the length of the phases in response to photoperiod. The two most common categories are ‘short-day’ and ‘long-day’ plants. Short-day plants reduce their rates of development (and extend the duration of phases which are sensitive) when photoperiod is lengthened, while long-day plants reduce the duration of their phases when photoperiod is lengthened. Crop species of temperate origin (e.g. wheat, barley, oats, canola, linseed, peas) are long-day plants, while crops of tropical origin (e.g. maize, sorghum, rice, soybean) are short-day plants. Within a particular crop species, genotypes could be classified as follows:

(i) Photoperiod insensitive or neutral, if they do not respond to photoperiod in any of its developmental phases; therefore, thermal time to flowering is fairly constant across locations or sowing dates (if insensitive to vernalisation), or

(ii) Photoperiod sensitive, if duration of at least some of its developmental phases increases (short-day species) or decreases (long-day species) in line with photoperiod. Within the sensitive genotypes, there is normally a huge range of genotypic variation.

The optimum photoperiod maximises the rate of development, and consequently minimises the duration of the sensitive phases; photoperiod sensitivity is the delay in duration of a certain stage of development per hour difference between actual and optimum photoperiod. Both optimum photoperiod and photoperiod sensitivity vary among genotypes (e.g. Major, 1980; Davidson et al., 1985; Worland et al., 1994; Slafer and Rawson, 1996; Summerfield et al., 1998; Kantolic and Slafer, 2005). In soybean, cultivars from low-maturity groups present a lower sensitivity and a higher photoperiod threshold than genotypes of high-maturity groups.

Photoperiod sensitivity could be different throughout the crop ontogeny. For instance, while wheat reduces the length of different phases from seedling emergence to flowering as photoperiod is increased, without any sensitivity described for the duration of grain filling, soybean shows photoperiod sensitivity during the whole crop cycle, including grain filling. The variation in sensitivity during different phases has been in fact proposed as a breeding goal to increase the duration of critical phases for yield determination at the expense of the duration of earlier phases (Section 5). Highly sensitive cultivars during early phases (e.g. before double ridges in wheat and before R1 in soybean) are usually highly sensitive during later phases (stem elongation in wheat and post-flowering phases in soybean), but the association is not strict (Kantolic and Slafer, 2001); combinations of different sensitivities at different phases might be possible (Slafer et al., 2001).

Both in wheat and in soybean, less-stimulating photoperiods, that is short in wheat and long in soybean, delay both floral initiation and flowering and increase the number of vegetative primordia generated in the apex (Borthwick and Parker, 1938; Rawson, 1971, 1993; Wall and Cartwright, 1974; Halloran, 1977; Thomas and Raper, 1977; Major, 1980; Hadley et al., 1984; Pinthus and Nerson, 1984; Raper and Kramer, 1987; Roberts and Summerfield, 1987; Caffaro and Nakayama, 1988; Sinclair et al., 1991; Evans and Blundell, 1994; Slafer and Rawson, 1994ab, 1995d, 1996; Upadhyay et al., 1994ab; Fleming et al., 1997; Kantolic and Slafer, 2001, 2005; Zhang et al., 2001; González et al., 2002; Miralles et al., 2001, 2003). In line with the extended periods, non-stimulating photoperiods modify the number of tillers the number of leaves per tiller in wheat and the number of branches and the number of nodes in the branches in soybean (Thomas and Raper, 1983; Board and Settimi, 1986; Settimi and Board, 1988; Caffaro and Nakayama, 1988; Miralles and Richards, 2000; Kantolic and Slafer, 2001, 2005, 2007).

In soybean, photoperiod also affects developmental rates after flowering: the duration of the flowering, pod-addition phases and the time from R1 to full maturity are increased by direct exposure to long photoperiod (e.g. Johnson et al., 1960; Major et al., 1975; Thomas and Raper, 1976; Lawn and Byth, 1973; Raper and Thomas, 1978; Guiamet and Nakayama, 1984a; Summerfield et al., 1998; Morandi et al., 1988; Kantolic and Slafer, 2001; Han et al., 2006; Kantolic and Slafer, 2007; Kumudini et al., 2007). During seed filling, long photoperiods increase the duration of the lag phase (Zheng et al., 2003; Kantolic, 2006) and delay leaf senescence (Han et al., 2006). It has been proposed that the synchronisation in seed maturation, which contrasts with the low degree of synchronism that prevails during the early stages of flowering and pod set, is attributable to photoperiod responses: late developing seeds are generally exposed to short photoperiods that increase their development rate (Gbikpi and Crookston, 1981; Raper and Kramer, 1987). In fact, asynchronous maturity has been described in soybeans exposed to long days under controlled environments (Guiamet and Nakayama, 1984b) and under field conditions (Mayers et al., 1991). In field experiments that included photoperiod manipulations, asynchronism was found to be quantitatively affected by photoperiod, and the response could be partially reverted by exposure to short photoperiod (Kantolic, 2006).

As photoperiod modulates flowering time and potential plant size, pre-flowering responses to photoperiod have a strong impact on adaptation and potential yield (Roberts et al., 1993). In fact, the classification of soybean cultivars in maturity groups defining broad-sense adaptation is based on pre-flowering developmental response to photoperiod (Summerfield and Roberts, 1985; Boote et al., 1998; Heatherly and Elmore, 2004).

3.3. Vernalisation

Vernalisation is the acceleration of development by exposing sensitive cultivars to cool temperatures during the early stages of crop ontogeny. The plant apex may sense vernalising temperatures from seed imbibition, throughout the vegetative phase. Vernalisation requirements are typical of crops with a temperate origin, for example wheat, other small-grained cereals, canola and peas. In many of these crops, there are 'winter' and 'spring' cultivars. It is frequently assumed that vernalisation requirements are characteristic of winter genotypes within a particular species. The difference between spring and winter types may be restricted, however, to the magnitude of vernalisation responsiveness (e.g. Levy and Peterson, 1972; Slafer and Rawson, 1994a).

Vernalisation may be reversed if the period of low temperature is interrupted, an effect known as 'devernalisation'. This was experimentally proven in wheat by Gregory and Purvis (1948) and Purvis and Gregory (1952); Dubert et al. (1992) showed that devernalisation may occur at temperatures between 20 and 30°C.

Excluding the effects of temperature per se by the calculation of the length of the phases in degree days, photoperiod and vernalisation are generally considered to account for most of the differences in development rate among cultivars; any 'residual' difference after the vernalisation and photoperiod requirements were satisfied would be the consequence of differences in 'basic development rate' or 'intrinsic earliness' (Major, 1980; Flood and Halloran, 1984; Masle et al., 1989, Slafer, 1996), which are discussed in Section 4.1.3.

4. GENETIC CONTROL OF DEVELOPMENTAL RATES

4.1. Genes affecting development in wheat and related species

The life cycle in wheat is determined by genes that regulate (i) photoperiod response (*Ppd*), (ii) vernalisation response (*Vrn*) and (iii) genotypic differences in developmental rates independent of these two environmental factors, called either intrinsic earliness, earliness per se or developmental rate genes (*Eps*). The latter are also affected by temperature depending on the gene and allele considered (Slafer and Rawson, 1995b; Appendino and Slafer, 2003). Most of the variation in developmental rates is explained by vernalisation and photoperiod response genes, with smaller, more subtle effects of *Eps* alleles.

Wheat is an allohexaploid with three genomes, A, B and D (Table 1); the simultaneous presence of more than one locus implicated in a particular trait (homeologous loci) generates a more complex inheritance pattern than in diploid related species. This polyploid genome determined an early interest in chromosome research in wheat, namely aneuploidy materials, genetic variability in vernalisation and photoperiod responses (Worland et al., 1987; Law et al., 1991). Interest in earliness per se is more recent, owing to smaller effects and more complex interactions requiring new molecular approaches to understand *Eps* alleles (Table 1).

Table 1 *Ppd*, *Vrn* and *Eps* Loci of *Triticum aestivum* (*T.a*; Allohexaploid: A, B and D genome), *Triticum monococcum* (*T.m*; Diploid: A$^{\mathrm{m}}$ genome) and *Hordeum vulgare* (*H.v*; Diploid: H genome)

	Genomes				
Chromosome		***T.a*** **2*n* = 6*x***		***T.m*** **2*n* = 2*x***	***H.v*** **2*n* = 2*x***
	A	**B**	**C**	**A$^{\mathrm{m}}$**	**H**
1					*Ppd-H2*
				Eps-A^{m}*1*	
2	Ppd-A1	*Ppd-B1*	*Ppd-D1*		*Ppd-H1*
		Eps2-B			*Eps2-HL*
					Eps2-HS
3	*Eps-AL*				*Eps3-HS*
4					*Eps4-HS*
					Vrn-H2
5	*Eps5*	*Eps5-BL*$_{1\text{–}2}$			*Eps5-HL*
	Vrn-A1	*Vrn-B1*	*Vrn-D1*	*Vrn-A*^{m}*1*	*Vrn-H1*
				Vrn-A^{m}*2*	
6					*Eps6-HL1*
					Eps6-HL2
7					*Eps7-HS*
					Eps7-HL
		Vrn-B3			*Vrn-H3*

All main genes were genetically mapped either as QTL or as major genes, except Ppd-A1*. Genes are grouped by character. The gene order in the table does not indicate the gene order in the respective chromosome. For gene nomenclature see text in Sections 4.1.1–4.1.3.*

4.1.1. Vernalisation response genes

Vernalisation requirement is the need of fulfilment of a low-temperature period in sensitive genotypes in order to avoid delays in development to reach floral initiation. This requirement prevents the exposure of developing flower organs to frost damage in sensitive cultivars. Most studies about the genetic systems controlling these requirements have been concentrated on the major genes *Vrn1* of *Triticum aestivum*. These are located on homeologous chromosomes 5A (*Vrn-A1*, formerly *Vrn1*), 5B (*Vrn-B1*, formerly *Vrn2*) and 5D (*Vrn-D1*, formerly *Vrn3*) (Flood and Halloran, 1986; Snape et al., 2001); they map to equivalent position than *Vrn-H1* in *Hordeum vulgare* and *Vrn-A*^{m}*1* in diplod wheat *Triticum monococcum* (Laurie, 1997; Dubcovsky et al., 1998). Additional loci in other chromosome groups like *Vrn2* (Yan et al., 2004b) and *Vrn3* (Yan et al., 2006) are also involved in the gene pathway of vernalisation requirement (Table 1).

The presence of dominance in one or more *Vrn-A1* loci eliminates partially or completely the vernalisation requirement, giving rise to spring genotypes, while winter wheat normally carries recessive alleles. These loci have been considered to have the greatest effect in the elimination of the vernalisation requirement (Law et al., 1976; Snape et al, 1976), with some alleles like *Vrn-A1a* conferring insensitivity to vernalisation (Appendino and Slafer, 2003; Yan et al., 2004a). Variability in these loci is spread in commercial germplasm but the allelic frequencies may vary depending on the region of cultivation in the world (Stelmak, 1990; Yan et al., 2004a).

A gene primary detected in *T. monococcum* (chromosome 5A) is *Vrn-A*^{m}*2*, which is also present in *H. vulgare* (*Vrn-H2*). This gene is, in contrast to *Vrn1*, a dominant repressor of flowering and is down-regulated by both vernalisation and short day (Yan et al., 2004a; Dubcovsky et al., 2006). This genetic factor also regulates flowering by vernalisation in polyploid winter wheat. There is no evidence of variability in hexaploid wheat but its presence has been demonstrated through RNAi transgenic wheat in winter cultivar Jagger (Yan et al., 2004a). Both in barley and diploid wheat, the determination of the vernalisation requirement involves an epistatic interaction between *Vrn1* and *Vrn2* (Tranquilli and Dubcovsky, 2000).

Vrn3 is a locus involved in the pathway of vernalisation requirement, up-regulated by long days. It is located on chromosome 7B (*Vrn-B3*, formerly *Vrn5*), is orthologous to the barley gene *Vrn-H3* located on chromosome 7H, and shows a dominant spring inheritance. The mutation that generates spring genotypes in wheat is not widely spread in commercial germplasm representing a potentially valuable source of genetic diversity (Yan et al., 2006).

4.1.2. Photoperiod response genes

In bread wheat, photoperiod sensitivity is mainly determined by a group of genes located on chromosome group 2 (Table 1), namely *Ppd-D1*, formerly *Ppd1* (chromosome 2D); *Ppd-B1*, formerly *Ppd2* (chromosome 2B); and *Ppd-A1*, formerly *Ppd3* (chromosome 2A). Photoperiod insensitivity is of dominant effect, and *Ppd-D1* is the main source of photoperiod insensitivity conferred by the *Ppd-D1a* allele (Worland and Law, 1985; Worland, 1999). *Ppd-B1* is also an important source of photoperiod insensitivity (Scarth and Law, 1984). Although chromosome 2A shows influence on photoperiod sensitivity (Law et al., 1978; Scarth and Law, 1984), to the best of our knowledge *Ppd-A1* has not been genetically mapped. Chromosomes of other groups (1, 3, 4 and 6) may also be involved in the determination of photoperiod response, either via modifiers or via major genes (Law, 1987). The adaptive roles of *Ppd-D1* and *Ppd-B1* loci were well evidenced by Law (1987) using substitution lines with contrasting genotypes in photoperiod response genes.

Two major loci regulating the photoperiod response in barley are *Ppd-H1* and *Ppd-H2* located on chromosomes 2H and 1H, respectively (Table 1; Laurie et al., 1995). *Ppd-H1* has been cloned (Turner et al., 2005), and the region of chromosome 2H that contains *Ppd-H1* is collinear with the region of chromosome 2D of wheat where *Ppd-D1* has been mapped (Laurie, 1997; Borner et al., 1998). However, these genes in barley and wheat have important differences in the photoperiod response. In the presence of *Ppd-D1a* (a semidominant allele), wheat plants flower rapidly on either short or long days, but the recessive genotype delays flowering on short days. In barley, the recessive *ppd-H1* delays flowering on long days, but has no effect on short days (Laurie et al., 1995; Turner et al., 2005). According to Beales et al. (2007), these wheat and barley *Ppd* genes have contrasting types of mutations, which cause, in wheat, the induction of a flowering locus, homologous to FT in *Arabidopsis* (Yan et al., 2006), irrespective of day length, and in barley, the failure to induce this gene correctly on long days.

Although sowing to heading or anthesis is often considered as a single phase, it is clear that sensitivity to photoperiod changes with developmental phases (e.g. Slafer and Rawson, 1996; Miralles et al., 2000; González et al., 2002). Understanding and manipulating the differential sensitivity to photoperiod at different stages might be useful in increasing yield potential (Section 5). However, most attempts to identify genes of photoperiod sensitivity in particular phases using near-isogenic or recombinant inbred lines for *Ppd* alleles have failed (Scarth et al., 1985; Whitechurch and Slafer, 2001, 2002; Foulkes et al., 2004; González et al., 2005c). This is likely because we only know (and have worked with) few of the hypothesised genes for photoperiod sensitivity (Table 1; Snape et al., 2001). There are other approaches to determine what genes are down- or up-regulated in response to photoperiod (Ghiglione et al., 2008) or to identify genes or QTLs for differences in length of different phases within mapping populations (Borrás et al., University of Lleida, unpublished results).

4.1.3. Earliness per se genes

Time to heading can differ among cultivars by several weeks depending on the interaction between photoperiod, vernalisation requirements and the ambient temperature. Where the vernalisation and photoperiod requirements have been adequately satisfied, significant differences in time to heading may still persist. The genetic factors underlying these differences have received different names: narrow sense earliness, earliness per se, intrinsic earliness or basic development rate genes (e.g. Slafer, 1996, and references quoted therein).

In polyploid species such as *T. aestivum* or diploid species such as *H. vulgare* or *T. monococcum*, this character exhibits a complex genetic base. Earliness per se genetic effects have been identified mainly on *T. aestivum* chromosomes of groups 2, 3 and 5 (Table 1); a few of them have been mapped as QTLs (Scarth and Law, 1984; Miura and Worland, 1994; Worland, 1996; Kato et al., 2002; Toth et al., 2003).

In *T. monococcum*, a QTL for earliness per se is located on the distal region of chromosome $1A^{m}L$ (*Eps-*A^{m}*1*) (Bullrich et al., 2002). Allelic variation at this locus resulted in differences in flowering time in controlled environment, with fully vernalised plants grown under long day. Also smaller differences under natural conditions, in interaction with photoperiod and vernalisation requirements were evidenced. *Eps-*A^{m}*1* was then mapped within a 0.8 cM interval using a high-density mapping population and markers generated from the rice collinear region (Valarik et al., 2006). In *H. vulgare*, Laurie et al. (1995) mapped several QTLs for *Eps* (Table 1), giving evidence of a wide dispersion of candidate genetic factors underlying this character in barley. Future studies will help in the identification of these potential *Eps* genes that, according to Snape et al. (2001), would also be expected to be present in wheat.

4.2. Genes affecting development in soybean

4.2.1. Photoperiod response genes

Genetic control of flowering has been widely used to improve crop adaptation in classical soybean breeding programmes (Curtis et al., 2000). The control of time of flowering involves at least seven major loci, each with two alleles: *E1/e1*, *E2/e2* (Bernard, 1971), *E3/e3* (Buzzell, 1971), *E4/e4* (Buzzell and Voldeng, 1980), *E5/e5* (McBlain and Bernard, 1987), *E6/e6* (Bonato and Vello, 1999) and *E7/e7*, closely linked to *E1/e1* (Cober and Voldeng, 2001). In most cases, the dominant or partially dominant allele lengthens time to flowering in response to photoperiod (Saindon et al., 1989; McBlain et al., 1987; Cober et al., 1996); an exception to this is *E6*, in which early flowering is dominant (Bonato and Vello, 1999). Apparently, the genes of the series E (also known as maturity genes) have no effects on the response of development to temperature (Upadhyay et al., 1994a).

Sensitivity of genotypes to photoperiod depends on the allelic composition of E-genes. Photoperiod sensitivity tends to increase with the number of dominant alleles (Summerfield et al., 1998; Cober et al., 2001; Stewart et al., 2003; Kumudini et al., 2007). The number and type of dominant alleles also seem to modify the photoperiod threshold for response (Messina et al., 2006). Lines with the dominant allele *E1* tended to have a longer juvenile period (Upadhyay et al., 1994b); modelling also supports the role of *E1* in extending the juvenile phase (Messina et al., 2006). Besides their direct effect on photoperiod response, some combination of alleles seem to have additional advantages in crop adaptation; for instance, the allelic combination of *E1e3e4* is preferable to *e1E3E4* to enhance yield under chilling conditions (Takahashi et al., 2005).

Several QTLs associated with flowering time and maturity have been mapped in soybean (Tasma et al., 2001; Keim et al., 1990; Mansur et al., 1996; Lee et al., 1996; Abe et al., 2003; Matsumura et al., 2008); molecular markers are available for marker-assisted breeding for photoperiod sensitivity. Although some association has been found between some loci E and those controlling flowering time in *Arabidopsis thaliana* (Tasma and Shoemaker, 2003), the molecular basis of photoperiodic response in soybean has not been elucidated.

Near-isogenic lines have been developed for the genes of the E-series by back-crosses with different commercial lines (Bernard, 1971; Saindon et al., 1989; Voldeng and Saindon, 1991; Voldeng et al., 1996). The response of the genes alone and in different combinations has been studied. Although the genes that control pre- and post-flowering development are apparently the same, their individual effects may differ depending on the developmental phase. For instance, the allele *E1* alone has a considerable effect on delaying flowering under long days, but has virtually no effects on delaying maturity. In contrast, the effects of *E2*, *E3*, *E4*, *E5* and *E7* on delaying flowering are less marked than those of E1 but they are effective in delaying maturity under long photoperiods (Bernard, 1971; McBlain and Bernard, 1987; Saindon et al., 1989; Upadhyay et al., 1994a., Summerfield et al., 1998; Cober et al., 1996; Cober and Voldeng, 2001). The effects of the genes are not purely additive; interactions between them differ depending on developmental stage (Bernard, 1971; Buzzell and Bernard, 1975; Buzzell and Voldeng, 1980; Upadhyay et al., 1994a).

4.2.2. Long-juvenile genes

There are some soybean genotypes that delay flowering under short days (Hartwig and Kiihl, 1979). This trait was first identified in a plant introduction designated as P1 159925, and has been subsequently referred to as 'long-juvenile' (Parvez and Gardner, 1987; Hinson, 1989; Wilkerson et al., 1989), although there is no evidence that the trait alters the length of the juvenile period. The long-juvenile trait retards the overall development of the plants towards flowering, so that under short days the duration of the emergence to flowering period is longer in long-juvenile compared with normal genotypes (Sinclair et al., 1991, 2005; Sinclair and Hinson, 1992; Cairo and Morandi, 2006). This trait is useful in tropical and sub-tropical areas, as flowering can be delayed in spite of the prevailing conditions of high temperature and short photoperiod.

Examining the segregation pattern of this trait in six F2 populations, from crosses between conventional lines and P1 159925, Ray et al. (1995) concluded that the trait is controlled by a single recessive gene (J/j): the conventional phenotype (JJ) has normal photoperiodic response, while the long-juvenile phenotype (jj) delays flowering under short days. Studying the inheritance of the long-juvenile trait under short days for BR80-677 and MG/BR 22 soybeans, Carpentieri-Pipolo et al. (2000, 2002) proposed that the long-juvenile trait may be controlled by three recessive genes; a genotype with single pair of recessive alleles did not show the long-juvenile characteristic. The recessive genetic combination in three loci causes a longer pre-flowering period than recombination in two loci.

Differences between normal and long-juvenile lines are small under long days (Cregan and Hartwig, 1984; Parvez and Gardner, 1987; Sinclair and Hinson, 1992; Cairo and Morandi, 2006). The genetic background has important effects on the quantitative expression of the trait (Sinclair and Hinson, 1992; Ray et al., 1995; Sinclair et al., 2005). To avoid environmental and genetic effects in the expression of the character, Cairo et al. (2002) have generated molecular markers linked to the juvenile locus in two genetic backgrounds of soybean that can be used for an early discrimination of long-juvenile plants in a segregating population.

4.2.3. Growth habit genes

The growth habit or stem termination in soybean is affected by two loci (*Dt1*, *Dt2*) (Bernard, 1972). Determinate growth habit is conditioned by the recessive allele (*dt1dt1*); the dominant gene pair *Dt1Dt1* produces the indeterminate phenotype. A second gene (dominant *Dt2*), independent of the *Dt1* locus, produces a semi-determinate phenotype in the presence of *Dt1*; *dt1* is epistatic to *Dt2-dt2*. However, Bernard (1972) observed that in some genetic backgrounds, *Dt2* and *dt1dt1* can be indistinguishable, and that *Dt1Dt1* may be modified by other genetic factors. A third allele (*dt1-t*) was reported at the *dt1* locus by Thompson et al. (1997); plants with this allele present a tall determinate phenotype. Although *dt1-tdt1-t* and *Dt2Dt2* phenotypes are similar in plant height, *dt1-tdt1-t* is more similar to *dt1dt1* when considering leaf and stem traits at the top of the plant.

5. CAN WE IMPROVE CROP ADAPTATION AND YIELD POTENTIAL THROUGH FINE-TUNING DEVELOPMENTAL RATES?

Although yield components are being formed all the time from sowing to maturity (e.g. Slafer et al., 1996; Slafer, 2003), there are particular phases that are more relevant for yield. This means that there is scope for improving yield through manipulation of phenology. The prerequisites for this to be effective is that we must (i) recognise the phases which are actually critical, (ii) be able to manipulate development to avoid stressful conditions (adaptation) or take advantage of resource availability (yield potential) in these critical phases and (iii) evaluate trade-offs between yield components when the developmental phases are modified. As yield seems in general more limited by the number of grains than by their average size, likely due to both evolutionary and breeding causes (Sadras, 2007), the timing of occurrence of flowering defines the broad adaptation of a given genotype; the critical phase for grain number determination (only slightly varying among crops) is crucial for yield potential. Thus, crop ontogeny should be tailored to the target environments to avoid unfavourable conditions during the most critical stages (Lawn and Imrie, 1994).

In wheat and soybean, the number of grains per unit area is the yield component most correlated with yield (Slafer and Andrade, 1993; Magrin et al., 1993; Egli, 1998). Number of grains per unit area is largely determined by the events occurring in a few weeks prior to anthesis in wheat, while in soybean, the critical phase for seed number goes from soon after flowering to early seed filling. Those periods within each species are known as 'critical period' for yield determination (see Figure 4 in Chapter 3). With good supply of nutrients and water, the number of grains per unit area is largely determined by the amount of solar radiation and mean temperature. The latter environmental factors influence plant growth and crop development, respectively; thus, their combined effects can be described by combining both variables in a photothermal quotient (Nix, 1976). Fischer (1984) demonstrated a strong correlation between the number of grains per unit area and the photothermal quotient during the critical period of wheat. In soybean, capture of solar radiation during the pod-setting stage is closely associated with the number of grains per unit area (Kantolic and Slafer, 2001; Calviño et al., 2003).

5.1. Crop development and adaptation

An important objective of crop adaptation is to match crop development phases or stages with optimum environmental conditions; among others, the timing of flowering is critical. If flowering is too early, plant growth may be insufficient to produce a minimum amount of biomass compatible with reasonable yields (Mayers et al., 1991). This is why early vigour of the crop is much more important for 'short-season' crops (e.g. those grown at high latitudes) than for 'full season' crops. Chapter 4 discusses in detail the challenges of growing temperate crops in northern Europe, including the role of phenology as the key adaptive trait in these extreme environments. On the contrary, if flowering is too late, the period available for grain growth may be too short, stressful, or both (Lawn et al., 1995). Section 3 in Chapter 5 discusses how threatening could be late sowing dates, and consequently high temperatures during grain filling, in cropping systems of Asia. Therefore, the above-mentioned extremes (early and late flowering) define the length of the growing season, and the pre-flowering development may be manipulated to improve adaptation by balancing the optimum time of flowering and the consequent duration of pre- and post-flowering phases.

Phenological adaptation is particularly critical in stressful environments. When water or nutrients are scarce, vegetative growth may become limiting, increasing the length of the pre-flowering phase, which may increase the size of both canopy and root system. Cultivars with longer vegetative period may have deeper root systems and better capacity of extracting water from deeper soil layers than early flowering ones (e.g. Giménez and Fereres, 1986; Dardanelli et al., 2004), which may be useful provided the soil holds water deep in the profile. In contrast, long-cycle cultivars may deplete more water before the critical periods (Edwards and Purcell, 2005), generating themselves a stronger stress when crop yield is most sensitive; under these circumstances early-flowering cultivars may produce larger yields when moisture stress develops late in the season (Kane and Grabau, 1992, Figure 1).

Crop development may also improve cultivar adaptation by reducing the risk of biotic stresses. Early-maturing wheat had been useful for escaping rust damage in Australia (Section 5.1.2 in Chapter 17), while management techniques based primarily on early-maturing cultivars of soybean effectively reduced the impact of stem rot (*Sclerotinia sclerotiorum*) in Argentina (Ploper, 2004).

In soybean, the stem-termination habit, which modifies the length of the phase of node production independently of the duration of pre-flowering stages, is not directly associated with potential yield, but confers some characteristics that may modify cultivar adaptation. Determinate growth habit is useful in reducing plant height and lodging but can result in excessive dwarfing in early-maturing soybean (Cober and Tanner, 1995). Indeterminate cultivars tend to yield better than determinate ones in yield-restricted environments and late plantings (Kilgore-Norquest and Sneller, 2002; Beaver and Johnson, 1981; Robinson and Wilcox, 1998). However, the relative value of stem termination types in conferring adaptability to different environments may also depend on genetic background (Heatherly and Elmore, 2004).

5.2. Crop development and yield potential

A large body of evidence indicates that reduction in canopy photosynthesis before the onset of stem elongation in wheat or before R1 in soybean seldom reduces the final number of seeds, while crop growth reduction during stem elongation in wheat or from R2 to R5 in soybean is directly related with the number of pods or seeds produced (Fischer, 1985; Savin and Slafer, 1991; Board and Tan, 1995; Egli and Zhen-wen, 1991; Jiang and Egli, 1993, 1995; Board et al., 1995; Abbate et al., 1997; Demotes-Mainard and Jeuffroy, 2004; González et al., 2005a; Miralles and Slafer, 2007). In wheat, where grain filling is mostly sink limited (Slafer and Savin, 1994; Borrás et al., 2004), reduction in grain number cannot be compensated by an increase of grain weight, except for small compensations that might occur if the decrease in grain number brings about increases in carpel size and concomitantly greater grain weight potential (Calderini and Reynolds, 2000; Calderini et al., 2001; Ugarte et al., 2007). In soybeans, where seed filling is usually more limited by source (Egli, 1999, 2004; Borrás et al., 2004; Egli and Bruening, 2006b), reductions in seed production by stresses during R1-R3 may be partially compensated by favourable conditions during seed filling.

Within this context, from the developmental point of view, it has been proposed that the length of the critical phase might be extended at the expense of the duration of earlier phases as a means of increasing yield potential both in wheat (Slafer et al., 2001, 2005; Miralles and Slafer, 2007) and in soybeans (Kantolic et al., 2007). Briefly, the length of the critical phase in both crops is (i) highly relevant in the determination of seed number per unit land area (Figure 4a) and (ii) sensitive to photoperiod (Figure 4b). In experiments where crops were exposed to different day lengths, the number of grains per square metre increased with increasing duration of the critical phase (Figure 4c). In soybean, the increase in seed number in response to long

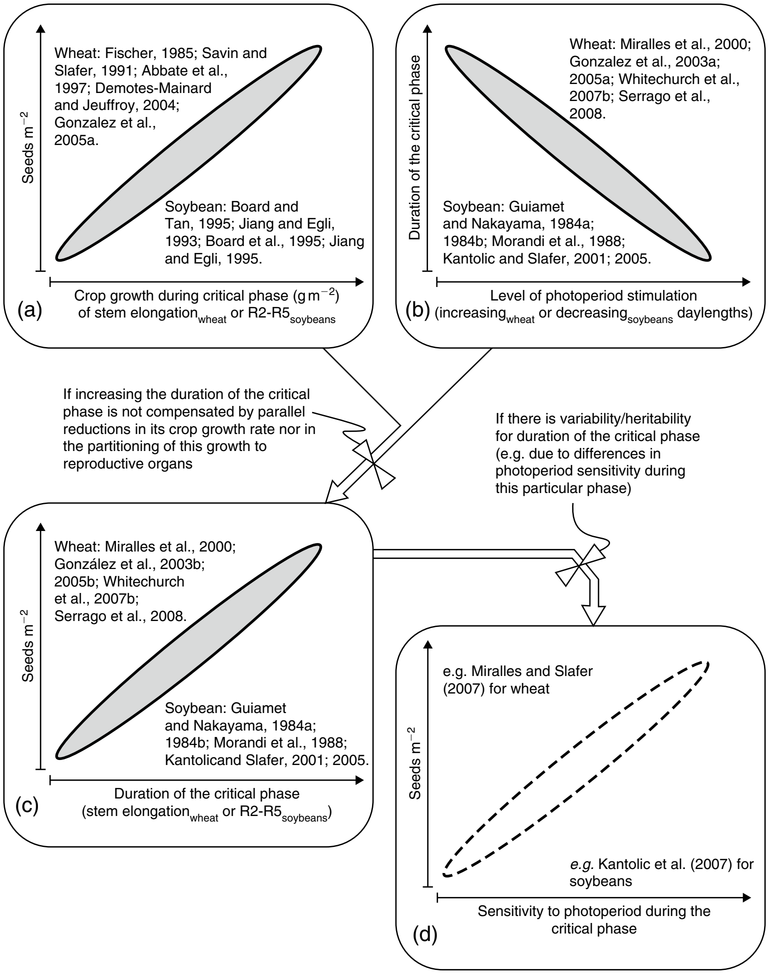


FIGURE 4

The top two panels of this figure summarise two established facts: (1) that seed number is strongly responsive to crop growth during a critical phase for seed number determination (top left panel, with some of the many references evidencing this relationship) and (2) that these phases in wheat and soybean are sensitive to photoperiod so that the less inductive the photoperiod the longer is the phase (top right panel). As there is no (at least not complete) compensation between crop duration and growth rate during the critical phase, the longer the duration of the critical phase the more seeds the crop produces, as shown when the length of the critical phase is altered by manipulating photoperiod only during this phase (bottom left panel). Thus, it is strongly suggested that increasing sensitivity to photoperiod during this particular phase would bring about increases in seed number per square metre by increasing accumulated growth during the critical phase, allowing in turn the set of more inflorescences or more seeds per inflorescence (bottom right panel). A more comprehensive treatment may be found in Slafer et al. (2001) and Miralles and Slafer (2007) for wheat and in Kantolic et al. (2007) for soybeans.

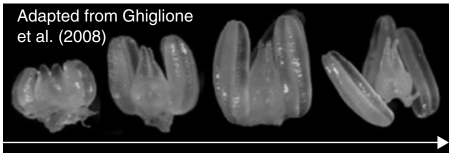
photoperiod is related to an increase in the number of nodes per plant and in the number of seeds per node, which actively accumulate during the critical period; this is strongly supported by experiments both in controlled environments (Guiamet and Nakayama, 1984a, 1984b; Morandi et al., 1988) and in the field (Kantolic and Slafer, 2001, 2005, 2007). In wheat, the increase in seed number in response to short photoperiod is mainly related to the fate of floret primordia during the 'floret mortality' period: with longer photoperiod and shorter phase, the proportion of floret primordia that develops towards fertile florets is consistently reduced (González et al., 2003b, 2005b; Serrago et al., 2008). Studies on the fate of floret primordia when the duration of the stem elongation phase was modified demonstrated that survival of florets positioned in the middle of the spikelet (mostly florets from the third to the fifth position from the rachis within the spikelet) may be improved by increasing assimilate allocation to the spike (González et al., 2005a), although more detailed mechanisms have been recently suggested (see Box 2). From the association between seed set, duration of critical phases and the photoperiodic control of these phases, it has been proposed that grain set could be increased indirectly, by selecting or manipulating for photoperiodic sensitivity (Figure 4d).

BOX 2 Live and let die: likely mechanisms of floret mortality in wheat

As in many other species, the number of grains per unit land area is the main yield component explaining the variations in wheat yield. Although each spikelet within the wheat spike has the capacity to produce a very large number of floret primordia (approximately 10–12 in central spikelets), many of these developing florets fail to reach the stage of fertile floret at anthesis. As (i) the number of floret primordia developed in each spikelet is much higher than the number of fertile florets at anthesis and (ii) the proportion of grain set (grains per fertile floret) is normally quite high, the capacity of floret primordia to survive and continue developing all its floret organs constitutes a major bottleneck for a high number of fertile florets, thereby grains.

Understanding the mechanisms of floret mortality from a combined approach including (i) anatomy changes of the primordia at cellular level, (ii) physiological development and (iii) gene expression (transcriptomic patterns) during the active spike growth period would be a way to gain insight into the process for increasing floret survival in wheat. Ghiglione et al. (2008) combined microarray, biochemical and anatomical approaches to investigate the origin of floret mortality. The authors modified the duration of the spike growth period by modifying the photoperiod only during the phase of spike growth. They found that the acceleration of floret primordia mortality induced by extending photoperiod (e.g. González et al., 2003b, 2005b), which is illustrated below, was associated with the expression of genes involved in photosynthesis, photo-protection and carbohydrate metabolism. The expression of marker genes associated with floral development, cell proliferation and programmed cell death was activated with long photoperiod, that is the signal that determined the mortality of distal floret within the spikelets.

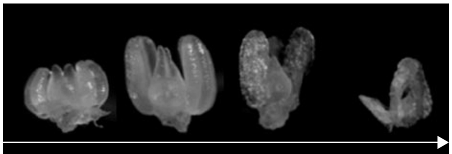
Plants grown under field conditions (i.e. relatively short days)



Adapted from Ghiglione et al. (2008)

Floret development in a plant growing under normal field conditions through stages 6, 7, 8 and 8.5 of the Waddington et al. (1983) scale

Plants grown under extended photoperiod during the spike growth period



Floret mortality in a similar floret that reached the stage 7 normally, illustrating the decay of floret organs and floret abortion, due to accelerated development

In relation to the anatomy and morphological changes in the primordia, the observation of cells of the ovaries of aborting florets revealed formation of the vacuoles (which become dense), an increase in size, incorporation of dense globular bodies (autophagosomes), condensation of chromatin in the nucleus and disappearance of nucleolus. This suggests that floret abortion was a programmed cell death by autophagy rather than passive

(Continued)

BOX 2 Continued

death or necrosis. Another mechanism involved in floret abortion is related to the level of soluble carbohydrates as the decrease of glucose and fructose during the spike growth period enhanced floret abortion of the primordia previously initiated; this is in line with previous studies showing that the fate of florets was largely determined by the acquisition of assimilates by the growing spike when affected by either genetic (Miralles et al., 1998; González et al., 2005c) or environmental (González et al., 2005a) factors.

Ghiglione et al.'s (2008) multidisciplinary approach revealed previously unnoticed mechanisms and allowed for a far-reaching interpretation from gene to phenotype. Thus, the identification of candidate genes controlling the process of survival of the floret primordia previously initiated might constitute a major step to further improve the number of grains per unit land area and yield in cereals and other crops. However, to effectively manipulate these traits, we need to understand the environmental and genetic controls as well as trade-offs involved in the gene-to-crop scales.

6. CONCLUDING REMARKS

In this chapter, the particularities of development of wheat and soybean have been discussed to highlight the importance of identifying the genetic and environmental controls of the phenological pattern. This knowledge is a prerequisite to understand, predict and manipulate the association between crop cycle, the resources and the environmental constraints to favour the coincidence of the critical period with the most favourable conditions. Although the cycle to match crops and environmental factors has been determined in most production systems, further improvement is feasible by manipulation of critical periods.

The critical period may occur before (e.g. in wheat) or after (e.g. in soybean) flowering, but it is clear that in both species, in spite of their large morphological and physiological differences, the growth during this period defines crop yield in most environments. Improving our knowledge of genetic and environmental drivers of the expression of the genes that control flowering time should improve our precision in positioning the critical period when the highest level of resources is expected, and stresses are less likely.

In both species, the length of the critical phase is positively related with the number of seeds, and its duration is modified by photoperiod. Manipulative experiments described in this chapter showed that increasing sensitivity to photoperiod during the critical phase for grain number determination may actually raise yield potential. The longer the critical phase, the more the crop may grow, supporting more grains to be established. So yield could be improved if this phase is lengthened without modifying the whole crop cycle duration. In wheat and barley, there is a large variability in duration of stem elongation independently of the total duration to anthesis (Kernich et al., 1997; Whitechurch et al., 2007a); at least this is in part due to photoperiod sensitivity during this phase (Whitechurch et al., 2007b). In fact, in exceptional cases, it seems that empirical breeding may have made use of this variability (Abeledo et al., 2001). In soybean, simulation studies have shown that shortening the pre-flowering period, without changing the duration of the whole cycle, could be a way for increasing yields in a broad range of latitudes and environmental conditions (Kantolic et al., 2007). The main problem for application of this alternative is to identify a more clear genetic basis of photoperiod sensitivity of the critical phase. This is not a simple challenge. However, even though no single major allele has been particularly linked with photoperiod sensitivity during the critical phase for yield determination, different sources of evidence reinforce the idea that photoperiod sensitivity of individual phases may be independent of each other. This would allow exploiting this trait to change the length of the critical period without altering the duration of the whole crop cycle. Moreover, identifying the genes involved in floret survival (e.g. Ghiglione et al., 2008) is the first step to understand their environmental modulation; putative trade-off is required for eventually manipulating the link between growth, development and genetic information (Table 1).

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CHAPTER 13

Vigorous Crop Root Systems: Form and Function for Improving the Capture of Water and Nutrients

Jairo Palta and Michelle Watt

1. INTRODUCTION

In 1987 O'Toole and Bland concluded their excellent review of genotypic variation in root systems and crop improvement on an optimistic note. Research on the growth and function of roots was progressing rapidly. They listed 11 types of genetic variation in wheat root systems alone, already reported in the literature. These types focused around anatomical and morphological characteristics relevant to the spatial and temporal expansion of root systems (Table 1 in O'Toole and Bland, 1987). The authors stated that root system characteristics appeared as heritable as shoot characteristics and as amenable to selection as other traits in breeding programs. However, they cautioned that controlled environments for phenotyping must incorporate the physical factors of field soils, and that interdisciplinary research among quantitative geneticists, soil physicists and root physiologists was essential. They saw root system characteristics offering many opportunities to become robust traits for breeders to select and for crop improvement in the future.

Two decades later, enthusiasm for root characteristics aimed at crop improvement remains, and new understanding of root form and function accumulates (Gregory, 2006). We are aware of seven root characteristics that have been progressed through to a 'trait' (Table 1), that is, a characteristic that has been selected in phenotypic screens for germplasm improvement, and validated for yield gain in the field. The trait to resist the cereal cyst nematode (CCN) root disease and the trait that confers root tolerance to the toxic element Al have molecular markers and are currently used by commercial breeding companies. The other five traits listed in Table 1 were selections of anatomical and morphological root characteristics to improve the capture of water or phosphorus: more deep water (Hurd, 1968, 1969), conserved water for grain filling (Richards and Passioura, 1989), larger roots for greater forage yield in water-limited environments (Caradus and Woodfield, 1998), longer root hairs that capture more rhizosphere phosphorus (Gahoonia and Nielsen, 2004) and shallow branch roots that capture surface phosphorus (Lynch, 2007). To our knowledge, only the shallow-angle trait is currently adopted by breeders who apply the phenotypic screen (J. Lynch, personal communication). Since O'Toole and Bland's review, however, many efforts have been done to identify root traits to increase capture of resources and crop yield.

In this chapter, we explore root vigour as a characteristic to increase resource capture and yield. Our definition of root vigour is early and fast root extension and proliferation, greater root biomass and greater root length density. We focus primarily on wheat root vigour, which has recently been greatly increased in novel germplasm developed through indirect selection for leaf vigour (Richards and Lukacs, 2002). We outline the

Table 1 Root Characteristics that have Become Traits for Crop Improvement, and are Correlated with Increases in Yield in the Field

Trait	Value	Crop and Growing Conditions	Phenotypic Selection and/or Molecular Marker	Adoption[a]	References
Malate released from root-tip cells chelates Al, reducing meristem damage	Al resistance	Wheat; acid soils	Extreme germplasm identified in the field; phenotypic screen for root elongation or malate efflux from root tips; molecular marker	Yes	Fisher and Scott (1987); Saski et al. (2006)
Stops nematode invading root cells	Cereal cyst nematode (CCN) resistance	Wheat; soils infested with CCN	Phenotypic screen and molecular marker	Yes	Ogbonnaya et al. (2001)
Rapidly penetrating root axes with denser roots at depth	Increases deep-water capture	Wheat; prairies of North America	Selection of diverse parents from small number of lines in root boxes with clear faces, followed by selection for yield at many field sites	No	Hurd (1969)
Reduced diameter of the largest xylem vessel in the seminal roots	Conserves water for flowering and grain filling	Wheat; northern Australia, where wheat grows on stored soil water	Phenotypic screen; many lines screened quickly by sectioning, staining and measuring vessel diameters; extreme lines and parents grown in the field to yield	No	Richards and Passioura (1989)
Large taproot diameter and high root-to-shoot weight ratio	Increases forage yield in water-limiting environments	White clover	Phenotypic screen, recurrent selection for taproot diameter; controlled-environment and field trials	No	Caradus and Woodfield (1998)
Weak root gravitropism enables branch roots to colonise surface soil where P is accumulated	Increases phosphorus acquisition	Bean; highly weathered soils where fertiliser P binds in surface layers	Phenotypic screen; root angle measured	Yes	Liao et al. (2004b)
Long root hairs	Increases phosphorus acquisition	Barley	Phenotypic screen; intermediate number of lines imaged with a video camera and microscope and root hair length measured	Unknown	Gahoonia and Nielsen (2004)

[a] *Adoption by a public or commercial breeding organisation.*

concepts of root vigour and resource capture, carbon allocation in vigorous root systems and the functions of root vigour in cropping systems, and finally examine where root vigour is in terms of becoming a 'trait' for germplasm improvement.

2. CAPTURE OF RESOURCES AND VIGOROUS ROOT SYSTEMS: THE CONCEPTS

2.1. Capture of resources

The interaction between crop root systems and their soil environment limits yields in many cropping areas of the world (Gregory, 2006). For instance, soil water shortage, waterlogging, salinity, soil structure, elemental toxicities and deficiencies are some of the primary factors limiting the capacity of root systems to effectively explore the soil resources. Even in soils free of these factors, there is a limitation caused by an uneven distribution of resources due to fertiliser applications, periodic saturation of topsoil with rainfall and the mobilisation of resources. However, crop root systems are plastic and respond to the uneven distribution of resources by producing and growing roots in relatively large patches of nutrients (Robinson, 1996) and water (Nobel, 1988). Root proliferation in response to a fertile patch was observed one day after the addition of aqueous fertiliser (Jackson and Caldwell, 1989) and just 5 h after the addition of water to dry soil (Nobel, 1988; Palta and Nobel, 1989). The uptake kinetics of roots may also respond within this time scale (Jackson et al., 1990). This plasticity of the root systems to proliferate and function where the soil resources are, and to gain control or possession of them before they escape, is the adopted meaning of 'capture of resources' in this chapter. The main root factors that regulate capture of soil resources are the root system extension rate and morphology (architecture), and the function and longevity of different regions along individual roots (Barley, 1970; Doussan et al., 2003).

2.2. Characterisation of vigour

'Vigour' is an Anglo-French word originated from the Latin word 'vigere', meaning 'to be strong'. When referring to plants, it literally means strength and healthy growth. The advantage found in the growth of barley over wheat when sown simultaneously in the same environment was attributed to greater seedling vigour of barley (Gregory et al., 1992; López-Castañeda and Richards, 1994). Early vigour describes fast development of leaf area and/or shoot biomass (Turner and Nicholas, 1998; Richards and Lukacs, 2002). For instance, vigorous wheat genotypes have larger leaf area and greater shoot biomass than non-vigorous genotypes (Rebetzke and Richards, 1999; Richards and Lukacs, 2002).

Wheats with vigorous shoots also have greater root biomass than the non-vigorous ones (Liao et al,. 2004a; Watt et al., 2005; Palta et al., 2007). The greater root biomass of vigorous wheats results mainly from more and longer branch roots rather than from heavier or thicker roots (Palta et al., 2004, 2007; Watt et al., 2005; Liao et al., 2006). Vigorous root systems in wheat have double the number of roots (Figure 1) because of their more profuse root branching (Palta et al., 2004, 2007; Liao et al., 2006). Root vigour describes early and fast root extension and proliferation, and greater root biomass and root length density (Figure 2).

3. CARBON COSTS OF VIGOROUS ROOT SYSTEMS

Production, growth and maintenance of more roots in a root system involve more investment of photosynthetic carbon (Smucker, 1984; Clarkson, 1985). The key factor that results in vigorous root systems in wheat is a larger amount of photosynthates invested in the extension of the roots. Although the proportion of root-to-total carbon was the same in vigorous and non-vigorous wheats, root systems of vigorous wheats can accumulate 59–66% more carbon than the non-vigorous ones (Table 2). The higher investment in root carbon was probably the result of greater carbon assimilation by the canopies of vigorous wheats, which

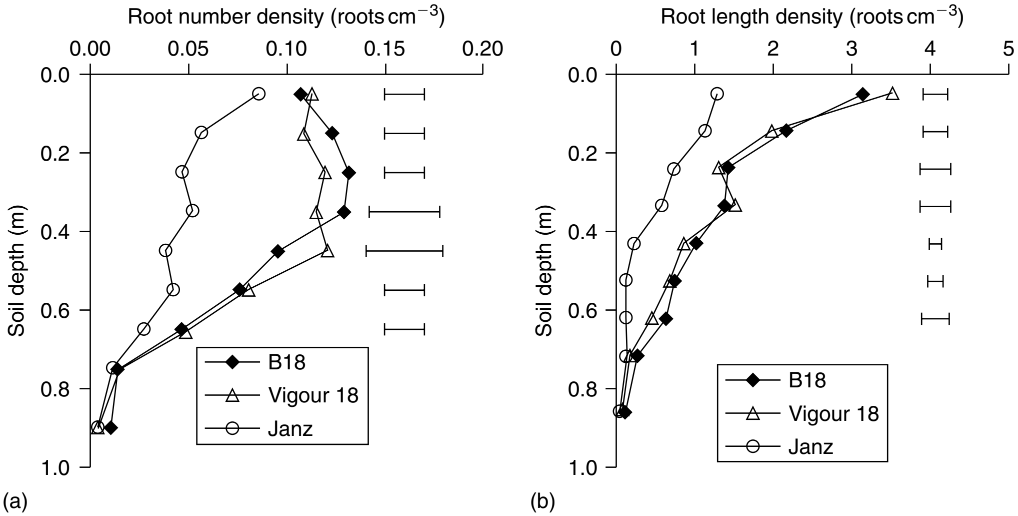

FIGURE 1

(a) Root number density and (b) root length density down the soil profile of the non-vigorous wheat cultivar Janz and the vigorous wheat breeding lines Vigour 18 and B18. Measurements were made at the beginning of stem elongation (Z31) on plants grown in specialised glass-windowed growth root boxes. The horizontal bars represent the l.s.d. ($P = 0.05$). (Source: Liao et al., 2006.)

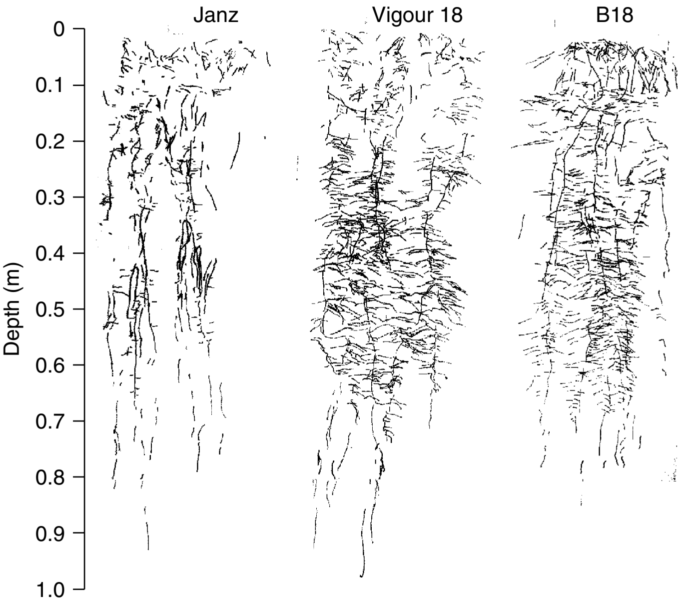

FIGURE 2

Rooting patterns of non-vigorous (cv. Janz) and vigorous breeding lines of wheat (Vigour 18 and B18). Measurements were made at the beginning of stem elongation (Z31) on plants grown in specialised glass-windowed growth root boxes. (Source: Liao et al., 2006.)

Table 2 Distribution of Photosynthetically Fixed Carbon in the Shoot and Roots of the Vigorous Wheat Breeding Lines Vigour 18 and B18 and the Non-Vigorous Wheat Cultivar Janz at the Beginning of Stem Elongation (Z31)

Genotypes	Photosynthetically Fixed Carbon ($g\,m^{-2}$)			Root/total Carbon (%)
	Shoot	Root	Total	
B18	17.8	8.01	25.8	31.0
Vigour 18	19.1	7.70	26.8	28.8
Janz	11.8	4.83	16.6	29.0
l.s.d. ($P = 0.05$)	2.1	0.02	3.1	3.1

Values are the absolute amounts of carbon derived from feeding the canopies with $^{13}CO_2$ for 24 h at the end of stem elongation. Source: Palta (unpublished).

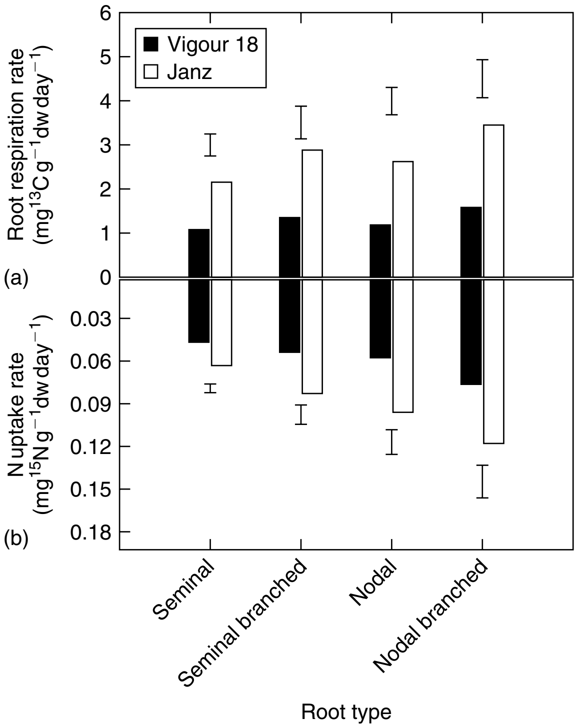

FIGURE 3

(a) Root respiration and (b) NO_3^- uptake by individual seminal and nodal roots with and without branches of non-vigorous wheat Janz and the vigorous breeding line Vigour 18. Measurements on non-branching and branched seminal roots were made before the onset of tillering and at mid-tillering, respectively. Measurements on non-branching and branched nodal roots were made at the beginning of stem elongation. The vertical bars represent the l.s.d. ($P = 0.05$) for comparison between genotypes. (Source: Palta, unpublished.)

can be 54–61% greater than that in the non-vigorous types at stem elongation (Palta, 2006, unpublished). The root carbon does not include the carbon used by root respiration or the carbon released as exudates. Root respiration in wheat has received little attention, despite its importance as a component of the whole plant carbon balance and its role in nutrient uptake (Smucker, 1984; Lambers, 1985b). For instance, losses of carbon by root respiration can represent 25% of current photosynthesis and 13.5% of total plant weight (Morgan and Austin, 1983; Smucker, 1984). Also low rates of root respiration are associated with high crop growth rates (Wilson, 1975; Lambers, 1985a; Amthor, 1989). $^{13}CO_2$ and $Ca(^{15}NO_3)_2$ have been used to simultaneously measure root respiration and NO_3^- uptake by individual roots of vigorous and non-vigorous root systems. Rates of root respiration of branched and unbranched seminal and nodal roots of non-vigorous root systems were twice faster than those of vigorous ones. Uptake of $^{15}NO_3^-$ by non-vigorous root systems was 40–57% faster than that in the vigorous types (Figure 3). However, seminal and nodal roots of vigorous root systems with free access to NO_3^- consumed less carbon in root respiration per unit of NO_3^- uptake than the non-vigorous wheats (Figure 4). This indicates that the carbon costs of maintaining the roots of vigorous root systems active are low, and this low respiratory cost was perhaps the cause of greater accumulation of root biomass and root length. These carbon studies suggest that genotypes selected for more vigorous shoot and root growth may be more efficient at nitrogen and water capture.

We can only speculate whether vigorous root genotypes release more carbon to the rhizosphere than non-vigorous genotypes. The total carbon released from wheat roots (water-soluble and -insoluble compounds such as root cap mucilage) is variable and depends on growing conditions and the age of the plant and the roots (Farrar et al., 2003). Studies in which canopies of wheat were pulse-fed with $^{13}CO_2$ showed that the total carbon released from roots increased from 0.8% of the fixed carbon in seedlings at Z13, Zadoks growth scale, (Zadoks et al., 1974) to 2.5% when the first node was detectable (Z32) (Palta and Gregory, 1997; Gregory et al., 1997). It could be assumed that a larger root system with greater length from which to release carbon would exude more carbon per plant. However, conditions such as nutrient stress and harder soils generally reduce root system vigour, but exudation per root length is greater. If roots extend more quickly

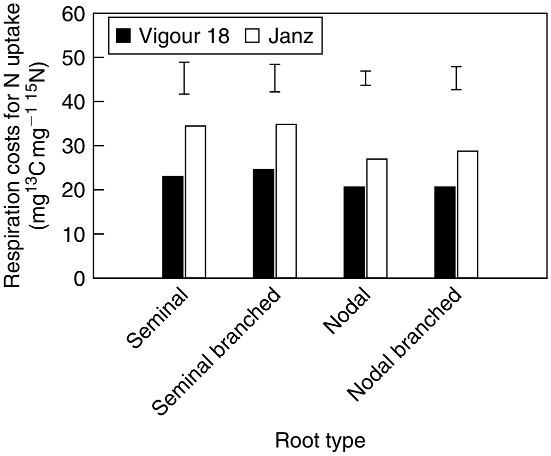

FIGURE 4

Respiration costs associated with NO_3^- *uptake by individual seminal and nodal roots with and without branches of non-vigorous wheat Janz and the vigorous breeding line Vigour 18. Measurements on non-branching and branched seminal roots were made before the onset of tillering and at mid-tillering respectively. Measurements on non-branching and branched nodal roots were made at the beginning of stem elongation. The vertical bars represent the l.s.d. (P = 0.05) for comparison between genotypes. (Source: Palta, unpublished.)*

through the soil, and maximum carbon is released from the root tips, the result may be less exudates per root length in vigorous root genotypes than non-vigorous roots (Watt et al., 2006). Vigorous root genotypes may exude less to the rhizosphere, as the percentage of total fixed carbon, and thus have greater carbon use efficiency (biomass carbon per exuded carbon). Studies that found fewer bacteria around the tips of vigorous roots than around non-vigorous roots support this hypothesis (Section 4.2). Careful studies of whole plant and rhizosphere fluxes of labelled carbon will help to measure rhizosphere carbon per root and plant with newly available near-isogenic lines varying in shoot or root vigour.

4. FUNCTIONS OF ROOT VIGOUR IN CROPPING SYSTEMS

This section outlines the putative value of vigorous root systems in capturing nitrogen and water, in improving crop performance in relation to soil-borne diseases in no-till systems and ultimately in increasing their value for crop yield.

4.1. The role of vigorous root systems in capturing nitrogen

Nitrogen use efficiency (NUE) or the grain yield per unit of nitrogen supplied consists of two components: the uptake efficiency and the utilisation efficiency; Chapter 8 (Section 4) presents a detailed analysis of NUE. While the uptake efficiency relates to the extraction of nitrogen from the soil, the utilisation efficiency relates to the conversion of the taken nitrogen into grain yield. Nitrogen uptake efficiency by cereal crops is low in several agricultural systems of the world (Hatfield and Prueger, 2004). An example is the agricultural system of the Mediterranean-climatic region of southwestern Australia, where annual rainfall is strongly concentrated (75%) between May and October, wheat is usually sown on the first major rainfall between mid-May and the end of June, and soils have high leaching potential (Anderson et al., 1998a, b; Asseng et al., 1998, 2001). During winter, crop growth is slow and its demand for nitrogen is low in relation to the availability of $NO_3{}^-$ in soils (Angus, 2001; Liao et al., 2004a, 2006). The pattern of rainfall in combination with sandy soils favours drainage, and the poor synchronisation between crop demand and the availability of nitrogen can lead to leaching of nitrate below the rooting zone equivalent to 40–60 $\mathrm{kg\,N\,ha^{-1}}$ (Anderson et al., 1998b). This leaching includes both the nitrogen available in the soil at the break of the season, chiefly NO_3^-, and the nitrogen applied as a fertiliser (Fillery, 2001). Typically, recovery of nitrogen fertiliser applied at sowing is 30–50% (Fillery and McInnes, 1992).

Nitrogen fertiliser is an expensive input in cereal cropping. Losses of nitrogen increase cropping costs, reduce crop yields, contribute to soil acidification and cause off-site pollution of groundwater and waterways. Measures to reduce the leakage of NO_3^- below the rooting zone by improving the efficiency of nitrogen uptake by wheat crops are being studied. One of these strategies is the agronomic practice of changing the time of supply of nitrogen fertiliser to match the availability of nitrogen in the soil with the demand by the crop. This practice is, however, limited by the rapid mobilisation of nitrogen within the soil profile and the time taken for the root system to grow and proliferate in response to nitrogen availability. Improving the ability of root systems to recover soil NO_3^- by earlier and faster uptake of NO_3^- is a more effective strategy to minimise NO_3^- losses and improve nitrogen uptake efficiency (Liao et al., 2004a). This strategy requires root systems to be vigorous, meaning to have early and fast growth and profuse proliferation to intercept and capture the NO_3^- before it moves below the rooting depth (Palta et al., 2004, 2007; Liao et al., 2006).

Genotypic variation in root growth has been reported in cereal crops such as wheat (Hurd, 1968; Sirohi et al., 1978; O'Toole and Bland, 1987; Miralles et al., 1997; Hoad et al., 2001; Gregory et al., 2005), barley (Gahoonia et al., 1997; Hackett, 1969) and maize (Costa et al., 2002; Zhu and Lynch, 2004), and there is an increasing interest in using this variation to select new varieties. However, none of the differences reported have been enough to categorise the root system as vigorous or to relate them to nitrogen capture. If breeding efforts are targeted to select for root systems with improved nitrogen uptake efficiency, then the important question is what is the role of vigorous root systems in capturing nitrogen? Comparative studies of vigorous and non-vigorous genotypes in their ability to capture nitrogen have been recently conducted (Liao et al., 2004a; Palta et al., 2004, 2007; Liao et al., 2006). These studies showed that nitrogen uptake and the uptake efficiency of nitrogen fertiliser was greater in vigorous wheats than in other genotypes when 50 kg N ha^{-1} was applied at seeding (Figure 5). The greater uptake efficiency of the nitrogen fertiliser by vigorous wheats was associated with a greater root biomass and higher root length density in the top 0.7 m of the soil profile (Liao et al., 2004a; Palta et al., 2004, 2007; Liao et al., 2006). Although the maximum rooting depth was similar in vigorous and non-vigorous genotypes, branching on the seminal roots commenced five to seven days earlier and was more profuse in the vigorous than in the non-vigorous wheats (Palta et al., 2004, 2007; Liao et al., 2006). Most of the root branching in vigorous wheats occurred in the top 0.7 m of the soil profile, leading to higher numbers of root tips and 42–60% more capture of nitrogen by the time plants were at stem elongation (Table 3).

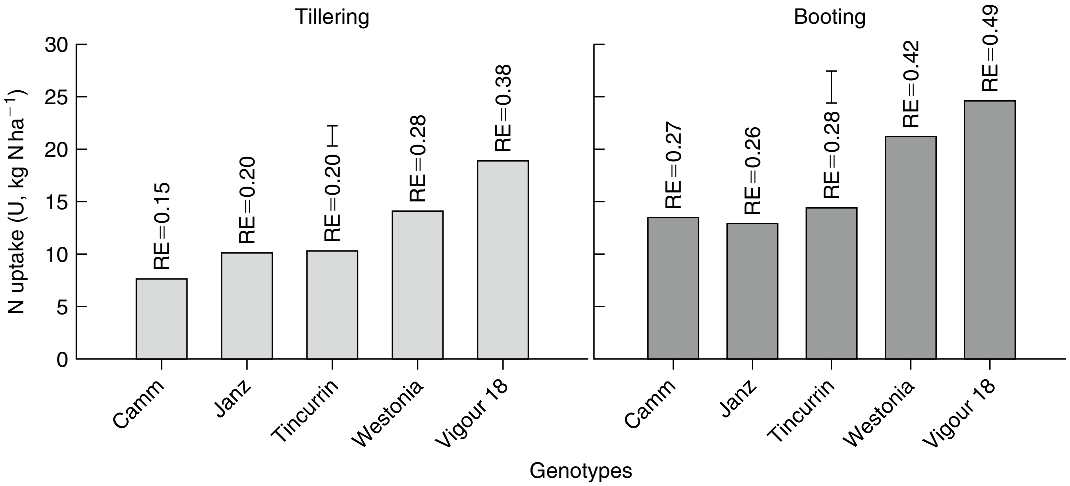

FIGURE 5

Nitrogen uptake of wheat genotypes grown on a nitrogen fertilised deep sandy soil with high leaching potential. Measurements were made at tillering and booting stage. The vertical bars represent the l.s.d. ($P = 0.05$) for comparison between genotypes. RE is the apparent recovery efficiency of the N-fertiliser applied at seeding calculated as kilogram increase in crop uptake per kilogram nutrient applied.

Table 3 Capture of Nitrogen Fertiliser by Vigorous and Non-Vigorous Wheat Root Systems from Different Depths in the Soil Profile up to Stem Elongation

Genotypes	N-Fertiliser Uptake (g m^{-2})		
	0–0.2 m	0.2–0.7 m	0.7–1.0 m
B18	0.56	2.04	0.28
Vigour 18	0.53	1.88	0.27
Janz	0.33	0.96	0.29
l.s.d. (P = 0.05)	0.095	0.41	n.s.

The role of crop root systems in the capture of nitrogen is controversial. For instance, Robinson et al. (1991) suggested that only 4–11% of the total root length is involved in nitrogen uptake. This estimate assumed that roots and nitrogen are distributed uniformly in the soil profile, a condition that is unrealistic under field conditions (Anderson et al., 1998a). ^{15}Nitrogen has been used to precisely measure the capture of nitrogen fertiliser by vigorous and non-vigorous roots from different soil depths. Vigorous roots from the top 0.2 m of the soil profile (24% of the total root length) were accountable for the capture of 19.5% of the total nitrogen in the plant. This capture was 60–68% more nitrogen fertiliser than that by the non-vigorous roots. Vigorous roots from the top 0.2–0.7 m of the soil profile (65% of the total root length) were responsible for capturing 71% of the total nitrogen in the plant. This was more than twice the nitrogen fertiliser captured by the non-vigorous roots in that segment of the soil profile (Table 3). Therefore, the roots captured nitrogen fertiliser mostly in soil layers where root tips were concentrated and where root length density was greater (Liao et al., 2006). Kinetic studies of NO_3^- uptake by vigorous and non-vigorous wheat genotypes indicated that intrinsic affinities for NO_3^- did not influence the greater capture of nitrogen by vigorous wheats (Palta and M. Liao, 2005, unpublished). Nitrogen capture by vigorous root systems is mainly controlled by the plant demand for nitrogen and the availability of the nitrogen. The plant demand for nitrogen is influence by plant growth, which in turn is the sink for the nitrogen uptake. If plant growth is disrupted, then the negative feedback that regulates nitrogen uptake suggested by Imsande and Touraine (1994) is likely to occur. Chapter 8 (Section 2) updates the feedback and feed-forward relationships between demand and supply of nitrogen and between carbon and nitrogen assimilation in crops.

Studies at the International Rice Research Institute (IRRI) aimed at understanding the causes of yield reduction in rice cultivars adapted to transplanting when they were direct seeded suggested that the too-early uptake of nitrogen by the direct-seeded crop locked up a lot of nitrogen, making it unavailable for the generation of grain yield (Dingkuhn et al., 1993). This presumably implies that root systems capable of capturing more nitrogen early in the crop cycle can improve grain yield. However, transplanting in rice imposes a stressful reduction in vigour (Ros et al., 2000), and it is possible that cultivars adapted to transplanting are genetically unable to respond with vigour with the early uptake of nitrogen. In wheat, early capture of nitrogen by roots results in high grain yield and grain protein content, particularly under terminal drought (Palta and Fillery, 1995a, b). This is because early capture of nitrogen by wheat crops stimulates early growth (Cooper et al., 1987; Palta and Fillery, 2005a). One of the reasons for early growth to improve grain yield is that assimilation of carbon and nitrogen during early growth is utilised for grain filling (Palta and Fillery, 1995a, b). Thus, the crop acts as a store of carbon and nitrogen for the period after flowering when the soil may dry and plant water deficits reduce carbon assimilation and the uptake of nitrogen from the soil.

4.2. The role of vigorous root systems in capturing water

The vigour of the root system contributes to the maintenance of growth into moist soil throughout the season. Early in the season, it facilitates seedling establishment. Around flowering and grain filling, additional water capture is particularly valuable because it is immediately used for grain development and filling (Passioura, 1983; Angus and van Herwaarden, 2001). In a direct quantification under SE Australian conditions, Kirkegaard et al. (2007) demonstrated that an additional 10 mm of water accessed by roots from the subsoil late in the season could contribute to grain yield approximately 0.5 t ha^{-1}. Modelling of cropping systems around the world supports these findings; where deeper water is available, genetic and agronomic efforts to capture it by roots will increase yields (King et al., 2003; Wang and Smith, 2004; Manschadi et al., 2006; Lilley and Kirkegaard, 2007).

One reason that roots of wheat and other determinate species fail to take up more available deep water is that they run out of time (Passioura, 1983). Around flowering, carbohydrate reserves are mobilised to the grain and root growth, generally ceases in cultivated wheats (Hurd, 1964; Gregory et al., 1978). In an experiment where the spike of wheat was removed just at flowering, root growth at depth doubled compared to intact plants (Richards et al., 2007). These studies indicate that there is not a constraint to growth in the soil for deep roots; rather deep roots require carbon, and around the time of flowering, apparently most carbon goes to the growing grains. An increase in root system vigour during vegetative growth would increase the time to grow more roots at depth for more water during grain filling. An alternative is to promote post-flowering root growth, such as that observed in the cultivar Seri (Manschadi et al., 2006), but the carbon costs of this investment in root growth and its water and yield revenues need to be evaluated.

Increased downward vigour of the seminal roots to arrive earlier in deep soil layers, with increased vigour of the branch roots to more fully exploit the soil layers for water, could achieve the increased length to capture water by the end of grain filling. The roots originating from the base of the embryo (seminal system) penetrate deepest in wheat, barley and triticale, and 50% of deep roots are small branch roots (Watt et al., 2008). Richards et al. (2007) selected wheats with high seminal-root vigour during vegetative growth, to generate deeper, more branched root systems by flowering and grain filling. They selected for vigorous root systems indirectly by using shoot characteristics such as high leaf area and low tillering and directly by measuring root length and mass in controlled environments, and depths and densities by coring in the field. The root length density at depth, around stem elongation, was 50% greater in germplasm with high leaf area, compared to that with low leaf area in sandy soil, cf. Janz versus Vigour 18 and B18 in Table 4, and the root length per ground area was double in germplasm carrying a gene that restricts tillering (*tin*) compared to near-isogenic lines without the *tin* gene in red-brown clay soil in southern Australia (Richards et al., 2007). The restricted-tillering gene (*tin*) in wheat reduces the number of tillers produced, and its effect on plant growth appears in the early development (Richards, 1988; Duggan et al., 2005). The current hypothesis is that high leaf area and the *tin* gene both provide additional carbon to the roots, which fuels greater root extension, primarily by the branches. Branch root growth can be restricted by carbohydrate supply (Tennant, 1976). It still remains to be demonstrated that germplasm with vigorous root systems during vegetative growth results in deeper root systems by flowering, and increases yield through greater deep-water capture during grain filling.

Capture of water at sowing for establishment and late in the season for grain filling may be the most important targets for root system traits. The location and the timing of these water sources within the soil profile depend on the soil and its capacity to hold water, the preceding crop and its water use, the water present at sowing and the pattern of rainfall during and after the crop growing season. Modelling can estimate when and where valuable water is likely to be present in the profile for targeting root traits (Lilley and Kirkegaard, 2007; Sadras and Rodriguez, 2007). Late-season water, for example, may be located mid-profile, or at the bottom of the root zone. This suggests that it would be beneficial to combine root vigour with other root characteristics to favour resource capture. The other characteristics may include weak root gravitropism to promote a more wide-spreading root system for shallower water uptake, or a strong gravitropism to promote deeper root penetration and deep-water uptake (Araki and Iijima, 2001; Ho et al., 2005; Manschadi et al., 2006), faster extension towards moisture (hydrotropism) (Eapen et al., 2005) and more or less nodal and seminal root axes (Hochholdinger et al., 2004). Combining, or pyramiding, a number of root characteristics for a

Table 4 Root Biomass and Nitrogen Uptake by Wheat Cultivar Janz and the Vigorous Wheat Breeding Lines Vigour 18 and B18 Grown in Glass-Walled Growth Boxes until the Beginning of Stem Elongation (Z31)

Genotypes	Root Biomass ($g\,m^{-2}$)	Root/total Biomass (%)	Root Length ($m\,m^{-2}$)	Specific Root Length ($m\,g^{-1}$)	N Uptake ($g\,m^{-2}$)	N Uptake per Unit Length ($mg\,N\,m^{-1}$)
B18	10.8	21.9	2025	187.5	2.30	1.13
Vigour 18	9.45	21.4	1965	207.9	2.03	1.03
Janz	6.15	21.1	810	131.7	1.42	1.76
l.s.d. ($P = 0.05$)	1.05	n.s	523	32.1	0.34	0.26

target environment can be achieved by phenotype selection in the short term. In future, molecular markers may be available for these characteristics since a gene regulating hydrotropism has been identified in Arabidopsis (Kobayashi et al., 2007); a gene regulating specific root types, including seminal versus nodal roots, has been identified in maize (Taramino et al., 2007); and a significant QTL associated with large root system size was identified in Arabidopsis growing in agar under high osmotic stress (Fitzgerald et al., 2006).

From the analyses in this section and Section 4.1, there is no doubt that vigorous root systems in wheat are better at capturing nitrogen and water, but what are the carbon costs of producing and maintaining such profusely branching root systems? Are water and nitrogen the appropriate currencies for a cost–revenue analysis of production of roots? These are important questions to be answered in the evaluation of genotypes with vigorous root systems. Other important questions concern the yield benefits if an additional carbon investment in the roots is diverted instead to the grain and how grain filling would be affected if an additional carbon investment is required in the root system after anthesis.

4.3. Root vigour and benefits in no-till farming systems

Growers worldwide have been encouraged to adopt no-till practices that include sowing seeds directly into unploughed soil, to conserve soil structure and water. However, in many regions of the world, early growth is slower and yield does not improve in no-till systems, compared to conventional systems where the soil is ploughed (Kirkegaard, 1995; Lekberg and Koide, 2005). Chan et al. (1989) demonstrated that the constraint to early growth of wheat was in the soil, and was a combination of the structure and organisms. Both loosening and sterilisation of the soil improved shoot growth. In some cropping systems, the biological constraints are well-known *Rhizoctonia* or *Pythium* fungal pathogens. However, in other cropping systems, a biological constraint remains in the absence of recognisable pathogens. In southern Australia (Simpfendorfer et al., 2002), the UK (Elliot and Lynch, 1984) and the Pacific North West of the USA (Cherrington and Elliot, 1987), *Pseudomonas* bacteria have been implicated as the causal agent of poor early vigour of wheat in no-till soil.

How are soil structure and microbiology interacting to reduce shoot growth in no-till systems? Watt et al. (2003) conducted a detailed study of root growth rates and the distribution of *Pseudomonas* along roots in no-till and conventionally cultivated soil. They demonstrated that the roots of wheat in no-till soil grew slower due to the hardness of the soil, and *Pseudomonas*, in particular, accumulated on the slow-growing root tips. The *Pseudomonas* accumulation was due apparently to an increase in exudates consumed by the bacteria around those slow-growing tips (Watt et al., 2006). These studies were conducted with the wheat Janz, the most widely adapted cultivar across Australia through the 1990s. Watt and colleagues explored the possibility that wheat genotypes with faster-growing seminal roots and high root vigour may overcome some of the soil structural constraints to root growth and perform better in no-till soil. They found that Vigour 18 has faster root growth in no-till soil than Janz, and that this faster root growth was associated with improved shoot growth (Watt et al., 2005). Genotypes with high root vigour may thus improve crop performance in no-till systems. In field and controlled studies of *Pseudomonas* bacteria on the tips of Janz and Vigour 18, it was observed that even when Vigour 18 roots were growing slowly, they did not accumulate *Pseudomonas* at their tips, suggesting that Vigour 18 varies in its exudates composition and quantity, compared to Janz (Watt, 2006, unpublished). Carbon allocation to Vigour 18 root exudates may be less than to the root exudates of Janz, raising interesting questions about patterns of carbon utilisation in vigorous and non-vigorous genotypes (Section 3).

The studies on no-till soils highlighted the value of knowledge of the rate of root growth relative to the rates of organism growth in the soil (Watt et al., 2006). Root extension in soil can be related to organism growth rates on root tips, densities at different depths in the soil profile and can guide the genetic improvement necessary to capture more of a resource and avoid soil biological constraints.

4.4. Root vigour and yield

Efforts to relate root system size and grain yield of cereals have been made. For example, Thangaraj et al. (1990) showed that the root length density of lowland rice at flowering was directly proportional to grain yield when water was not a limiting factor. However, as the amount of irrigation water was reduced, the soil mechanical strength increased and the root mass per unit of root length, which is an indirect measure of root thickness, also increased. The production and maintenance of thicker roots in response to soil mechanical impedance represent an additional investment of carbon in the roots, which may reduce shoot growth (Atwell, 1990). Xiong et al. (2006) measured root growth of old and modern Chinese wheat cultivars and found that the size of the root system was correlated with grain yield under low irrigation, but not under high irrigation. They interpreted this finding as indicating that when water supply was limited, cultivars with large root systems explored deeply the soil profile and maintained water supply to the plant. This implies that extra carbon was invested in the growth and maintenance of deeper roots, with a possible effect on shoot growth. These two examples show that large root systems in cereals may be associated with yield, but this association has under some circumstances an additional carbon investment in the root system.

5. CHALLENGES IN INCORPORATING THE VIGOROUS ROOT CHARACTERISTIC INTO BREEDING

The challenge facing the root researchers developing better cultivars for the farmer is the adoption of their root trait by a breeding company. To our knowledge, only one root anatomical and morphological characteristic relevant to the spatial and temporal expansion of root systems was selected for released varieties (Table 1). Why is this? It is instructive to look at the history of the traits listed in Table 1 to understand the factors contributing to a trait that was adopted by breeders and guide what is needed for the root vigour characteristic. In the case of the root traits to resist the CCN root disease or soil acidity, adopted by commercial breeding companies, strongly contrasting germplasm was first identified in the field, and rapid, controlled-environment phenotypic screens were developed. Soil diseases and toxic elements are sufficiently detrimental to plant growth that phenotypic screens clearly segregate germplasm, and are strongly linked to yield in the field where the disease or toxic element is present. The clear-cut phenotypic screens meant that major genes regulating the underlying mechanisms were identified and robust markers developed. Breeding companies now use these markers.

To our knowledge, only one of the five anatomical and morphological traits is currently incorporated into breeding – that of shallow branch root angle in bean root systems to capture surface phosphorus (Lynch, 2007). Public breeding organisations in Latin America, the origin of the research, and Africa and China, where phosphorus is bound to surface, highly weathered soil, use the phenotypic screen to select for root angle to improve bean cultivars (J. Lynch, personal communication). The Lynch group engages breeders from the target regions early in the research program, often directly training breeders in phenotyping. The other four anatomical and morphological root traits are not currently incorporated into breeding programs. Hurd (1968, 1969) selected among a small group of genotypes growing to maturity in large root boxes with clear faces for fast vertical growth of the root axes and proliferation of roots below 30 cm. He crossed the superior genotypes and then selected only for yield in the field for a number of generations, seasons and water-limited sites, continually eliminating the poor lines. To our knowledge, Hurd did not validate his high-yielding progeny for deep, vigorous roots in the field at the end of the breeding program, and no screen was provided to breeders. In the case of Richards and Passioura (1989), advanced lines with narrow xylem vessels were developed and the extremes tested for yield in the field. As they were to release superior lines to a breeding company, the genetic background fell to a new strain of the rust fungus (R. Richards and J. Passioura, personal communication). The research program could not keep up with the numbers of lines needed to advance the trait in current cultivar backgrounds and stay ahead of disease resistances. Possibly, the phenotypic screen, although simple in a laboratory, was not simple enough for a breeding company. The case of Caradus and Woodfield (1998) is similar to that of Richards and Passioura (J. Caradus, personal communication). The research program was not able to cross the lines with larger taproots into cultivars that had the latest disease and quality traits quickly enough to provide to breeding companies. It may be worth revisiting the phenotypes of Richards and Passioura (1989) and Caradus and Woodfield (1998) for strongly associated QTL for marker development, given the large potential value of these traits for increased water use efficiency and total water capture.

The examples in Table 1 suggest that (i) valuable traits with strongly linked molecular markers were incorporated into breeding programs; (ii) few public research programs can handle the numbers of lines needed to incorporate a new trait in an advanced cultivar with the latest disease and quality traits, either by phenotypic or marker-assisted selection (Bonnett et al., 2005); and (iii) breeding organisations generally do not phenotype for developmental and physiological traits without extensive training and involvement with the research group. Since there are currently no molecular markers for root vigour, and it may be controlled by a number of QTLs of small effect as observed in rice (Yadav et al., 1997), researchers and breeders will rely on phenotypic screening in controlled environments and the field in the immediate future. A 'bridge' program could be created between the researchers and the breeding companies to share their expertise to phenotype for traits such as root vigour, with the capacity to handle large numbers of lines to test for yield in the field and continually incorporate the latest disease resistance and quality traits into the new germplasm (R. Richards, personal communication).

Phenotyping for root vigour in young wheat root systems in controlled environments is straightforward and rapid in sandy soil or germination paper conditions that enable easy access to roots for axis length, branch root scoring or total root weight measurements. A limited number of young root systems can be dug out of the field with cores or shovel to validate the controlled-environment measurements, but this is not an option for breeders. Good relationships have been observed between controlled-environment vigour and field root vigour up to the five-leaf stage in wheat, particularly when using closely related genetic material (recombinant inbred lines and near-isogenic lines) within new populations developed specifically for increased leaf or root vigour (Watt, 2007, unpublished). Root system traits are more likely to be significantly expressed in the field when near-isogenic material is compared (Price et al., 1999; Richards et al., 2007). As mentioned in this chapter, the challenge is establishing a relationship between young root system vigour and mature crop root system vigour, water and nitrogen uptake, and yield. The root system depth and the root length density at anthesis can be directly measured from cores (Kirkegaard and Lilley, 2007); however, the number of lines screened is limited and not attractive to breeders. Canopy temperature offers promise to quickly, non-invasively phenotype lines in the field for root systems that access more water (Olivares-Villegas et al., 2007); however, it requires direct validation to determine if cool canopy temperature is directly related to roots accessing extra water, and some specialised skill to interpret. Ground-penetrating radar is used in forestry to detect soil moisture levels non-invasively and may complement canopy temperature to quickly measure moisture extraction by more vigorous root systems over large numbers of plots (Hagrey, 2007). Repeatable controlled environment or field phenotyping will be the key to identifying QTLs associated with root vigour for marker-assisted selection. Chapter 15 further discusses breeding for specific root traits (Section 5.1.3) and indirect phenotyping approaches (Section 6) for these otherwise difficult-to-measure traits.

Expensive systems that use X-rays (Grose et al., 1996), nuclear magnetic resonance (Scheenen et al., 2007) or near-infra-red reflection (Lemna Tec™, personal communication) to non-invasively measure the growth or water content of roots and rhizospheres in pots will likely reveal genetic variation in root vigour and provide new insights into root function. Expressions in these systems will need to be validated in the field with young and mature plants. In the meantime, progress towards providing root traits such as root vigour to breeders will continue through collaboration with physiologists, soil scientists, microbiologists, agronomists, geneticists and molecular biologists.

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Integrated Views in Plant Breeding: Modern Approaches for an Old Topic

Grazia M. Borrelli, Pasquale De Vita, Anna M. Mastrangelo and Luigi Cattivelli

1. INTRODUCTION

Following their initial domestication, which involved wholesale phenotypic changes in a suite of traits collectively known as the 'domestication syndrome' (Harlan, 1976, 1992; Hawkes, 1983), all major crop lineages have experienced more recent, intensive selection on a variety of agronomic traits. These include a set of new characters that assured their adaptation to cultivation and increased their usefulness for farmers and consumers. Some of these include changes in plant architecture: apical dominance increase in maize and sunflower, gigantism in the useful plant organs, for example fruit size in tomato and fruit species, and seed dispersal reduction by selecting non-shattering or non-dehiscent forms in common bean, sunflower and cereals. Thus, crop improvement can be divided into three major phases: the initial period of domestication, a subsequent period when crop species have been selected by environmental factors, by inter- and intra-specific competition and by empirical farmer selection, and a more recent phase when the application of principles of quantitative genetics and agricultural practices led to the intentional development of cultivars more suited to grow as a population stand aimed at solving human needs than to survive and reproduce in the wild. This last period can be defined as plant breeding (Slafer et al., 1994).

Crop plants have evolved from their wild ancestors during domestication and selective breeding over the last ~10,000 years. For most of this time, this has been a 'hit or miss' process. Initially, wild plants carrying promising traits were cultivated, leading eventually to locally adapted landraces. These lost many undesirable alleles, and useful alleles became enriched in the cultivated gene pool (Tanksley and McCouch, 1997). Modern breeding has largely continued this process of crossing the 'best with the best' and the successes have been impressive. During the last century, particularly in the second half, genetic progress has been extremely effective for many crops where improved cultivars significantly outyield the corresponding landraces (Gale and Youssefian, 1985; Sinclair, 1998). Frequently, genetic gain has been quantified as the slope of the regression between yield and year of release of cultivars of different breeding eras grown in the same trial (e.g. Austin et al., 1980; Table 3 in Chapter 2; Figure 1 in Chapter 15). A similar approach has been used to estimate breeding effects on other traits such as grain nitrogen and phosphorous content, disease tolerance, phenology and water use efficiency (e.g. Austin et al., 1980; Siddique et al., 1990; Slafer et al., 1990; Calderini et al., 1995; Ortiz-Monasterio et al., 1997; Sayre et al., 1998; Sadras et al., 2000). In general, a genetic gain from 10 to 50 $\text{kg}\,\text{ha}^{-1}\,\text{year}^{-1}$ has been recorded for cereals and legumes over the last century in most countries, including those characterised by vast low-rainfall regions. These changes were often associated with important variations in morpho-physiological traits (Chapter 15); for instance in barley and wheat the reduction in plant height and the corresponding increase in harvest index were the main features (Cattivelli et al., 1994; Calderini et al, 1999; De Vita et al., 2007; Section 3.2 in Chapter 15), as illustrated in Figure 1. This process was associated with the introgression in the elite germplasm of a few key genes affecting plant height, mainly *Rht* (Slafer et al., 1994).

Although important achievements have been made, the accumulation of useful alleles in the cultivated varieties is far from complete; rather, there is an increasing interest to search for useful alleles and traits in the available germplasm and for those introduced in the elite varieties. Many studies have demonstrated the value of alleles originating from wild relatives in plant breeding programmes (e.g. Tanksley and Nelson, 1996; Tanksley and McCouch, 1997), showing that centuries of selective breeding have thrown away useful alleles in addition to useless ones. In recent years, the pace of such research has accelerated in parallel with the development of genomic resources and a significant progress has been made in the use of molecular approaches for plant breeding. These approaches involve two main strategies: (i) a variety of transgenic/cisgenic plants that carry genes, which a plant breeder hitherto could not introduce by available conventional methods; (ii) molecular markers closely linked to useful traits which allow indirect selection and pyramiding of desirable traits through marker-assisted selection (MAS). Indirect selection is often more effective due to the absence of confounding environmental effects; it also allows pyramiding desirable genes, for instance, to enhance the resistance of the crop to disease.

The application of molecular tools to plant breeding has been envisaged as the most promising way for continuing genetic improvement of crops. Two decades after the development of the first transgenic plants (Vaech et al., 1987) this optimistic view needs to be reconsidered from a more realistic perspective. This chapter provides an overview of the breeding progress for some of the most important agronomic traits and summarises molecular technologies associated with plant breeding highlighting future perspectives that could result from the integration of recent advances in physiology, genomics and biotechnology.

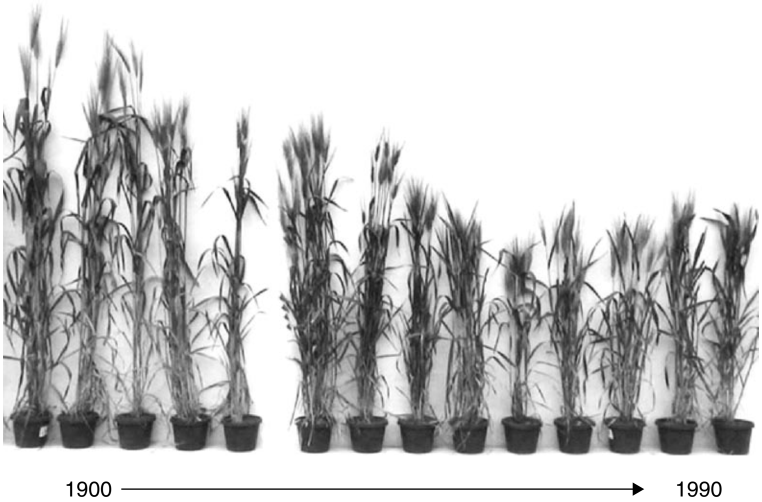

FIGURE 1

Morphological changes associated with the genetic progress in durum wheat cultivars released in Italy from 1900 to 1990. (Source: CRA, Centre for Cereal Research, Foggia.)

2. MODERN VIEWS IN PLANT BREEDING

Plant breeding can be described as the continuous accumulation of superior alleles (i.e. genes encoding useful traits) in the gene pool of the cultivated elite lines. The cultivated germplasm represents only a minimal part of the whole germplasm of a given crop species. Under these conditions, breeding has two main targets: to search for new useful alleles worthy to be introduced into the elite lines (also called 'pre-breeding') and to promote the recombination within the elite germplasm to find the best combinations among the best alleles (breeding) (Figure 2). Exploiting biodiversity for genetic gain is not a new concept in plant breeding. In fact, it was both recognised and practised for over a century and several major genes have been introgressed from wild relatives into the cultivated gene pools of many crops (Hajjar and Hodgkin, 2007). Pre-breeding refers to the transfer or introgression of genes and gene combinations from un-adapted sources into breeding materials (FAO, 1996). There are two distinct approaches for using wild species, exotic, and landrace germplasm in plant breeding: introgression and incorporation (Simmonds, 1993). Introgression indicates the transfer of one or few alleles from exotic genotypes to adapted bred cultivars that lack the allele(s) controlling a specific trait. Incorporation refers to a large-scale effort aiming at developing locally adapted genotypes using exotic germplasm, which will broaden the genetic base of new breeding materials. The broadening of the genetic base will contribute to increase crop stability and performance (Ortiz, 2002; Singh, 2001). The need for pre-breeding arises from the fact that many traits have a complex genetic base (i.e. quantitative) and that they can be found in exotic germplasm. Crosses with exotic material, in fact, can result in the parallel introduction of inferior alleles and the disruption of useful co-adapted gene complexes (Duvick, 1984). Thus, these traits cannot be transferred directly into elite cultivars, which represent a complex combination of desirable traits. Instead, intermediate steps have to be followed to introduce the trait

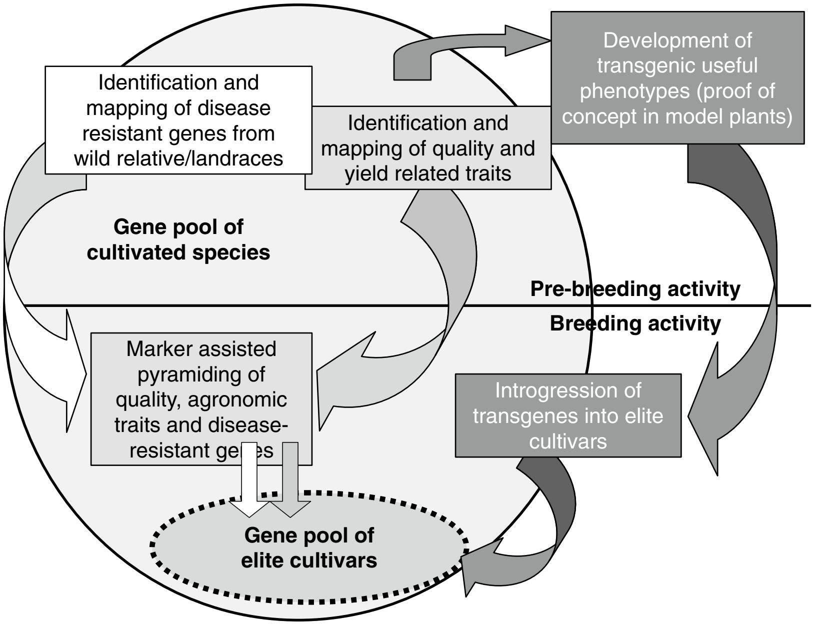

FIGURE 2

Pre-breeding (top half) searches for new useful alleles, and breeding (bottom half) promotes the recombination within the elite germplasm to find the best combinations among the best alleles.

into a genetic background that allows full expression of the trait, confers adaptation, and is more similar to that of the elite cultivars (Simmonds, 1993).

Considering available molecular options, different strategies can be used to search for useful traits and transfer them into the cultivated germplasm. New genes and traits identified in genetically distant genotypes and species can be assessed in model plants (e.g. Arabidopsis) and then introduced in the modern cultivars via genetic transformation. Alternatively, genes (e.g. resistance genes and quality-related and yield-related genes) from wild relatives and landraces can be identified at phenotypic level and then tagged with molecular markers for a safe and fast introgression into the modern cultivars.

Moving from the definition of possible research directions to practical applications, a number of difficulties can be found and relatively few successful stories are known so far. Positive examples are the development of transgenic plants with insect or herbicide resistance and the MAS for many disease resistance genes (Vasil et al., 1993; Altpeter et al., 1999; Sharma et al., 2002; Campbell et al., 2002). On the other hand, when the same strategies have been used to target more complex traits, successful results have been scarce; for example, the use of molecular tools for yield improvement in low-rainfall environments (Cattivelli et al., 2008). Due to its complex genetics, plant tolerance to water deficit is considered the most difficult trait to improve. This challenge becomes even greater due to the unpredictability of water stress, whose timing, duration and intensity varies in space and time. Classically, the mechanisms associated to water stress resistance have been classified as escape, dehydration avoidance and dehydration tolerance (Levitt, 1972; Ludlow and Muchow, 1990). Earliness, a typical escape strategy, can be effective for enhancing yield stability only in environments where crops are exposed to terminal water deficit. In this condition, shortening crop duration allows to synchronise the plant cycle with the most favourable environmental conditions (see Figure 1 in Chapter 12). Dehydration avoidance depends on maintenance of tissue turgor through an increase in water uptake, a reduction in water loss or both. Dehydration tolerance relies on biochemical mechanisms allowing the cells to tolerate water loss. Plants usually combine a range of response types, and the water stress tolerance of a particular genotype is determined by a plethora of traits acting and interacting at the biochemical, physiological and morphological levels (Ludlow, 1989). Nevertheless, a great emphasis is now being laid upon the mechanisms leading to increase yield per se, rather than the characteristics that enhance plant survival under extreme water stress, since the latter entails a negative trade-off under less severe circumstances and a lower intrinsic water use efficiency of the selected materials (Passioura, 2002). In fact, successful examples of yield improvement under water deficit are more related with improved productivity, than with improved water stress tolerance or traits associated with plant–water relations. For wheat, successful examples include (i) a reduced xylem vessel diameter in the seminal roots that slows water use when the soil is dry thereby saving more water for grain filling and therefore resulting in a higher harvest index (Richards and Passioura, 1989), (ii) osmotic adjustment associated with improved water relations at flowering time and hence improving fertility (Morgan, 2000) and (iii) a reduced carbon isotope discrimination, a trait associated to an improved transpiration efficiency (Rebetzke et al., 2002). All traits fit the framework proposed by Passioura (1977) whereby improved yield under water stress is a function of (i) water extracted from soil, (ii) water use efficiency and (iii) harvest index (Richards, 2006). Notably, despite ‘drought resistance’ being one of the hottest research topics at molecular level, the contribution of molecular breeding for yield improvement in dry environments has, so far, been negligible (Reynolds and Tuberosa, 2008).

The objectives of plant breeding are changing continuously according to social requirements. While in the past yield improvement was the main aim, more recently quality, environmental sustainability and the development of new kind of products (e.g. plants for bioenergy) represent additional targets for breeders (Chapter 1). To face these challenges there is a need to introduce new genes and traits in the modern cultivars or hybrids and, for most crop species, future genetic progress rely on the combination of pre-breeding and breeding. Progress in genomics has allowed to rapidly accumulate information about structures of the genomes, and several functional approaches have been initiated to decode the linear sequence establishing a connection between genes and phenotypes (Borevitz and Ecker, 2004). The accumulated genome information has drastically changed the strategy of modern plant breeding, from the traditional field selection mainly based on phenotype (often yield) to an integrated approach where cultivar development is based on genetically improved germplasm and assisted by the deep understanding of genetic processes at molecular level (Duvick, 1990). Although the past two decades have shown potentiality as well as limitations of molecular-based genetic improvement, we believe that the future breeding perspective will largely depend on the integration between genomic knowledge and classical breeding. In this view, the key point is the development of two fundamental connections: (i) the relation between genes and phenotypes and (ii) the relationship between the gene-dependent phenotype and the field performance. While the first one is currently tackled, the second relation is still largely unexplored. Functional genomics has developed many tools (i.e. transformation, insertional mutagenesis, RNAi, TILLING, etc.) (Varshney et al., 2005; Boutros and Ahringer, 2008; Jung et al., 2008) that allow the finding of the phenotype associated to a given gene (a strategy known as 'reverse genetics'), while from a phenotype of interest with a simple genetic basis (i.e. disease resistance) it is possible to clone the corresponding gene (forward genetics). Most of this work, however, is carried out at low levels of organisation (Figure 4 in Chapter 1).

3. MOLECULAR-ASSISTED GENETIC IMPROVEMENT

Biotechnology offers tools based on molecular markers for the assessment of the genetic variation among individual plants, accessions, populations and species (McCouch et al., 1997; Olufowote et al., 1997) and for monitoring genetic diversity over time and space (Smith and Beavis, 1996; McCouch et al., 1997). Molecular markers have the capability of revealing polymorphisms in the nucleotide sequence and allowing therefore discrimination between different alleles at a given locus. They are largely unaffected by environmental factors and developmental stages. Molecular markers are widely used for multiple purposes: to confirm identity between parents and progeny, to determine evolutionary relationships and genetic distances and to construct genetic and physical maps to localise genes or genomic regions responsible for the expression of a trait of interest. The application of molecular markers to plant breeding can significantly increase the speed and the effectiveness of pre-breeding and breeding programmes. Introgression, selection of traits with simple genetic bases or both are routinely carried out based on MAS particularly for disease resistance. Molecular marker characteristics and applications have been extensively reviewed (Korzun, 2002; Röder et al., 2004; Francia et al., 2005; Varshney et al., 2005; Khlestkina and Salina, 2006); they are summarised in Table 1. Virtually, every kind of molecular marker can be used for MAS; nevertheless, easiness, robustness, low cost per sample and possibility of automation are essential features for MAS applications. Therefore PCR-based markers, particularly SSRs and SNPs, are much more suitable for use in MAS programmes than other techniques (Table 1).

The success of a MAS breeding programme depends first of all on the nature of the trait to be improved. While the transfer of monogenic traits is simple and well documented (Campbell et al., 2002; Bonafede et al., 2007), MAS programmes for traits with a complex genetic basis are much more difficult due to the high cost, the genotype×environment and gene–gene (i.e. epistasis) interactions, trade-offs between different organisation levels, which, in turn, result in a low efficiency. Other parts of this book present physiological perspectives to disentangle these interactions and trade-offs, that is case studies in Chapter 11 (Section 3.1) and a more systematic modelling approach outlined in Chapter 10.

Another critical factor for MAS breeding is the degree of association between the markers and the major gene(s) or quantitative trait loci (QTLs) of interest; the closer are the marker and the gene, the lower is the probability of marker and gene being separated by recombination. If the gene controlling the trait has been isolated, it is possible to design a so-called 'perfect' marker directly within the gene; in this way the association between the gene and the marker cannot be lost. At the same time, it should be possible to monitor the entire genome to select rare progenies resulting from recombination near the target gene when backcrossing is carried out. Notably, the fast technological progress leading to new high-throughput equipment is lowering significantly the cost per sample and this will open new perspectives for molecular markers.

Table 1 Molecular Markers Used in Plant Breeding and Their Important Features

Marker	Description	Suitability for Employment in MAS
RFLPs	Restriction fragment length polymorphism	Despite the high reproducibility and the co-dominant nature, RFLPs are not suitable for MAS due to their complex analysis protocols, high cost per sample and low amenability to automation
RAPDs	Rapid amplification of genomic DNA with random primers	RAPDs are markers easy to analyse and with a low cost for reaction. Nevertheless their use in MAS programmes is unreliable due to a low reproducibility
AFLPs	Amplified fragment length polymorphism following DNA digestion and adapter ligation	AFLPs detect a good level of polymorphism (up to 100 loci per reaction); nevertheless AFLPs are dominant markers, not fully suitable for automation and high-throughput analysis at low cost
SSRs	Simple sequence repeat polymorphism	Also known as microsatellite markers, they are based on a single PCR reaction. SSRs detect a good polymorphism level and are suitable for automation and high-throughput analysis at low cost. Together with the co-dominant behaviour, these features make SSRs highly recommended markers for MAS programmes
SNPs	Single nucleotide polymorphism	SNP markers can be dominant or co-dominant depending on the analysis protocol. Development costs are generally high, but once developed, the marker can be used in high-throughput analysis at low cost per sample, being therefore highly recommended for MAS programmes
DArT	Diversity array technology markers, based on microarray hybridisation of genomic DNA	The use of these markers is linked to the work of laboratories that supply the analysis on samples of a number of species in short time and at low cost (www.triticarte.com). Despite their dominant behaviour, DArT markers have been used in some MAS protocols developed for key agronomic traits in wheat at Triticarte lab
TRAP	Target region amplification polymorphism, based on amplification of genomic DNA with a random primer and a gene specific primer	Similar to AFLPs and RAPDs, these markers allow analyzing a high number of loci per reaction, with a single PCR reaction and with high reproducibility. The low cost and the suitability to automation make them good candidate for MAS, despite their being mainly co-dominant

3.1. Identification of phenotype-associated markers

The search for molecular markers strictly associated with a locus controlling important phenotypic traits is a key objective in molecular genetics and can be carried out with methods based on segregation mapping, genomic introgression and association mapping (Morgante and Salamini, 2003) (Figure 3). Segregation mapping is based on the availability of large mapping populations such as F2s, recombinant inbred lines (RILs), backcross inbred lines (BILs) or doubled haploid lines (DHLs). These segregating populations are used to develop linkage maps in which the relative position of hundreds of molecular markers is indicated on each chromosome. Then, the gene(s) and QTL(s) position can be determined through the combination of phenotypic characteristics and segregation data of molecular markers. Many QTLs can affect the expression of a single trait and their importance may vary when assessed in different environments (QTL×environment interaction; Section 3.1 in Chapter 11).

The ability of an organism with a given genotype to change its phenotype in response to changes in the environment is known as phenotypic plasticity (Schlichting, 1986; Pigliucci, 2005). Differential detection of QTLs in a stressful and optimal conditions are often considered as related to adaptive traits. Reymond et al.

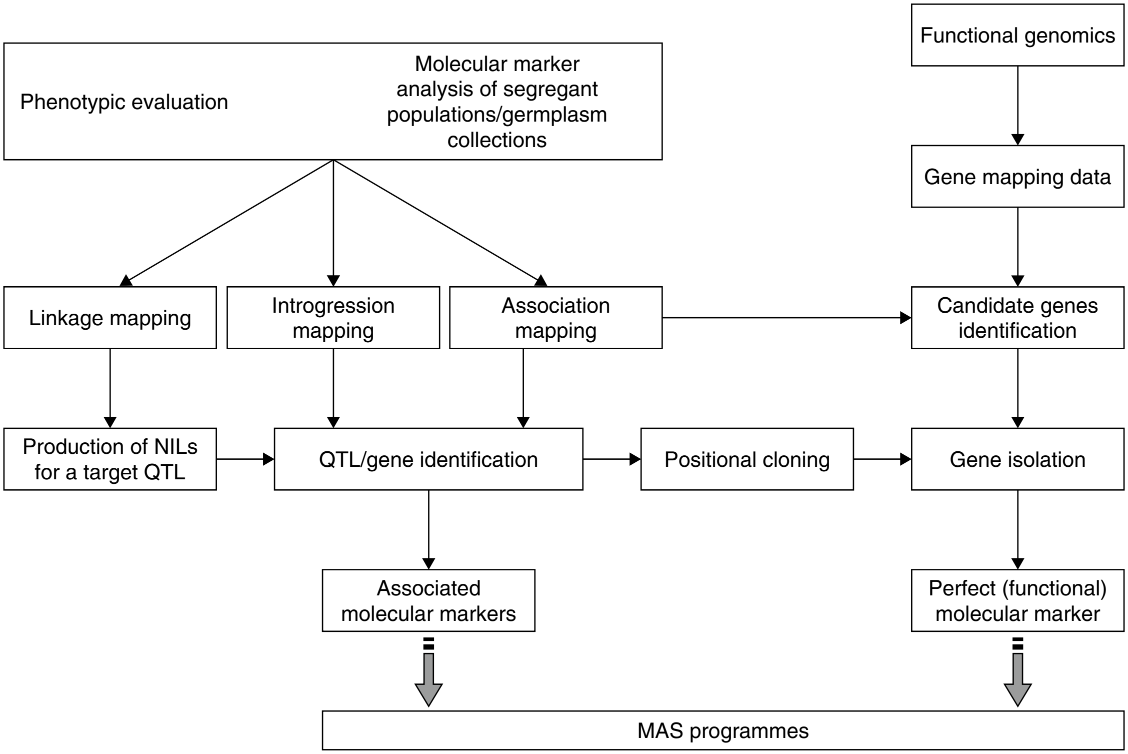

FIGURE 3
Summary of possible strategies for the development of molecular markers linked to genes controlling traits of interest.

(2003, 2004) have proposed a new approach in which QTLs are identified through the correlation between the molecular data and the parameters describing the response curve of the trait to the environmental conditions, rather than the raw phenotypic data per se. This approach allows the characterisation of the genotype per se rather than its behaviour in a given environment. The authors have successfully applied this method to the evaluation of leaf elongation rate in response to temperature, evaporative demand and soil water status. These results raise the question whether such model could be applied to more complex traits such as grain yield. A number of regression techniques of yield against environmental indices have been developed to evaluate the genotype adaptability. They are based on yield performance of a given genotype under stress and non-stress conditions, and on quantification of the degree of stress (e.g. water deficit) based on specific environmental factors (Cattivelli et al., 2008). For instance, Rizza et al. (2004) have suggested an integrated water stress index (WSI), based on a simple soil water balance and the integrated reduction in plant transpiration relative to potential transpiration. They proposed that yield potential and adaptability of cultivars could be related to water stress by means of the intercept and slope of a linear regression of yield versus WSI. By providing yield analysis as a function of an environmental index these different approaches could enable a genetic analysis of plant adaptability to different water stress conditions.

A crucial step to provide reliable QTL-associated markers for breeding is the validation of each QTL through the gain of more precise information on their relative importance on field performance. Near isogenic lines (NILs) can be produced backcrossing a donor plant with a recurrent parent. Each NIL carries only one target

QTL in the genomic background of the recurrent parent, behaving as a single Mendelian factor; therefore, the effect of the target QTL can be precisely evaluated, and the gene/QTL finely mapped and isolated (Salvi and Tuberosa, 2005).

The whole QTL analysis process, from the construction of the primary mapping population to the achievement of NILs, is labour intensive and requires many generations and years. An alternative and effective approach for identification of target QTLs is the development of introgressing lines (ILs), a set of lines obtained through the marker-assisted backcross of a donor parent, usually a wild relative, with a recurrent parent. After two to three backcross generations, each line will contain a specific genomic region of donor parent in the recurrent genetic background and the whole set of ILs is organised to represent the whole donor genome (Zamir, 2001). Because the identification of QTLs using ILs does not require a pre-existing linkage map, this is a more user-friendly method for practical breeding works. For instance, a collection of tomato ILs, containing chromosome segments of a wild species in the genetic background of a cultivated variety, have been utilised to identify more than 1000 loci controlling quantitative fruit metabolic traits and yield-associated traits (Schauer et al., 2006). Once a QTL has been identified, the IL carrying the region of interest can be used for fine mapping and cloning of QTL/gene as well as donor line in breeding programmes.

Besides linkage mapping studies, an emerging approach for the identification of genes underlying phenotypic variations in complex traits is represented by linkage disequilibrium (LD, i.e. non-random association between alleles at linked loci) mapping (Syvänen, 2005). LD infers associations between genotypes (haplotypes) and phenotypic variations examining the genetic polymorphisms that have been generated into different genetic backgrounds through thousands of generations of recombination. A whole genome may be scanned to identify regions that are associated with a particular phenotype by using molecular markers, covering the whole genome. Otherwise, alleles at a few selected candidate genes may be tested for association with a phenotype (Rafalski, 2002). Candidate genes for a trait of interest are usually referred to sequences whose expression profile or protein function can be associated to the trait and whose position on the genome co-maps with a QTL controlling the trait. The extent of LD is affected by many factors, including the population history and the frequency of recombination in the examined genome segment. In plant species where population bottlenecks are common, such as sugarcane and sugar beet, LD extending for several cM was found (Jannoo et al., 1999; Kraft et al., 2000). On the contrary, maize studies have shown that LD decays within 1500 bp distance, allowing successful identification of QTLs associated with variation in flowering date (Thornsberry et al., 2001). LD has been successfully employed in finding marker-trait associations for yield and yield stability in a collection of 146 modern two-row spring barley germplasm: the association was evaluated on a mean of 15 environments for each variety in Northern Europe (Kraakman et al., 2004), and for grain morphology and milling quality in a selected sample of 95 cultivars of soft winter wheat (Breseghello and Sorrells, 2006), indicating that association mapping approaches can be a viable alternative to classical QTL approaches based on segregating population studies.

Isolating the gene behind a QTL represents the final goal for the understanding of molecular basis of the trait and for identification of precise molecular markers to be used in breeding programmes. Recently several QTLs regulating agronomic traits have been cloned in tomato, rice and maize for invertase activity, control of flowering time, and grain yield components (Fridman et al., 2004; Ashikari et al., 2005; Fan et al., 2006; Ashikari and Matsuoka, 2006; Salvi et al., 2007). Their importance and application in MAS programmes will be discussed in Section 3.3.

3.2. MAS for improvement of qualitative traits

Most of the successful applications of MAS to plant breeding relate to resistance to diseases regulated by one major resistance (*R*) gene. Disease resistance is a typical example of traits that have a consistent effect across levels of organisation (Chapter 1). Based on 'gene-for-gene' theory (Flor, 1956; Punja, 2004), for any given plant and potential pathogen pair, an incompatible interaction is the result of the simultaneous presence of the plant resistance locus (*R*) and the pathogen avirulence determinant (*avr*) that activates signalling pathways leading to the phenotypic resistance in the host. The *R* gene products are hypothesised to act as receptors for the product of the avirulence locus (ligand). If the plant lacks the *R* locus or the pathogen lacks the *avr* determinant, a compatible interaction with disease appearance on the host is observed. This resistance mechanism is usually controlled by one gene with evident effects. Section 3 in Chapter 17 deals with genetic basis of disease resistance in detail; it shows that oligogenic resistance (including single gene resistance) is usually race specific, whereas many genes with individually small phenotypic effect can be combined to produce progeny with effective, normally more durable polygenic resistance.

Transferring *R* genes in elite cultivars generally requires 10 to 15 generations with conventional selection and the evaluation of the progenies by means of natural infection or artificial inoculation test. The availability of molecular markers tightly linked to resistance loci has facilitated their incorporation in the elite cultivars by MAS (Campbell et al., 2002). A typical marker-assisted backcross programme takes three to five generations, allowing rapid introgression of multiple genes from diverse sources, with advantages in particular when recessive genes have to be introgressed. Many efforts are made internationally, in order to incorporate modern selection technologies in breeding programmes. An example is the WHEAT CAP project (www.maswheat.ucdavis.edu/), aimed to prepare MAS protocols to incorporate valuable genes in the best wheat breeding lines for traits such as resistance to diseases and insects, quality and tolerance to abiotic stresses. These lines are being used in the WHEAT CAP project to deploy the targeted genes into thousands of lines using high-throughput forward breeding strategies. For instance, more than 50 leaf rust resistance genes have been characterised from *Triticum* species or introgressed into wheat from wild relatives (www.cdl.umn.edu/res_gene/wlr.html). Most of them were roughly mapped to specific chromosomes, few were fine-mapped to more specific genetic locations and three *R* genes were cloned (*Lr21* – Huang et al., 2003; *Lr10* – Feuillet et al., 2003; *Lr1* – Cloutier et al., 2007). When information on the genotype carrying the *R* gene and the associated molecular marker is available, a MAS programme can be developed.

The barley *Mlo* gene is a recessive gene encoding for durable resistance to powdery mildew, whose diffusion has been facilitated by the development of molecular markers located within the gene or closely linked to the gene (see Section 4.4 in Chapter 17). The durability of *Mlo* resistance provides an advantage over race-specific resistance genes that are typically overcome by selection of virulent races of the pathogen within several years of their deployment (Wolfe and McDermott, 1994). The *Mlo* gene was cloned and the mutation giving rise to the *mlo-9* resistance allele was discovered (Büschges et al., 1997). On the basis of this knowledge a mass spectrometry primer extension assay has been developed as a diagnostic co-dominant marker for *mlo-9* detection (Paris et al., 2003) and subjected to proprietary restrictions (US patent 6791007). Nevertheless, the availability of barley genomic sequences in public databases helped Tacconi et al. (2006) to search for polymorphisms in three predicted low-copy sequences adjacent to the *Mlo* gene and develop PCR-based markers capable of identifying *mlo*-resistant genotypes in segregating populations. Genes determining pre-invasion resistance to powdery mildew and leaf rust have been characterised in other species (Collins et al., 2007).

Monogenic race-specific resistance is not durable in the field where high levels of pathogen pressure are common (Chapter 17). In this case pathogen frequently responds to selection pressure by altering or eliminating the avirulence determinant. These dynamic genetic changes of the pathogen, in turn, impose a selective pressure on plant populations, leading to a continuous plant-pathogen co-evolution (Michelmore, 2000; Richter and Ronald, 2000). To slow down the development of resistance in pathogen populations, gene pyramiding has been proposed whereby multiple resistance loci, each locus recognising a unique range of isolates of a pathogen species or different pathogen species, may be incorporated into a single cultivar. The combination of the individual specificity of many *R* genes can efficiently give durable, broad-spectrum resistance (Singh et al., 2001). For instance, a MAS-assisted backcross programme has been used to pyramid into the high yielding rice cultivar PR106 three bacterial blight resistance genes (*Xa21*, *xa13* and *xa5*) conferring resistance to all bacterial races present in the specific cultivation area (Singh et al., 2001). The pyramiding of different sources of resistance to the same pathogen is, obviously, very attractive because it can lead to broad resistance. Nevertheless, this approach would expose simultaneously many *R* genes to the evolution of new pathogen virulent races. This strategy minimises the short-term risk of new virulent genes in the pathogen, but might be more risky in the long term since a virulent race may ultimately evolve able to overcome many *R* genes at the same time, strongly reducing the available sources of resistance.

Besides pathogen resistance, marker-assisted introgression has been used for genes controlling morphological and quality characters. For instance, wheat puroindoline genes (*Pina* and *Pinb*) at the *Hardness* (*Ha*) locus control the hardness/softness of the grain, an important trait determining many end-use properties of wheat (Bonafede et al., 2007). The fine mapping of the *Pin* genes with molecular markers designed within the *Pin* sequences and in adjacent regions allowed the introgression of a functional *Pin* allele from the diploid wheat *Triticum monococcum* into hexaploid wheat resulting in softer grains without any detrimental effects due to the linkage drag of undesired genes (Bonafede et al., 2007).

3.3. MAS for improvement of quantitative traits

Many traits of agronomic relevance, such as yield, abiotic stress tolerance and quality components, are explained by a number of QTLs each of which explains a part of the observed variation. Capacity for fast, reliable and affordable phenotyping represents the most limiting factor for the genetic analysis of quantitative traits (Cattivelli et al., 2008). Relevant phenotyping needs to account for timing, intensity and duration of stresses, and signal-to-noise ratio, which can be partially managed by selecting research plots with low spatial variability, consistent agronomy and experimental design controlling within-replica variability (Edmeades et al., 2004).

Low heritability and high sensitivity to environmental conditions strongly limit the application of QTLs in MAS programmes, though approaches have been proposed that produce more robust QTLs based on the analysis of parameters describing the change of the trait in relation to environmental drivers (Reymond et al, 2004).

Among abiotic stresses cold tolerance is probably the one with the simplest genetic basis in *Triticeae*. However, frost can take place at different developmental stages leading to different physiological and molecular responses. During winter the ability of the plants to survive depends on a number of factors, including freezing duration and severity and the duration of the hardening period prior to frost. Otherwise, frost can happen in spring, when plant fertility can be severely damaged. Despite the different factors involved in frost tolerance, most of the observed variability in temperate cereals can be explained by two tightly linked QTLs located on the long arm of homeologous chromosome group 5 (Vágújfalvi et al., 2003; Francia et al., 2004). Even frost-induced floret sterility and grain damage at the reproductive stage in barley were associated with a QTL on the long arm of chromosome 5H (Reinheimer et al., 2004). It is remarkable that different frost tolerance–related traits and measures such as field over-winter survival, membrane damage after hardening and freezing in controlled conditions and the expression level of a cold-induced protein, all have the same genetic basis (Francia et al., 2004). This indicates that these two QTLs may control frost tolerance at different levels of organisation, from cell to crop. One QTL exactly overlaps the locus carrying a gene family, encoding the most important transcription factors controlling the cold stress response (*CBFs*) (Vágújfalvi et al., 2003; Francia et al., 2004). The second frost tolerance–related QTL overlaps *Vrn1*, a locus controlling the vernalisation requirement, confirming that frost tolerance and vernalisation are two interconnected traits. Molecular analyses suggest that *Vrn1* acts in part to repress or attenuate *CBFs* expression (Stockinger et al., 2007). These findings make *CBFs* the best candidate for the QTL and markers designed on *CBF* the best tool for the selection of frost resistance genotypes (Vágújfalvi et al., 2005; Knox et al., 2008).

A more complex frame has been depicted for genetic control of water deficit tolerance, with a high number of QTLs widespread on many chromosomes (Cattivelli et al., 2002, 2008). The limited success with bottom-up approaches to improve crop performance under limited water supply is related to (i) the wide range of morphological, physiological and biochemical mechanisms involved, for example phenological development (Section 1 in Chapter 12), root architecture (Section 4 in Chapter 13), (ii) the complexity of the adaptive landscape derived from large G × E × M interaction (Chapter 10) and (iii) the buffering of trait relevance in scaling up to the crop level (Chapter 1) and trade-offs (Chapter 9). The genetic basis of traits with putative influence on water stress tolerance remains elusive, even if molecular markers may have resolution for osmotic adjustment (Morgan and Tan, 1996), tiller inhibition (Spielmeyer and Richards, 2004), GA responsive dwarfing genes (Ellis et al., 2002, 2005) and early vigour (Spielmeyer et al., 2007).

In rice, MAS was used to transfer several QTLs for deep roots from the *japonica* upland cultivar 'Azucena', adapted to rainfed conditions, to the lowland *indica* variety 'IR64'. MAS selected lines showed a greater root mass in low-rainfall trials (Courtois et al., 2003; Steele et al., 2006). In maize, several marker-assisted recurrent selection strategies have been proposed where the best genotypes selected with molecular markers are then intermated randomly to produce the next generation (Ribaut and Ragot, 2007). In a marker-assisted backcross experiment the drought-tolerant line Ac7643, donor parent, and the drought-susceptible line CML247, the recurrent parent, characterised by a very large male–female flowering asyncrony interval (anthesis-silking – ASI), were crossed. The increase in ASI with increasing stress and intra-specific variation for this trait have been recognised in early studies (Du Plessis and Dijkhuis, 1967; Hall et al., 1982). Five QTLs for ASI, located on different chromosomes and co-localised with QTLs for yield components, were selected, each of them explaining >5% of the phenotypic variance for ASI. Plants with the highest proportion of CML247 alleles at 60 markers distributed throughout the genome, and with good agronomic traits and yield performance were selected in two backcrosses. When compared with controls, hybrids obtained from these selected lines showed a consistently higher mean grain yield under severe water stress conditions (the best five MAS-derived hybrids yielded at least 50% more than control hybrids), with no significant differences in grain yield under mild water stress and well-watered conditions (Ribaut and Ragot, 2007).

Isolating the gene(s) behind a QTL and designing a marker within it (them) could represent the best approach to pyramid different QTLs into the same genotype through MAS. For instance, QTLs associated with grain number (*Gn1a*) and grain size (*GS3*) have been cloned in rice (Ashikari et al., 2005; Fan et al., 2006). When *Gn1a* was pyramidised with a QTL for plant height (*Ph1*), grain yield increased (23%) and plant height was reduced (20%) compared to controls, but the field performance of this genotype is unknown. The increased grain number was associated with cytokinin accumulation in floral meristems, in turn related to the reduced expression of the cytokin oxidase/dehydrogenase *OsCKX2* encoded by *Gn1a* (Ashikari et al., 2005).

4. TRANSGENIC-ASSISTED GENETIC ENHANCEMENT

A peculiar contribution of molecular biology to plant breeding is the deeper and more precise understanding of gene action and function which, in turn, has suggested the introduction of relevant genes via genetic transformation as a possible breeding practice. Genetic transformation, the non-sexual insertion of alien genes, gene-regulating systems or both, may be applied to endow the new cultivars with useful traits. Plant transformation provides new variability and a wide array of novel genes not previously accessible to plant breeders, also from related plants or other species even in other taxonomic phyla, which can be easily inserted and functionally expressed into agronomic background in a single event, without associated deleterious genes (Sharma et al., 2002). This process also allows changing the level and the spatial and temporal pattern of transgene expression by choosing suitable promoters, constitutive or inducible, or adding introns into the constructs (Sahrawat et al., 2003). The engineered genetic enhancement may solve many plant breeding problems particularly when the gene controlling the trait of interest is not present or is very difficult to access in the gene pool of the major crops. Pest, disease and herbicide resistance provide examples in which transgenic crops have been obtained and successfully adopted worldwide.

Remarkable efforts have been made over the past two decades in manipulating genes and inserting them into crop plants to confer desirable attributes, although the success of the transgenic breeding is largely dependent on the trait considered. While transgenic plants modified for herbicide tolerance and insect resistance have been adopted worldwide, other transgenic events are at a pre-commercial phase and many more are still at laboratory level and most likely few of them will be successfully validated in field trials. Almost all plant features have been targeted with a transgenic approach: (i) increased resistance to biotic and abiotic stress and increased tolerance to herbicides; (ii) enhanced nutritional value of crops and improved post-harvest quality; (iii) enhanced efficiency of soil phosphorus uptake and nitrogen fixation; (iv) improved adaptation to soil salinity and aluminium toxicity; (v) increased photosynthetic rate, sugar and starch production; (vi) male sterility and apomixis to fix hybrid vigour in inbred crops; (vii) production of pharmaceuticals and vaccines (Sharma et al., 2002). The development of many transgenic plants has contributed to the understanding of genes and their function but from a farmer's point of view still few transgenic cultivars are available. There are a number of reasons to explain this. Transgenic approach is, by definition, based on a single (rarely few) gene that controls a specific metabolic reaction or cellular process. Therefore only when the cellular phenotype is positively reflected at plant population and community levels, the transgenic plants have a chance to result in a new transgenic crop (Chapman et al., 2002). Genes conferring resistance to pathogens are relevant across levels of organisation, while modification of a single step of a complex metabolic pathway (e.g. photosynthesis) can be buffered in the scaling up to the crop level (Chapter 1) or cancelled by trade-offs (Box 1 in Chapter 9).

Furthermore the transgenic-based breeding is nowadays troubled by public constraints related to the commercialisation of transgenic crops, particularly in Europe. The commercial success of these products will depend upon the development of clearly defined and scientifically based regulatory frameworks for the introduction of genetically modified plants in the environment and onto market, and upon public acceptance of transgenic plant products.

4.1. Plant transformation: basic concepts

The technology is based on the delivery of biologically active and functional foreign genes into plant cells, the integration of the genes into plant genome, and subsequently the plant regeneration from transformed cells or tissues with the recovery of transgenic plants stably expressing the foreign gene, useful for cultivation or as donor parent (reviewed by Sahrawat et al., 2003). One of the most efficient methods for gene transfer employs *Agrobacteriun tumefaciens* to deliver the transgene into the host genome. In nature, this soil bacterium causes tumour formation (so-called crown galls) on a large number of dicotyledonous as well as some monocotyledonous species and Gymnosperms by transferring a specific DNA fragment, the T-DNA (transferred DNA), from its tumour-inducing (Ti) plasmid to the plant cells (Gelvin, 1998, 2000). Recombinant *Agrobacterium* strains, in which the native T-DNA has been removed and replaced with genes of interest, are the most efficient vehicles used for the introduction of foreign genes into plants (Lacroix et al., 2005). The use of *Agrobacterium* vectors for genetic transformation is superior compared with other techniques in terms of stable genome integration and single/low-copy number of the intact transgene, though it may lead to variable expression level due to the genomic position effect and transgene silencing. In crops recalcitrant to *Agrobacterium* infection several physical methods for DNA delivery into cells have been developed, including microprojectile bombardment (Sanford et al., 1987; Vasil et al., 1993). This approach delivers the genetic material using highly accelerated gold or tungsten particles so that they penetrate through the cell wall. The foreign DNA coated on their surface will then be freed and in some rare cases will recombine with the chromosomal DNA of the target cells.

4.2. Transgenic applications

In 2006 the global area of transgenic crops was about 102 million ha (Clive, 2006). More than 95% of commercialised transgenic crops are concentrated in USA, Argentina, Brazil, Canada, India and China (Table 2), representing 55% of the world population. In spite of the wide diffusion of the transgenic crops, it is noticeable that 99% of these was represented by four species, soybean (56% of global transgenic crop area), maize (25%), cotton (13%) and canola (5%). The main traits involved are herbicide tolerance (mainly to glyphosate and gluphosinate) (68%), insect resistance (19%) and the two traits combined (13%). Considering the actual trend, more than 200 million ha and about 20 million farmers are expected to grow transgenic crops by 2015 (Clive, 2006). Chapter 3 (Section 1) outlines the substantial changes in the agricultural

Table 2 Global Area of Transgenic Crops in 2006

Country	Area (Mha)	Crop
USA	54.6	Soybean, maize, cotton, canola, squash, papaya, alfalfa
Argentina	18.0	Soybean, maize, cotton
Brazil	11.5	Soybean, cotton
Canada	6.1	Canola, maize, soybean
India	3.8	Cotton
China	3.5	Cotton
Paraguay	2.0	Soybean
South Africa	1.4	Maize, soybean, cotton
Uruguay	0.4	Soybean, maize
Philippines	0.2	Maize
Australia	0.2	Cotton

Source: Clive (2006).

landscape of Argentina associated with transgenic soybean. In the following sections the perspectives of transgenic-assisted genetic enhancement are outlined for selected traits.

4.2.1. Photosynthesis

Increasing leaf photosynthetic rate was considered a strategic way for increasing crop yield (Kruger and Volin, 2006; Long et al., 2006), and a number of avenues have been explored to achieve this aim including the introduction of C_4-like photosynthesis in C3 plants (Matsuoka et al., 2001; Häusler et al., 2002; Leegood, 2002; Van Camp, 2005), and manipulation of key photosynthetic enzymes such as rubisco (Parry et al., 2007), NADP malate dehydrogenase and catalase (Laporte et al., 2002; Sharma et al., 2002). Transgenic C_3 plants expressing the C_4 phosphoenolpyruvate carboxylase gene were produced, although they did not improve photosynthetic rate or grain yield (Ishimaru et al., 1997, 1998; Ku et al., 1999). This is not surprising because many photosynthesis-related traits (e.g. rubisco and chlorophyll content) are relevant at low levels of organisation (e.g. leaf) but much less at crop level (Pettigrew et al., 1989; Denison et al., 2003; Sinclair et al., 2004). This is accounted for metabolic buffering (Jenner, 2003), scaling-up processes and trade-offs discussed in other chapters (Section 6 in Chapter 7, Box 1 in Chapter 9 and Section 5.1.2 in Chapter 15).

Maintenance of photosynthesis associated with the stay-green trait could improve grain yield in source-limited crops under terminal stress (Sharma et al., 2002; Sakulsingharoj et al., 2004; Wang et al., 2007); this trait is discussed in Chapter 15 (Section 3.2.2) where the relationship with maintenance of root activity and nitrogen uptake during grain filling in sorghum highlights the complex involvement of root and shoot traits.

4.2.2. Source:sink

Manipulation of the source–sink relationships and assimilate partitioning to increase starch biosynthesis and accumulation have been considered (Regierer et al., 2002; Jenner, 2003). ADP-glucose pyrophosphorylase (AGP) produces the substrate for starch synthesis and is thought to catalyse a rate-limiting step in the starch biosynthetic pathway. The introduction of a mutant form of the large subunit of AGP less sensitive to allosteric inhibition by orthophosphate has led to increase in starch biosynthesis and yield in many crops (potato – Stark et al., 1992; maize – Giroux et al., 1996; wheat – Smidansky et al., 2002).

4.2.3. Morphological and developmental modifications

Plant morphology and architecture and the transcriptional networks controlling plant development have been targeted in yield improvement studies. Examples concern the modification of root growth, by affecting cell expansion, and of leaf and stem architecture, by acting on gibberellin's and brassinosteroid's signalling pathways (Van Camp, 2005). The identification of the genes responsible for plant dwarfing, related to plant response to gibberellin, or affecting the formation of tillers and lateral branches carrying inflorescences has opened promising ways for yield improvement (Takeda et al., 2003; Sakamoto and Matsuoka, 2004). The alteration of phytochrome *phyA* and *phyB* gene expression also represents a powerful strategy to alter plant morphology. By means of phytochrome photoreceptors, plants sense the reduction in the ratio of red (R) to far-red (FR) light when they are shaded by their neighbours and respond by increasing their stem extension, reducing branching, accelerating leaf senescence and reducing allocation of resources to yield organs (Smith, 2000; Libenson et al., 2002). Transgenic overexpression of oat *phyA* in tobacco showed an enhanced allocation of assimilates to leaves with a consequent increase in fresh leaf harvest index, particularly when plants were grown at high density in the field (Robson et al., 1996). Positive effects on leaf morphology, photosynthetic performance and tuber yield were found in transgenic potatoes overexpressing *Arabidopsis phyB* (Thiele et al., 1999; Schittenhelm et al., 2004) that were confirmed in field studies at high plant population density (Boccalandro et al., 2003). The enhanced *phyB* expression not only altered the ability of plants to respond to light signals, but also modified the light environment itself, resulting in higher maximum photosynthesis in leaves of all strata of the canopy, largely due to increased leaf stomatal conductance, and a yield increase due to the increased tuber number.

4.2.4. Resistance to biotic stress

Conventional breeding, wide crossing involving inter-specific and inter-genetic hybridisation (Trethowan and Mujeeb-Kazi, 2008) and physiological trait-based approaches (Richards, 2006) are largely used to introgress useful genes in cultivated germplasm. However, the direct introduction of genes by genetic engineering might represent a more attractive and straight solution for improving biotic stress tolerance (Dunwell, 2000; Wang et al., 2003). Insect-resistance genes were successfully inserted into a wide array of crop plants, including maize, cotton, potato, tomato, groundnut, chickpea, tobacco, rice, broccoli, lettuce, walnuts, apples, alfalfa and soybean (Sharma and Ortiz, 2000; Sharma et al., 2002). A consistent number of transgenic crops carrying the *Bacillus thuringiensis* δ-endotoxin gene (Bt-toxin) have been released for on-farm production (Altpeter et al., 1999; Dunwell, 2000; Sharma et al., 2002). Other insect-resistant transgenic plants containing genes which interfere with nutritional requirements of the insects, such as protease inhibitors, chitinases, secondary plant metabolites (e.g. flavonoids and lectins) have been proposed (Hilder and Boulter, 1999; Sharma et al., 2000), even though many of these candidate genes either are too specific or are only mildly effective against the target insect pests compared to Bt-toxin.

Besides the specific pathogen–host (*R*/*avr*) interaction described in Section 3.2, signalling components that function downstream of *R* genes without race-specific mechanism, giving a broad-spectrum defence response, have been identified. The systemic acquired resistance (SAR) is associated with a rise of internal levels of salicylic acid (SA) and with the increased expression of a set of genes termed pathogenesis-related (PR), several of which encode proteins with antimicrobial activity or enzymes involved in biosynthesis of antimicrobial compounds (phytoalexins). Although some of the physical and chemical defence mechanisms are constitutive cellular components (e.g. cell wall, tannins and phenolics) other defences are deployed only after the pathogen contact. The inducible defence system includes reactive oxygen species, phytoalexins, cell wall components (i.e. callose, glycine or hydroxyproline-rich proteins) and PR proteins. It has been argued that the efficacy of the inducible defence mechanisms is often insufficient (too weak or too late). Hence the proposal that overexpression of regulatory genes that are upstream of defence genes in signalling pathways can be a successful approach to engineer disease resistance (Campbell et al., 2002). For instance, these approaches were used to enhance resistance to pathogens in some cereals (Lin et al., 1995; Chen et al., 1998; Datta et al., 1999, 2000; Dahleen et al., 2001; Muthukrishnan et al., 2001;

Anand et al., 2003). This approach overlooks, however, the cost and trade-offs of **constitutive defences** (Section 2 in Chapter 9).

4.2.5. Resistance to abiotic stress

Transgenic and genomic technologies have generated extensive information on the molecular basis of abiotic stress adaptation (Parry et al., 2005; Bohnert et al., 2006; Umezawa et al., 2006). Molecular mechanisms involved in abiotic stress tolerance are based on the activation and regulation of specific stress-related genes including components of the signalling pathways (e.g. kinases), transcription factors, stress-responsive proteins, proteins involved in free-radicals and toxic-compounds scavenging, enzymes controlling osmolyte accumulation, water and ion uptake and transport (Apse and Blumwald, 2002; Wang et al., 2003; Zhang et al., 2004; Vinocur and Altman, 2005; Cattivelli et al., 2008). The knowledge of these responsive mechanisms has prompted the development of transgenic plants designed either to up-regulate the general stress response or to reproduce specific metabolic or physiological processes related to stress tolerance.

However, the evaluation of 'drought tolerance' of transgenic plants has often been based on survival capacity (Gaxiola et al., 2001; Laporte et al., 2002; Park et al., 2005; Wang et al., 2005; Hu et al., 2006; Rivero et al., 2007), with very limited analyses of the transgene effects on yield. Many abiotic stress studies are performed under controlled conditions, where a single constraint is applied as 'shock' treatment that does not reflect the real conditions in the field where the crops are routinely subjected to a combination of different constraints (Mittler, 2006). Passioura (2007) pointed out that about 3000 patents and patent applications emerge in CAMBIA's BiOS patent database on searching for 'drought tolerance' and 'drought resistance'. Of these, a large proportion is concerned with metabolic or stress-induced genes having doubtful functional significance under field conditions. Although this suggests inefficient use of research resources and opportunities for improvement, some encouraging results are emerging (Bahieldin et al., 2005; Wang et al., 2005; Nelson et al., 2007; Hu et al., 2006). In their review of the impact of translational research on crop productivity in drought-prone environments, Reynolds and Tuberosa (2008) emphasised the magnitude of information on the molecular basis of abiotic stress adaptation generated by transgenic and genomic technologies and envisaged forthcoming impacts in the field.

4.2.6. Qualitative and nutritional improvement

Genetic engineering can change a metabolic pathway to increase the amount of various secondary metabolites used in medicine, food and aromatic industry, or to inhibit the production of toxic metabolites (Sharma et al., 2002). Increased protein content, modification in fatty acids composition, improvement of vitamin and essential amino acid contents, alteration of amylose to amylopectin ratio in starch, increased amount of oligosaccharides and removal of anti-nutritional factors are all relevant targets for transgenic approach. Improvement of these traits will, ultimately, increase the value of food through the modification of the chemical composition of plant products to meet nutritional and industrial requirements (Sharma et al., 2002; Rahman et al., 2007).

Relevant improvements in yield, protection and nutritional value were obtained with a combination of MAS and transformation in rice (Zhang, 2007). Through a pyramiding of different transgenes, a new rice genotype able to produce β-carotene and with enhanced iron availability was released (Goto et al., 1999; Datta and Khush, 2002; Datta et al., 2002, 2003). Transgenic potato with deep yellow tubers and higher carotenoid and β-carotene content was obtained (Ducreux et al., 2005; Diretto et al., 2007; Lopez et al., 2008). Transgenic approaches could be adopted to develop food crops with increased Zn and Fe content (Cakmak, 2008). The overexpression of the gene encoding a Zn–transporter protein involved in the uptake and transport of cationic micronutrients (Schachtman and Barker, 1999) in roots of barley increased grain Zn concentration (Ramesh et al., 2004), and the overexpression of the ferritin gene increased Fe and Zn seed content in rice (Vasconcelos et al., 2003) and maize (Drakakaki et al., 2005). A NAC (NAM-B1) transcription factor encoded by the *Gpc-B1* locus from *Triticum dicoccoides* increased grain Zn and Fe concentration, perhaps by stimulating leaf senescence and remobilising Zn and Fe from flag leaves to seeds (Uauy et al., 2006). This information will be related with grain yield to assess any potential dilution or concentration effects. However, even though grain yield and grain Zn and Fe concentrations are inversely related (Distelfeld et al., 2007), it was possible identifying genotypes with high grain Zn concentration, independently of their yield potential (McDonald et al., 2008). Trade-offs between yield and grain quality traits are analysed in Chapter 16 (Section 4).

A further significant example of quality modification through genetic engineering is the alteration of the wheat storage protein composition (HMW glutenin) and of the endosperm texture to improve the gluten quality and the technological properties of the wheat flour and of transformed products (Vasil et al., 2002; Sahrawat et al., 2003; Rakszegi et al., 2008; Yue et al., 2008; Beecher et al., 2002; Xia et al., 2008).

5. PRE-BREEDING: A LINK BETWEEN GENETIC RESOURCES AND CROP IMPROVEMENT

Over the past century, plant breeding has significantly contributed to increase crop productivity and the utilisation efficiency of agricultural inputs (Warburton et al., 2002; Figure 1 in Chapter 15). However, these gains have often been accompanied by decreased genetic diversity within elite gene pools (Lee, 1998; Fernie et al., 2006). A complementary discussion on the effect of plant breeding on genetic diversity is presented in Chapter 15 (Section 4.1) that shows cases where genetic diversity has been unchanged or increased by breeding and selection and a brief discussion on the different means of estimating genetic diversity.

It has been suggested that the elite germplasm of the major crops, especially self-pollinating cereals, has experienced an overall reduction in its genetic basis as a result of high selection pressures, recurrent use of the adapted elite germplasm and the adoption of breeding schemes not favouring genetic recombination (Rosegrant et al., 1997; Hoisington et al., 1999). For example, the majority of hard red winter wheat cultivars in the United States have been derived from two main lines imported from Eastern Europe (Harlan, 1987). In rice, molecular analyses comparing modern varieties and wild types reveal that the cultivated gene pool has a limited genetic variation compared to wild relatives (Wang et al., 1992). Even in maize, which is considered to be a highly polymorphic species, there has been roughly a 30% drop in diversity at the average locus from maize's wild relatives (Buckler et al., 2001). Certainly, the loss in diversity was not experienced equally by all genes in the genome. For genes that do not influence favoured phenotypes (neutral genes), the loss in diversity is simply a function of the strength of the bottleneck in terms of the population size and duration (Doebley et al., 2006). On the contrary, genes that influence desirable phenotypes experienced a more drastic loss of diversity because plants carrying favoured alleles contributed the most progeny to each subsequent generation while the other alleles were eliminated by selection (Wright et al., 2005).

Crop domestication and plant breeding have been extremely successful at increasing the frequency of beneficial alleles at many loci and breeders have persisted in making crosses among closely related, high yielding varieties. Nevertheless, wild relatives and landraces are thought to still carry agricultural desirable alleles (Xiao et al., 1996; Tanksley and McCouch, 1997). In wild species, favourable loci or QTL alleles often remain cryptic due to several factors including their low frequency, masking effects of deleterious alleles and negative epistatic interactions (Xiao et al., 1998; Gottlieb et al., 2002; Lauter and Doebley, 2002; Peng and Khush, 2003). These alleles have the potential to contribute to crop improvement when transferred to cultivated varieties (Xiao et al., 1996, 1998; Poncet et al., 2000, 2002; Peng and Khush, 2003). Thus, although wild and exotic germplasm is perceived to be a poor bet for the improvement of most traits based on phenotypic examination, it is quite possible that some favourable genes (alleles) lie buried amidst the thousands of accessions maintained in gene banks which, if they could be found, might be of great value to crop improvement.

Examples of the use of wild germplasm in traditional breeding have been reported for various cereal species. In wheat, almost 30 independent disease resistance genes have been identified, which were transferred using introgressions from the wild relatives (reviewed in Fedak, 1999, and Hoisington et al., 1999). In rice, genes for resistance to eight pathogens have been introgressed into cultivated germplasm from wild species (Brar and Khush, 1997). Barley genetic improvement has also benefited from genes derived from wild barley and Middle Eastern landraces (Ellis et al., 2000), as exemplified by the development of the *mlo*-mediated resistance to powdery mildew (Büschges et al., 1997; reviewed in Thomas et al., 1998).

Despite some highly significant successes, mostly based on single gene traits including the incorporation of dwarfing genes into wheat and genes conferring durable resistance against a wide spectrum of diseases as described earlier, traditional breeding programmes have not always been successful in extracting useful traits from exotic germplasm. The use of beneficial alleles from wild species requires repeated backcrossing to recover most of the desirable agronomic traits and an efficient selection procedure is needed to retain the target allele from the exotic donor. Even when these are applicable, linkage drag may compromise the final result. These problems are exacerbated, in the case of complex agronomic traits, by the existence of numerous interacting QTLs, whose expression is also significantly influenced by the environment (e.g. Section 3.1 in Chapter 11). One example of how undesirable linkages limit access to useful traits is the low protein quality of cultivated maize grains (Or et al., 1993). Storage proteins (zeins) containing high proportion of the essential amino acids methionine and lysine have been identified in unselected wild germplasm, but not in domesticated germplasm. It is thought that undesirable genetic linkages between the zein loci and other loci have, since domestication, prevented both farmers and plant breeders from selecting for this trait using conventional breeding techniques (Swarup et al., 1995).

These drawbacks can be in part solved using molecular tools (Xiao et al., 1996, 1998; Zamir, 2001). Two molecular-map-based studies have been conducted for simultaneous identification and transfer of wild QTLs into a cultivated genetic background. In the advanced backcross QTL method (Tanksley and Nelson, 1996), molecular linkage maps are used to analyse populations obtained by repeatedly backcrossing a wild parent to a recurrent domesticated parent. The outcome of this procedure is a subset of alleles from the wild species that can be mapped and evaluated in a cultivated genetic background (Tanksley and Nelson, 1996). The rationale of this strategy is that beneficial wild alleles can be recovered from transgressive segregations that outperform the cultivated parent (Tanksley and Nelson, 1996; Tanksley and McCouch, 1997). Using this method, yield of a highly productive rice hybrid has been enhanced by the introduction of two QTL alleles from the low-yielding *O. rufipogon*, each increasing yield by about 17% compared with the original hybrid (Xiao et al., 1996, 1998). A second advanced backcross experiment has shown that *O. rufipogon* can contribute favourable alleles for the improvement of rice cultivation under low inputs (Moncada et al., 2001). In both studies, about 50% of trait enhancing QTL alleles were derived from the phenotypically inferior wild parent (Xiao et al., 1998; Moncada et al., 2001). The advanced backcross method has also been applied to barley (von Korff et al., 2005, 2006) and wheat, with positive results for yield improvement (Huang et al., 2003; Pillen et al., 2003; Narasimhamoorthy et al., 2006; Leonova et al., 2007).

6. BREEDING BY DESIGN

Conventional plant breeding has typically used phenotypic observations, sometimes backed by sophisticated statistical analysis, to select for improved germplasm in segregating populations and the improvements in yield obtained were likely due to an increase in yield potential through the unconscious pyramiding of yield-related traits. This approach has been and remains effective. The gene pool represented by the modern varieties is surely the starting point for the development of new and improved materials and recombination among elite cultivars is still a powerful engine to support genetic progress. In barley, incremental genetic gains were made for several agronomic traits within a very narrow genetic pool (Rasmusson and Phillips, 1997). Similarly, in maize about 100 years of recurrent selection in the Illinois populations for high and low protein content still gives some genetic progress (Dudley and Lambert, 2004). This suggests that genomes are more plastic and amenable to selection than previously believed (Rasmusson and Phillips, 1997).

In this view, sorting out the favourable genes from the modern variety and capturing the few genes desired from the germplasm resources represents a major objective for the future, and the molecular knowledge will be an essential tool to assure further progress in plant breeding. Molecular tools are currently used in reconstructing novel genotypes through allele pyramiding of useful loci from many donors, and transgenic crops are a true option, at least for some simple traits. When, in the 1980s the first molecular tools were applied to plant breeding an expectation of 'easy solution' for difficult tasks was generated. Three decades later molecular breeding has revealed both successful and unsuccessful stories. Regardless of the approach used (transformation vs. molecular markers) most of the traits with a Mendelian genetic base were efficiently targeted with molecular breeding technologies, while quantitative traits still represent a challenge. The improvement in disease resistance through molecular tools has certainly contributed to improve yield reliability. Nevertheless the improvement of yield potential, or yield in low-rainfall environments, is still mainly based on traditional selection assisted by physiological knowledge on yield components and stress responses.

Further perspectives in plant breeding will explore the new possibilities derived from genome-wide knowledge. Indeed, the application of the genomic tools to plant breeding, besides improving the selection process, opens the possibility to plan and develop novel varieties bearing pre-defined traits. The understanding of the genetic bases of all agronomic traits and the analysis of allele variations at the corresponding loci would enable the breeders to design new ideotypes first in silico (Chapter 10), then to construct the new genotypes in planta. For instance a combination of approaches has been followed to develop new rice cultivars referred to as 'Green Super Rice', possessing resistance to multiple insects and diseases, high nutrient efficiency and drought resistance, promising to greatly reduce the consumption of pesticides, fertilisers and water (Zhang, 2007). The goals of Green Super Rice can be achieved as a two-stage process. In the first stage, which has been partially realised, elite lines carrying single genes of interest are developed and evaluated, which are useful cultivars on their own. In the second stage, the genes introduced into these lines will be combined in various ways to develop cultivars with the desired traits for Green Super Rice.

Compared with the later 1990s, breeders have a range of new perspectives for plant improvement. Firstly, they have new tools such as markers for single loci and QTLs as well as genes for plant transformation that will provide an opportunity to move the selection from phenotype to genotype, taking into account the buffering nature of many agronomical traits when scaling up from gene to crop. Secondly, they will have a new role, to blend together all knowledge of the traits sustaining yield and quality and to accumulate randomly dispersed QTLs, transgenes or both into elite genotypes. This 'breeding by design' strategy (Peleman and Van der Voort, 2003) is important in the face of the future breeding challenges. Notably, it becomes more evident that successful breeding will only be possible when a true integration of traditional breeding with physiology and genomics is achieved. Thus, to ensure sufficient yield in the future requires a multidisciplinary approach based on plant genomics, physiology and modelling (Yin et al., 2004; Wollenweber et al., 2005).

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Genetic Improvement of Grain Crops: Yield Potential

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1. RATIONALE FOR RAISING YIELD POTENTIAL

The UN forecasts that the world population will reach 9.4 thousand million by 2050. The world must therefore develop the capacity to feed 10 thousand million within the next 40–50 years. The increase in production has to come not only from greater yields on existing cropland, but also without proportionate increases in the use of water or fertiliser, and within the context of climate change (Chapter 20; Hirel et al., 2007; Cattivelli et al., 2008). A substantial increase in yield potential is therefore required, along with better use of water and fertiliser to ensure food security and environmental protection in future decades. The aims of this chapter are to (i) review the physiological basis of genetic gains in yield potential in grain crops to date, (ii) consider the genetic basis of yield potential and the implications for breeding, (iii) identify barriers to future gains in yield potential and (iv) assess the scope for the use of physiological tools to select for high yield potential.

Yield potential is the yield of a cultivar when grown in environments to which it is adapted (solar radiation, temperature, photoperiod) with nutrients and water non-limiting and with pests, diseases, weeds and other stresses effectively controlled (Evans and Fischer, 1999). It is somewhat theoretical since 'optimal' radiation and temperatures, for example, most likely interact with genotype and growth stage. This differs from the attainable yield, which corresponds to the best yield achieved through skilful use of the best available technology (Box 1 in Chapter 1). On-farm yields normally realise from 60 to 80% of attainable yield; the gap relates to the physical environment being suboptimal on most farms and to moderate use of fertiliser and crop protection measures in environmentally sensitive farming. The yield gap may therefore be quite large, especially in the more marginal environments. For example, Sadras and Angus (2006) showed an average yield gap of 40% for wheat in dry environments of the world. The best farmers in high-potential environments achieve yields that are at par with experiment-station yields, but the majority lag behind by as much as 2–3 $\mathrm{t\,ha^{-1}}$ for the major cereal crops (Pingali and Heisey, 2001). Slafer and Calderini (2005; Figure 1) carried out an analysis of the yield gap for wheat throughout the twentieth century, that is between what is potential and what is actually achieved on farmers' fields, in a set of cultivars released at different times in Argentina and the UK. The analysis showed the importance of increasing potential yield through breeding as a means to increase on-farm yields, since increases in potential yields were closely tracked by actual yields in both environments in the last decades. Therefore, yield potential remains the principal target for breeders in high-potential environments directly linked to both attainable and on-farm yields.

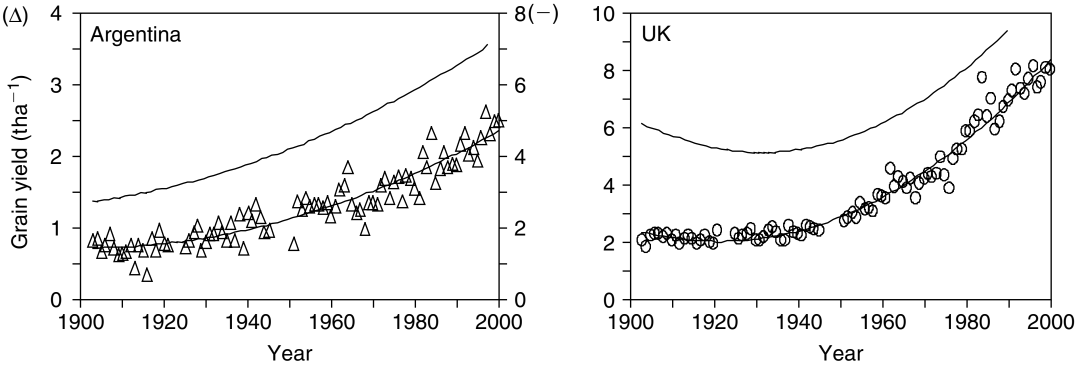

FIGURE 1

Grain yields of wheat throughout the twentieth century at farm level (symbols) and at potential conditions in a set of cultivars released at different times (line) in Argentina and the UK. Note different scales for potential and actual yields in Argentina. Data for fitting the line showing the effect of wheat breeding on yield potential are from Austin et al. (1980, 1989) for the UK and from Calderini et al. (1995) for Argentina. (Source: Slafer and Calderini, 2005.)

2. RELATIONSHIP BETWEEN YIELD POTENTIAL AND YIELD UNDER ABIOTIC STRESSES

Selection for greater yield potential has frequently resulted in higher production in environments subject to abiotic stress (usually water and heat) in wheat (Calderini and Slafer, 1999; Slafer et al., 1999; Richards et al., 2002; Araus et al., 2002; Reynolds and Borlaug, 2006). The point at which there is a crossover interaction implying that selection for yield potential will result in cultivars which in absolute terms perform less well than those selected under drought is estimated to be in environments with yields <2.0 t ha^{-1} (Araus et al., 2002), that is in severely stressed environments. Breeding strategies to improve plant performance through increased transpiration efficiency (biomass:transpiration) associated with reduced stomatal conductance have had some success in severe drought environments. For example, selection for low ^{13}C:^{12}C isotope discrimination (high transpiration efficiency) was associated with yield gains in Australia under severe drought (Rebetzke et al., 2002). However, in a typical Mediterranean environment with mild-to-moderate drought conditions characterised by a grain yield between 2 and 4 t ha^{-1}, it seems likely that most rapid progress will depend on the introduction of high-yielding genotypes of traits able to improve drought tolerance without detrimental effects on yield potential, thus reducing the gap between yield potential and actual yield in drought-prone environments.

Likewise there is a general agreement that for barley a high yield potential is advantageous under moderate-stress conditions, and that advantages of drought-tolerant cultivars with low yield potential are expressed only when stress is severe (Voltas et al., 1999). Thus, breeding efforts to improve tolerance of severe stress have been most successful for drought-prone environments with barley yields often below 1.0 t ha^{-1} (Ceccarelli and Grando, 1996); and in these conditions locally adapted germplasm has been used (Ceccarelli et al., 1998). Tambussi et al. (2005) similarly concluded that for growing areas other than the very drought-prone environments, barley 'ideotypes' should have minimal genotype by environment interaction, and should show both high yield potential and yield stability. CIMMYT's experience with maize shows that genetic correlations between yield in stressed and unstressed environments remain positive but tend to non-significance when stress reduces yields by about 50%, probably due to radical changes in relative allocation of assimilates to male versus female reproductive structures (Edmeades et al., 2000).

Therefore, an important outcome of breeding for yield potential is higher attainable yields under moderate abiotic stresses. One strategy shown to be successful in production of wheat germplasm better adapted to intermittent drought stress in northwest Mexico is selection of segregating generations under alternating high yield potential and drought-stress conditions (Kirigwi et al., 2004). In many farms in drought environments because of the overriding impact of low rainfall, growers make most of their profit in a few ‘good’ seasons. Hayman (2007), for example, estimated that in a series of 18 seasons, the business profit for grain growers in Western Australia ranged from slight loss (about $10K) to over $200K profit. The top five seasons accounted for 52% of the series profit. Therefore, in addition to the biological considerations, there is a strong economic justification to maintain the capacity to capture the benefits of good seasons, even in the dry environments.

3. PHYSIOLOGICAL BASIS OF GENETIC GAINS IN YIELD POTENTIAL

3.1. The contribution of ‘crop design’ to breeding

To date improvement of yield potential has been mainly empirically based on yield *per se* (Evans, 1993). However, yield has a relatively low heritability and this approach may not be the most efficient as there is a high genotype × environment interaction (Jackson et al., 1996; Slafer, 2003). There is therefore a strong case that understanding of traits at the physiological level may help to identify indirect selection criteria that could be applied to accelerate breeding progress. Such an integrated approach may complement empirical breeding and hasten progress (Araus et al., 2002; Reynolds and Borlaug, 2006). Furthermore, yield can only be precisely measured in later progeny populations of core breeding programs, so measurement of physiological traits in intermediate generations, before lines are purified, offers the possibility of selecting physiologically adapted material before yield testing begins.

In order to combine effectively desirable traits in new cultivars, breeders must understand their genetic control, and ideally have markers to facilitate their selection amongst progeny of targeted crosses. Most yield-related traits are under multi-gene control and their genetic analysis has to date normally been addressed by the application of molecular-marker approaches to detect quantitative trait loci (QTLs). The rational application of QTLs in breeding programs and their introgression into elite material will depend on an improved understanding of relationships between yield-enhancing traits and their expression at the crop level. This will be critical too in guiding the selection of synergistic parental genotypes in breeding programs for grain crops. The application of physiological principles to accelerate breeding progress has also been demonstrated outside grain crops, for example the transformation of the potato plant based on fundamental physiological principles of plant-to-plant relationships in crop populations (Boccalandro et al., 2003).

3.2. Changes in traits with genetic gains in yield potential

3.2.1. Changes in biomass and grain partitioning

During the Green Revolution of the 1960s and 1970s the first semi-dwarf cultivars were released in the small-grain cereals (Borlaug, 1968; Peng and Khush, 2003). The yield increases were associated with reduction in stature and lodging, and hence a greater responsiveness to high fertility. In the absence of lodging, yield was also higher due to reduced competition from the growing stem, resulting in greater ear or panicle growth, more grains per unit area and higher harvest index (HI) (Riggs et al., 1981; Gale and Youseffian, 1985; Peng et al., 2000). Improved grain number was associated mainly with more grains per spikelet in wheat and rice (Fischer and Stockman, 1986; Peng et al., 2000) and more ears per unit area in barley (Abeledo et al., 2002). Since the Green Revolution, yield potential in small-grain cereals has continued to increase mainly due to improvements in HI (Reynolds et al., 1999; Abeledo et al., 2002). Future yield gains in modern semi-dwarfs through HI is less promising, since HI of modern cultivars is considered already close to theoretical maxima (Mann, 1999; Austin, 1980; Evans and Fischer, 1999). Austin (1980) predicted a maximum HI of 0.62 in winter wheat based on an extrapolation from the mean value (0.49) observed for the four most modern winter wheat cultivars characterised by Austin et al. (1980) in the UK. They assumed that (i) there is no change in shoot dry matter (DM), (ii) leaf lamina (physiological) and chaff (structural) DM cannot be decreased, (iii) stem and leaf sheath DM can be reduced by 50% and (iv) chaff DM can be increased *pro rata* to accommodate extra grain. In Table 1 we present results for modern UK winter wheat cultivars released between 1985 and 1996 together with Austin's observed and theoretical values. A HI of 0.56 has already been achieved for the modern UK winter wheat Consort, with progress based entirely on reduced partitioning to stem and sheath DM from a value of 0.30 observed by Austin et al. (1980) to 0.25 for Consort. Austin (1980) assumed that chaff must increase *pro rata* to grain with breeding, and broadly chaff dry weight as a proportion of grain dry weight at harvest appears to have been maintained at about 0.20 with breeding in the last decades in the UK (Table 1).

A feasible strategy for future HI improvement is to continue reducing the structural stem DM as a competing sink to the ear, although only small further increases in HI may be possible through this avenue. How much more can be achieved will depend partly on the constraints imposed by the need to maintain adequate lodging resistance. In summary, raising yield potential in small-grain cereals will mainly have to involve an increase in biomass production in future years.

In wheat, most investigations of genetic yield progress under high-yielding conditions have historically failed to show positive correlation between biomass and yield (e.g. Waddington et al., 1986; Austin et al., 1989; Slafer et al., 1994; Brancourt-Hulmel et al., 2003), whereas a few more recent studies have demonstrated greater biomass for more modern cultivars (e.g. Donmez et al., 2001; Shearman et al., 2005). Biomass increases have been found too with introductions of alien genes into wheat germplasm, for example the 1BL.1RS wheat-rye translocation in Mexico and the Great Plains (Carver and Rayburn, 1994; Villareal et al., 1998) and the 7DL.7Ag wheat-*Agropyron elongatum* translocation in Mexico (Reynolds et al., 2001a). In other small-grain cereals, genetic yield progress in the twentieth century was principally a result of higher HI, but again yield gains in the last decades were associated with biomass in rice (Song et al., 1990; Yamauchi, 1994; Peng et al., 2000) and barley (Boukerrou and Rasmusson, 1990). The yield advantage of new 'super rice' hybrid cultivars developed in China was attributed to a substantial increase of biomass rather than HI (Cheng et al., 2007; Yang et al., 2007).

Table 1 Comparison of Aboveground Dry Matter (AGDM) Production and Dry Matter Partitioning at Harvest in Sets of Winter Wheat Cultivars in the UK with Values of Austin (1980) Corresponding to a Theoretical Maximum HI of 0.62

Crop component	Austin et al. (1980) (Four Most Modern Cultivars[a])		Austin (1980) (Theoretical Maximum HI)		Shearman et al. (2005) (Four Most Modern Cultivars[b])		Consort[c] Herefordshire, UK mean 1996/1997 and 1997/1998	
	$g m^{-2}$	%	$g m^{-2}$	%	$g m^{-2}$	%	$g m^{-2}$	%
Grain	707	49	895	62	888	51	1103	56
Chaff	143	10	181	13	171	10	195	10
Leaf lamina	139	10	139	10	151	9	183	9
Stem+sheath	453	31	226	15	536	30	490	25
AGDM	1442	–	1441	–	1746	–	1971	–

[a] *730/3637, 989/10, Armada, Benoist 10483.*
[b] *Riband, Haven, Brigadier, Rialto.*
[c] *Released 1996.*

In maize and soybean, genetic gains in yield potential in the USA have historically resulted from increased biomass, rather than HI, associated with increased assimilate supply during the grain-filling period (Crosbie, 1982; Tollenaar, 1991; Tollenaar and Aguilera, 1992; Hu et al., 1998; Specht et al., 1999). Modern maize hybrids are strongly population-dependent as their maximum grain yield is achieved only under a narrow spectrum of high plant populations, followed by adverse effects on hybrids' productivity and stability. Improved yield in maize hybrids is therefore mainly due to increased optimum plant population rather than greater biomass and grain yield per plant (Tollenaar, 1991; Pagano et al., 2007). At higher plant populations, there is a risk that reduced grain yield may result from the increased pollen-to-silking interval and the consequent reduction in grain set. As a result, maize breeding generally seeks hybrids that combine population-tolerance and improved yield potential per plant, so that a wider range of optimum plant populations ensure both high productivity and stable performance. Leaf orientation in maize responds to the red (R) to far-red (FR) ratio of light and is part of a strategy that minimises mutual shading among plants (Maddonni et al., 2002). Maize plants receive higher R:FR ratios from the inter-row spaces than within the rows. Maddonni et al. (2002) showed that the leaves of the hybrid DK696 turned away from the low R:FR ratio signals within the rows, whereas those of the hybrid Exp980 remained unaffected. These findings indicate that phytochrome-mediated responses to low R:FR could be manipulated to raise biomass and crop yield in maize by minimising mutual shading between plants within rows and maximising interception between rows. The possibility that reduced photomorphogenic responses could increase field crop yield has also been suggested in potato (*Solanum tuberosum*). Boccalandro et al. (2003) reported that ectopic expression of the Arabidopsis *PHYB* (phytochrome B) gene, a photoreceptor involved in detecting R:FR ratio associated with plant density, increased tuber yield in field-grown transgenic potato crops. Results suggested that enhanced *PHYB* expression could be used in breeding programs to shift optimum planting densities to higher levels.

3.2.2. Changes in grain number associated with yield gains

Grain yield improvement is highly associated with grain number per unit area in wheat (Canevara et al., 1994; Sayre et al., 1997; Brancourt-Hulmel et al., 2003; Shearman et al., 2005; Peltonen-Sainio et al., 2007), barley (Riggs et al., 1981; Bulman et al., 1993; Jedel and Helm, 1994; Martinello et al., 1987; Boukerrou and Rasmusson, 1990; Peltonen-Sainio et al., 2007), oats (Peltonen-Sainio et al., 2007), rice (Horie et al., 1997; Peng et al., 2000), maize (Andrade et al., 1999; Echarte et al., 2000; Tollenaar et al., 2000), soybean (Egli, 1998) and sunflower (López Pereira et al., 1999). In wheat, current evidence suggests grain sink strength remains a critical yield-limiting factor (Fischer, 1985; Slafer and Savin, 1994; Abbate et al., 1995; Miralles et al., 2000; Borrás et al., 2004; Miralles and Slafer, 2007) and that improving the balance between source and sink is a promising approach for raising yield, biomass and radiation-use efficiency (biomass per unit radiation interception; RUE) (Reynolds et al., 2001a, 2005). In maize hybrids, Ding et al. (2007) found that, although photosynthetic efficiency did not directly cause genetic increases in grain number in the pre-anthesis period, enhanced photosynthetic efficiency in the post-anthesis period as a result of improved grain sink strength was positively associated with yield gains. Yield gains associated with new super 'hybrid' rice in China were also associated with an enhanced post-anthesis rate of flag-leaf photosynthesis (Wang et al., 2002).

The period before the start of the grain-filling is very important for the determination of grain number. Despite some uncertainty about the actual beginning and the end of this critical period, it is generally accepted that it covers the period from late stem elongation to early post-flowering in wheat (Fischer, 1985; Savin and Slafer, 1991; Slafer et al., 1999), from early stem elongation to anthesis in barley (Bingham et al., 2007a), of the 14 days prior to full heading in rice (Takai et al., 2006), from −230 to 100°Cd from silking (the active ear elongation period) in maize (Otegui and Bonhomme, 1998), from initial bloom to the beginning of seed filling in soybean (Egli, 1998) and from floral initiation (~30 days before anthesis) to about 20 days after first anthesis in sunflower (Cantagallo et al., 1997). Chapter 12 (Section 5) discusses the concept of critical period of grain number determination in wheat and soybean, and the opportunities for its genetic manipulation. Chapter 16 applies the concept of critical period to quality traits. Greater ear or panicle DM growth during the critical period is associated well with higher grain number in wheat

(Calderini et al., 1997; Reynolds et al., 2001a; Fischer, 2007), rice (Tanaka, 1983; Takai et al., 2006), maize (Simmons and Jones, 1985; Tollenaar et al., 1992; Aluko and Fischer, 1988; Otegui and Bonhomme, 1998; Andrade et al., 1999), sorghum (Vanderlip et al., 1984) and sunflower (Cantagallo et al., 1997). In maize, a feature of the relationship between grain number and plant growth rate is a significant plant growth rate threshold for grain set which reflects an abrupt decrease in DM partitioning to the ear when resource per plant is low (Edmeades and Daynard, 1979; Tollenaar et al., 1992; Andrade et al., 1999). The threshold may be lower for the newer compared to the older hybrids (Echarte and Andrade, 2003).

Genetic gains in ear or panicle biomass at anthesis have been historically achieved in small-grain cereals through enhanced partitioning of DM to these organs in the critical period during stem elongation. There is some evidence that RUE may now be directly contributing to gains in ear or panicle DM accumulation as well during the critical period (Horie et al., 2003; Shearman et al., 2005; Takai et al., 2006). In this situation, increased RUE during the critical pre-anthesis period may directly cause increases in grain number, which then in turn may enhance RUE in the post-anthesis period as a result of improved grain sink strength. In rice, Horie et al. (2003) observed a significant positive relationship between crop growth rate (biomass per unit area per day; CGR) during the period from two weeks before heading to final heading and grain yield, and stressed the importance of higher CGR on the basis of spikelet formation. Takai et al. (2006) examining eight genotypes also found a positive association between CGR from 14 days before heading to heading and grain yield in rice; genotypes having higher CGR produced more spikelets per square metre. Interestingly, the large genotypic variability in CGR during the 14-day period was mainly derived from RUE. Likewise a positive association between RUE during the period from the onset of stem elongation to flowering and each of grains per square metre and yield was observed in winter wheat amongst a set of cultivars released from 1972 and 1995 in the UK (Shearman et al., 2005). Chapter 7 reviews environmental and crop factors influencing RUE in general, and Section 5.1.2 explores further the possible physiological mechanisms by which breeding may enhance RUE during the critical period.

3.2.3. Changes in post-anthesis assimilate supply associated with yield gains

Grain crops are in general little limited by the source during grain filling in the absence of terminal stresses (Dreccer et al., 1997; Borrás et al., 2004; Calderini et al., 2006). In these crop species, it would only be anticipated that delayed canopy senescence during grain filling could contribute to gains in yield potential in crops which are not sink limited, for example by boosting source to match improvements in grain sink size so that crops avoid becoming source-limited. There is some evidence that maize may fall into this category, since new maize hybrids in the USA produce more biomass because they remain photosynthetically active longer during mid-to-late grain filling (Fakorede and Mock, 1980; Duvick, 1992; Tollenaar and Aguilera, 1992; Rajcan and Tollenaar, 1999). Yield gains associated with super 'hybrid' rice have also been attributed in part to slow leaf senescence (Wang et al., 2002). In experiments on sets of historical cultivars in wheat and barley senescence variables have only rarely been assessed. In wheat, leaf area duration during grain filling was not different between cultivars released at different eras in Argentina (Calderini et al., 1997). Although Shearman (2001) found differences in senescence patterns amongst wheat cultivars released at different eras in the UK, these were not correlated with yield.

The stay-green trait (i.e. delayed senescence associated with extended photosynthesis) has been studied principally to date as a trait for increasing abiotic stress tolerance rather than yield potential. Studies offer some valuable insights into the physiological and genetic mechanisms underlying stay-green. Stay-green is important as an indicator of heat tolerance in wheat (Reynolds et al., 2001b) and drought tolerance in sorghum (Borrell et al., 2000) and wheat (Verma et al., 2004). In sorghum, stay-green is related to maintenance of N uptake after anthesis, suggesting some complexity in the trait that might result from a combination of root and shoot traits. Four stay-green mutants were identified in durum wheat (*Triticum turgidum* spp. turgidum) (Spano et al., 2003), which showed an extended capacity to photosynthesise during grain filling and increased grain weight per plant in glasshouse experiments. In the wild emmer wheat ancestor (*T. turgidum* ssp. dicoccoides), a transcription factor (NAM-B1) accelerates senescence and increases nutrient remobilisation from leaves to developing grains (Uauy et al., 2006). Although the reintroduction of the functional allele would not prolong canopy survival, the gene provides an entry point to characterise the genes regulating senescence.

In many grain crops, assimilate from current photosynthesis during grain filling is supplemented by remobilisation of assimilate reserves from vegetative tissues. Thus, by flowering, reserves of non-structural carbohydrate (fructans and starches, NSC) have accumulated in vegetative organs (stems and leaf sheaths) of cereals. Maximal amounts are amassed in wheat and barley shortly after flowering (Austin et al., 1977; Ehdaie et al., 2006), in rice at around heading (Samonte et al., 2001) and in maize at around silking (Kiniry and Otegui, 2000). In sunflower, accumulation of NSC peaks before or shortly after flowering in stems, and normally well into grain filling in receptacles (Hall et al., 1989; López Pereira et al., 2008). Genetic variation in the percentage of NSC in the stem at around anthesis is reported from 5 to 43% in wheat (Foulkes et al., 1998; Reynolds et al., 2007; Ehdaie et al., 2006; Ruuska et al., 2006), from 20 to 35% in barley (Austin et al., 1977; Gay et al., 1999) and from 15 to 20% in maize (Williams et al., 1968; Campbell and Hulme, 1970; Swank et al., 1982; Jones and Simmonds, 1983). Differences may arise because of differences in carbon availability or the available capacity for carbon reserve storage being different between genotypes. NSCs disappearing from the stems are important contributors to grain growth under severe drought in wheat, barley, rice and sunflower (Blum, 1998; Hall et al., 1989; Yang et al., 2000). In maize, Kiniry and Otegui (2000) suggested that there was little benefit from selecting cultivars with greater amounts of stem NSC at anthesis, and that much of the NSC was used in maintenance. This was supported by a study with selections having different amounts of stem NSC at anthesis where there was no evidence that reduced NSC per plant was associated with reduced drought tolerance during grain filling (Edmeades and Lafitte, 1993). However, sucrose which continues to accumulate after stem elongation in maize can be remobilized to support grain development during grain filling under drought (Westgate, 1994).

Under favourable post-anthesis conditions, the value of stem NSC at anthesis for grain yield differs according to crops, species and environment, but NSC can be a major contributor to yield in modern cultivars of wheat, barley and rice. Thus, in winter wheat positive correlations between stem NSC content and grain yield were observed amongst cultivars released at different eras (Shearman et al., 2005; Foulkes et al., 2006, 2007a), and stem NSC was estimated to contribute 28% of yield (Foulkes et al., 2002). Stem NSC has been estimated to contribute about 20% of yield in UK winter barley (Gay et al., 1999) and in rice from 24 to 27% (Cock and Yoshida, 1972) and 20 to 30% (Murthy, 1976). Pre-anthesis NSC contributed about 15–20% of the total carbon uptake of sunflower grain in irrigated crops (Hall et al., 1989, 1990). However, there is a need to determine the optimum NSC concentration that produces the highest yield in each of wheat, barley and rice, because the presence of NSC beyond a specific limit may indicate reduced allocation to the ear or to structural vegetative organs potentially associated with increased lodging risk or premature senescence of leaves. The potential optimisation of stem NSC and the use of this candidate trait in future breeding are discussed further in Section 5.1.3. A summary of the physiological traits discussed above relevant for yield potential is provided in Table 2.

4. GENETIC BASIS OF YIELD POTENTIAL AND IMPLICATIONS FOR BREEDING

4.1. Gains associated with the broadening of genetic background

It has been suggested that plant breeding reduces genetic diversity in elite cultivars potentially jeopardising the continued ability to improve crops (Section 5 in Chapter 14). Considering the transition from domestication of cereals to cultivation of landraces to modern breeding, there is evidence to support a narrowing

Table 2 Physiological Traits Relevant for Yield Potential

Trait	Crop	Effects Relevant for Yield	References
Plant height	Wheat, barley, rice	Reduced height decreases competition from stem, increased ear or panicle DM and grain number; improved lodging resistance	Fischer and Stockman (1986), Austin et al. (1989), Peng et al. (2000), Abeledo et al. (2002)
Optimum plant population	Maize	Increased yield and biomass per plant and per unit area; yield stability	Tollenaar (1991), Pagano et al. (2007)
Timing of phenological phases	Wheat	Increased duration of stem elongation as proportion of thermal time to flowering increases ear DM, increased grain number	Slafer et al. (2005)
Anthesis-silking interval	Maize	Grain set in subapical ear depends on synchronous silking and pollination of both ear shoots. Reduction in grain set when pollination interval between early- and late-appearing silks in the apical ear is decreased	Cárcova and Otegui (2001), Cárcova (2003)
Crop growth during critical period before grain filling	Wheat, barley, rice, maize, sorghum, sunflower	Infructescence DM growth during the critical period positively associated with grain number	Tanaka (1983), Vanderlip et al. (1984), Simmons and Jones (1985), Tollenaar et al. (1992), Calderini et al. (1997), Cantagallo et al. (1997), Aluko and Fischer (1998), Otegui and Bonhomme (1998), Andrade et al. (1999), Reynolds et al. (2001a), Fischer (2007)
Radiation-use efficiency pre-anthesis	Wheat, rice	Increase ear or panicle DM, increased grain number	Horie et al. (2003), Shearman et al. (2005)
Leaf response to R/FR ratio	Maize	Minimise mutual shading	Maddonni et al. (2002)
Leaf specific weight	Wheat, rice	Increased leaf specific weight leads to higher A_{max}	Murata (1961), Khan and Tsunoda (1970)
Crop growth rate pre-anthesis	Rice	Increase panicle DM, increased grain number	Horie et al. (2003), Takai et al. (2006)
Leaf posture	Wheat, barley	Erect leaf posture reduces light saturation of upper leaves	Angus et al. (1972), Evans (1983), Araus et al. (1993)
Leaf photosynthetic rate post-anthesis	Maize, wheat, rice	Enhanced photosynthetic rate in the post-anthesis period as a result of increased sink strength; maintenance of grain weight at high grain number per unit area	Reynolds et al. (2001a), Wang et al. (2002), Reynolds et al. (2005), Ding et al. (2007)
Stem non-structural carbohydrate	Wheat, rice, barley	Stem NSC positively associated with grain yield under favourable post-anthesis conditions	Gay et al. (1999), Horie et al. (2003), Shearman et al. (2005)
Stay-green	Maize, durum wheat	Delayed canopy senescence associated with increased leaf photosynthesis or yield under favourable post-anthesis conditions	Tollenaar and Aguilera (1992), Rajcan and Tollenaar (1999), Spano et al. (2003)

of the genetic base in wheat (Reif et al., 2005) and rice (Sun et al., 2001; Sundaram et al., 2007). The main maize hybrids cultivated in the world involve a restricted number of key inbred lines. Therefore, genetic diversity of those cultivars is probably limited, in comparison to the large genetic diversity available in gene banks. Nevertheless, plant breeding does not inevitably lead to a loss of genetic diversity. For example, Donini et al. (2000) detected no significant narrowing of genetic diversity among winter wheat cultivars released in UK between 1934 and 1994. Similar results were presented by Manifesto et al. (2001) working on 105 Argentinean wheat cultivars released between 1932 and 1995. Maccaferri et al. (2003) even demonstrated that the level of genetic diversity present in modern cultivars of durum wheat was increasing over time. A study that addressed different means of estimating genetic diversity in wheat indicated that as modern plant breeding matures, it tends to increase rather than decreases the genetic diversity of new germplasm, good examples being proliferation of the number of landraces that can be found in the pedigrees of modern cultivars as well as evidence from molecular diversity studies (Smale et al., 2002).

Assuming that overall some reduction in diversity has occurred due to intensive selection in plant breeding, one strategy to counterbalance this would be by the introgression of novel germplasm. This has been facilitated by the advent of molecular breeding technologies, to transfer genes from wild wheat, rice and barley species together with the availability of a wide range of germplasm in gene banks, for example at CIMMYT for wheat and IRRI for rice. The most widespread development and use of synthetics is currently in wheat. Under optimal conditions, synthetic hexaploid lines (*Triticum durum* × *T. tauschii*) have been associated with high thousand grain weight (Calderini and Reynolds, 2000) and high photosynthetic rate (Blanco et al., 2000). Consequently, these materials represent useful sources for broadening the genetic base of elite wheat breeding germplasm. A new generation of wheat cultivars generated using synthetic wheat produced by intercrosses between synthetic derivatives and common wheat is now available at CIMMYT. Over the last 10 years, the proportion of synthetic wheat derivatives to total number of wheat lines that CIMMYT has distributed to rainfed wheat improvement programs around the world has increased from approximately 10 to 40%. Evidence is building from CIMMYT's global wheat yield trials that synthetic derivatives can contribute to yield potential in well-watered, highly productive environments (Ogbonnaya et al., 2007). In a comparison of synthetic-derived wheat with recurrent parents, final biomass and grain weight were larger under both irrigated and moisture-stressed conditions (Reynolds et al., 2007). Future work should aim to dissect the genetic and physiological basis of the traits to allow their rapid introgression into breeding programs worldwide.

4.2. Hybrid breeding versus inbreeding

Heterosis (or hybrid vigour) is a major reason for the success of the maize industry as well as for recent advances in yield potential in rice. Switching from inbreds to hybrids provides a one-time boost to primary production and yield potential of about 10% (Cassman, 1999) to over 20% (López Pereira et al., 1999). There is relatively little information on the physiological basis of this phenomenon. Development of a reliable method for predicting hybrid performance without testing hundreds of thousands of single crosses would therefore be of great value. This has been the goal of numerous studies using combinations of marker and phenotypic data, particularly in maize. This subject has been extensively reviewed and will not be discussed in detail here (see review by Stuber et al., 1999). In summary, results from these studies have demonstrated that quantitative traits such as yield can be improved by using genotypic (marker) data, and theoretical and analytical investigations have shown that the maximum rate of improvement may be obtained by integrating both phenotype and marker data. In wheat, hybrid production is often mentioned as an alternative. The yield advantage of hybrid wheat has been estimated to be 10–13% in the USA (Bruns and Peterson, 1998) and 5–12% in Europe (Eavis et al., 1996). The yield advantage is attributed in part to better temporal and spatial stability. Although successful examples of the development of hybrid wheat can be found regarding both yield and economy, for example Trigomax in Argentina (Calderini et al., 1995), hybrid wheat production may not be economically feasible in many cases due to higher seed costs and because heterosis may in theory be fixed in polyploid plants, giving hybrids no advantage over inbred lines.

5. BARRIERS TO AND OPPORTUNITIES FOR FUTURE GENETIC GAINS IN YIELD POTENTIAL

5.1. Strategies to increase grain number per unit area: framework

The number of grains per unit land area in grain crops is strongly associated with the DM accumulated in the ear or panicle at around anthesis (Section 3.2.2). The following model can be broadly applied in small-grain cereals to describe quantitatively the physiological basis of grain number.

$$\mathrm{GN} = \mathrm{RAD} \times \mathrm{FI} \times \mathrm{RUE} \times \mathrm{EP} \times \mathrm{GEDM} \tag{1}$$

where GN is the number of grains per square metre, RAD the incident radiation in the period from onset of stem elongation (GS31) to anthesis (GS61) ($\mathrm{MJ\,m^{-2}}$), FI the fraction of RAD intercepted, RUE the radiation-use efficiency in the period from onset of stem elongation (GS31) to anthesis (GS61) ($\mathrm{g\,MJ^{-1}}$), EP the ear partitioning coefficient (fraction of shoot DM accumulated from GS31 to GS61 partitioned to the ear or panicle) and GEDM the grains to ear or panicle DM ratio at anthesis (grains per gram).

Increasing CGR during the critical phase of stem elongation is probably the main mechanism by which most breeding programs may impact on yield of grain crops in future years. We will now consider the prospects for manipulating the processes in Eq. 1 underlying grain number per unit area through future breeding as well as the likely interactions affecting their joint optimisation. The model relates most directly to small-grain cereals, although the physiological principles involved will also generally apply to other grain crops where the critical phase determining grain number extends partly beyond anthesis, for example maize.

5.1.1. Increasing fractional radiation interception

Increasing the thermal duration of the stem-elongation period is one logical strategy to increase radiation interception during this period. Ways to manipulate patterns of development to achieve this, for example manipulating photoperiod responses affected by photoperiod-sensitivity genes, are discussed in Chapter 12, and are therefore not discussed further here. Increasing radiation interception during the stem-elongation period could also be achieved without changing the relative durations of phenophases by increasing the average fractional interception during the period.

For 95% radiation interception assuming an extinction coefficient (K) of 0.5, a green area index (GAI) of 6 is required.

$$K = -\ln\left(\frac{I/I_{\mathrm{o}}}{L}\right) \tag{2}$$

where I_{o} is the incident radiation and I is the amount of radiation transmitted below a GAI value of L.

At anthesis, modern cultivars of rice (Mitchell et al., 1998), wheat (Gaju, 2007; Whaley et al., 2000), barley (Bingham et al., 2007a) and maize (Ogola et al., 2002) all produce canopies with GAI in the region of 6 hence achieve full interception at this stage. So the only way to increase FI is by increasing fractional interception at the start of the stem-elongation phase when less than full interception occurs. A mathematical function for crop growth developed by Goudriaan and Monteith (1990) included the concept of the time 'lost' for growth while the canopy is closing, which is proportional to the logarithm of the initial fractional radiation interception (Eq. 3).

$$t_{\mathrm{b}} = -\ln\left(\frac{\mathrm{FI_o}/(1-\mathrm{FI_o})}{R_{\mathrm{m}}}\right) \tag{3}$$

where t_b is the time 'lost' for growth while the canopy is closing, FI_o the initial fractional light interception and R_m the initial maximum relative growth rate.

Typically fractional interception at the start of stem elongation is in the region of 0.6–0.7 in wheat and barley (Gaju, 2007; Whaley et al., 2000; Shearman et al., 2005) and 0.4–0.6 in rice (Mitchell et al., 1998), so only marginal improvements in FI_o and time 'lost' for growth (hence 'lost' biomass) seem possible. Physiological avenues worth investigating may include a larger specific leaf area (leaf area per mass) and/or more prostrate non-culm leaves. Phenotypic differences in specific leaf area in temperate cereals have been associated with embryo size (López-Castañeda et al., 1996) and genetic variation in embryo size could be exploited to achieve earlier canopy closure (Rebetzke et al., 1996; Rebetzke and Richards, 1999). The PAR (photosynthetically active radiation) extinction coefficient, K_{PAR}, which is mainly influenced by leaf angle, for modern cultivars is approximately 0.65 for maize (Varlet-Grancher et al., 1989) and 0.55 for wheat, barley and rice (Abbate et al., 1998; Mitchell et al., 1998; Bingham et al., 2007a). These values are associated with semi-erect to erect leaf angles which help to reduce light saturation in the upper canopy leaves hence boost RUE; and a shift back to higher values of K_{PAR} seems unlikely to be desirable overall due to the trade-off with RUE. Studies on the seasonal dynamics of K generally showed no change over the stem-elongation period, for example in maize (Flenet et al., 1996) and wheat (Thorne et al., 1988). So breeding for more prostrate leaves during early vegetative growth and more upright leaves during later vegetative growth although desirable may be difficult to achieve in practice. A shorter phyllochron (the thermal duration between successive emerging leaves) would favour earlier canopy closure through more rapid leaf emergence and/or tiller production, although some care would be needed here as increased production of non-grain-bearing tillers is likely detrimental to yield potential (Berry et al., 2003). In summary, although gains in grain number per unit area may be possible through increasing the average fractional interception during stem elongation, they seem likely to be small.

5.1.2. Increasing radiation-use efficiency

If radiation interception and HI are approaching an upper limit, yield ultimately must be improved mainly by increasing RUE. Currently RUE_{PAR} in modern cultivars are in the region of $2.2\,g\,MJ^{-1}$ for rice, $2.5\,g\,MJ^{-1}$ for wheat and barley and $3.3\,g\,MJ^{-1}$ for maize (Mitchell et al., 1998; Shearman et al., 2005; Bingham et al., 2007a). The higher RUE for maize is associated with C_4 metabolism, and the lower value for rice than for wheat is thought to be associated with higher losses from photorespiration (Mitchell et al., 1998). Chapter 7 discusses physiological and environmental drivers of RUE in detail.

There are three main potential avenues to increase RUE in crops: (i) increase leaf photosynthetic rate, (ii) increase canopy net photosynthetic rate due to a more uniform distribution of incident light across the leaf canopy and (iii) decrease respiration.

5.1.2.1. Increase leaf photosynthetic rate

The enhanced growth of C_3 crops observed at elevated CO_2, without any decrease in leaf area, shows the potential for increases in photosynthesis through manipulating leaf photosynthesis, for example improved grain yield observed with elevated CO_2 in irrigated wheat (Pinter et al., 1996) and lowland paddy rice (Baker et al., 1990). With C_4 crops such as maize it may be more difficult to increase photosynthesis; elevated CO_2 has not generally resulted in large increases in leaf photosynthesis. The dependence of leaf photosynthesis on light intensity can be generally described by a rectangular hyperbola. The minimum number of parameters is two: the quantum efficiency in low light intensity (ϵ) and the light-saturated rate of photosynthesis (A_{max}). Despite significant differences in A_{max}, there is little if any genetic variation in quantum efficiency at low light in unstressed leaves reported in grain crops. In wheat, a positive correlation between A_{max} and crop yield in field investigations was not found by Austin et al. (1989), Lawlor (1993) and Richards (2000), whereas a positive correlation was observed for measurements of A_{max} during grain filling and yield by Gutierrez-Rodriguez et al. (2000). In maize, Crosbie et al. (1981) raised A_{max} by 8% after five generations of selection, and in soybean Secor et al. (1982) raised A_{max} by about 10% compared with a population selected for low photosynthesis. However, in both cases a positive correlation was not found between photosynthesis and yield. One problem is that the response curve between A_{max} and RUE flattens at high rates of photosynthesis, mainly because individual leaves normally operate well below light saturation in the canopy and due to the need to account for dark respiration (Reynolds et al., 2000). There are also trade-offs between leaf photosynthetic rate and leaf size, for example higher A_{max} in diploid wheat species compared to hexaploid bread wheat is associated with smaller leaves (Austin et al., 1982). A benefit from high A_{max} may only be significant if the climate in which the crop is grown is relatively sunny. Chapter 9 (Box 1) outlines trade-offs associated with improvement in photosynthesis-related traits, and discusses the link between photosynthesis and yield from an evolutionary perspective.

There are reports of both positive and neutral associations between A_{max} and specific leaf weight (mass per area). Positive associations were observed in wheat (Khan and Tsunoda, 1970) and rice (Murata, 1961), whereas no association was found in wheat (Dunstone et al., 1973; Fischer et al., 1981) and maize (Crosbie et al., 1978). Fischer (2001) suggested the heritability of specific leaf weight was likely to be moderate to low in wheat. It is encouraging that in wheat genetic progress in RUE was positively associated with specific leaf weight in the UK in the last decades (Shearman et al., 2005). So this trait may merit further investigation for improving RUE. Since leaf size and thickness are associated with anatomical structure, there may be merit in investigating the cellular basis of differences in leaf specific weight including the number of chloroplasts per cell. However, sacrificing leaf size to gain a higher rate of leaf photosynthesis in future breeding strategies must be considered carefully.

5.1.2.2. Increase canopy photosynthesis via canopy architecture

Altering canopy architecture or DM partitioning (leaves, stems and ears) to raise RUE could be easier than altering single metabolic processes such as leaf photosynthesis. For large crop canopies, RUE is potentially higher with more erect leaves, associated with reduced light saturation of the upper leaves (Evans, 1973). This is supported by findings for a trend for lower canopy temperature with more erect leaves in pairs of wheat lines differing in leaf angle measured 10 days after anthesis under irrigation in northwest Mexico by Araus et al. (1993). However, most modern cereals cultivars worldwide already have semi-erect or erect flag leaves. So there is likely limited scope for improvement of RUE via this route. Altering DM partitioning to minimise any sink limitation in the extending stem internodes could offer an alternative avenue to raise RUE during stem elongation. There is a large body of evidence that greater sink strength may support higher photosynthetic rates via feedback regulation. Thus, RUE was observed to increase during pre-anthesis shading of field plots of winter wheat (Beed et al., 2007), and post-anthesis RUE increased in wheat in response to opening rows in the booting-to-ear emergence phase to increase light interception, ear growth and grain number (Reynolds et al., 2005). So, strategies to minimise sink limitation and to optimise source-sink balance, particularly during the latter stages of stem elongation, could potentially boost ear biomass and grain number in future breeding.

5.1.2.3. Decrease respiration

At the metabolic level, there are several avenues to increase photosynthetic efficiency. These include (i) relaxing the photo-protected state more rapidly, (ii) reducing photorespiration through rubisco with decreased oxygenase activity, (iii) introducing higher catalytic rate forms of rubisco and (iv) introducing C_4 photochemistry into C_3 plants (see recent reviews by Reynolds et al., 2000; Parry et al., 2002; Long et al., 2006). Largest potential improvements are available from reduced photorespiration (≈30%), with improvement from other mechanisms estimated to be in the range 15–22% (Long et al., 2006). There is considerable interest in decreasing the wasteful oxygenase activity of rubisco. In spite of the lack of any formal enzyme binding site for the gaseous substrates, rubisco has an inherent ability to discriminate between CO_2 and O_2 as described by the specificity factor. Attempts to select for specificity and low photorespiration in crop plants have historically met with little success (e.g. Evans, 1983). However, thermophilic red algae, for example *Galderia partita*, have rubisco which is up to three times more efficient than that in C_3 cereals due to greater specificity for CO_2 (Uemura et al., 1997). If rubisco in wheat plants had the specificity factor of that of red alga, the leaf A_{max} would be increased by about 20% (Austin, 1999). On the other hand, red algal rubisco has a lower reaction rate than the rubisco in terrestrial plants, so there could be a trade-off between specificity and reaction rate. Prospects of boosting RUE of crop plants by introducing rubisco with greater specificity for CO_2 may therefore depend on addressing this apparent trade-off (Box 1 in Chapter 9). It should be noted that plants selected for superior performance on the basis of superior leaf photosynthetic rate in a high-radiation environment would not necessarily be superior in more temperate, lower-radiation environments. This would be the case if differences in leaf photosynthesis were not apparent at relatively low light intensities. Alternatively, if higher leaf photosynthetic rate reflects a higher quantum efficiency as a result of less carbon loss in photorespiration, and these effects were consistent at lower temperatures, then higher leaf photosynthesis should result in benefits in temperate environments as well. For the most rapid gains in RUE, an additional issue is to define leaf photosynthetic traits in terms that are relevant to the canopy so that their impact on canopy photosynthetic rate may be quantified. Traits that scale to the canopy and promote high rates of canopy photosynthesis should be prioritised in future physiological investigations applied to breeding, and integrative measurements such as leaf cooling exploited in the assessment of photosynthetic traits at the crop level (see Section 6).

Early attempts to introduce C_4 genes into C_3 plants failed (Hatch et al., 1972), but elaborate biotechnological approaches are now seeking to exploit the greater carbon efficiency found in C_4 compared to C_3 plants. The introduction of genes for all of the steps of C_4 metabolism into single cells within leaves of C_3 plants has been attempted by several groups (Leegood, 2002). For example, in rice, non-functioning silent C_4 genes have been replaced with functioning equivalents from maize and PEPC was highly expressed in the transformed plants and oxygenation was cut by a third (Ku et al., 2000; Matsuoka et al., 2000). Even if all of the steps are introduced and are functional in the leaves of C_3 plants, improved efficiency seems unlikely to be achieved without additional structural changes (Evans and Von Caemmerer, 2000). While these approaches are scientifically sound there are still numerous obstacles to overcome before they could be immediately exploited by breeders (Lawlor, 2002). A major challenge is to introduce the C_4 (Kranz) anatomy into C_3 plants. Current work at the International Rice Research Institute (IRRI) is focusing on screening a wide range of germplasm including wild relatives of rice for such C_4 characteristics (Hibberd et al., 2008).

5.1.3. Traits to increase ear or panicle partitioning

The proportion of shoot biomass partitioned to the ear or panicle at anthesis is typically in the range 15–20% in modern wheat, barley and rice cultivars (Peng et al., 2000; Spink et al., 2000; Shearman et al., 2005; Gaju, 2007; Bingham et al., 2007a). To increase partitioning of assimilate to the ear or panicle further, future avenues would include reducing partitioning of assimilate to competing sinks: roots, stems (structural and non-structural carbohydrate components) and leaves. Reducing partitioning to the leaf lamina may be incompatible with raising RUE (although it may be possible to modify leaf traits, e.g. specific leaf area, to boost RUE while maintaining leaf partitioning). Potential avenues for increasing ear or panicle partitioning therefore seem mainly to rely on reducing partitioning to the roots or stems.

5.1.3.1. Root partitioning

Genetic variation in root system size has been widely reported in grain crops (e.g. O'Toole and Bland, 1987; Ehdaie et al., 2003; Waines and Ehdaie, 2007), but root distribution varies strongly with soil characteristics such as water and nutrient availability and mechanical impedance (Gregory, 1994). The root dry weight ratio (root to total dry weight ratio; RDW) of wheat, barley and upland rice plants is typically about 30% during early vegetative growth, decreasing to ≈10% by anthesis (Gregory et al., 1978; Gregory and Brown, 1989; Miralles et al., 1997; Price et al., 2002). One way to reduce root partitioning could be through accelerated development rate, since nodal root production is synchronized with leaf and tiller production. Thus, earlier development in near isolines contrasting for vernalisation requirement in wheat was associated with reduced RDW (Gomez-MacPherson et al., 1998). Effects of increasing plant height on root partitioning have been studied using isolines and are generally either neutral or negative in wheat (Bush and Evans, 1988; McCaig and Morgan, 1993; Siddique et al., 1990; Miralles et al., 1997). However, some caution is required when suggesting decreased root partitioning as a strategy to increase ear or panicle partitioning. This is because genetic gains in shoot biomass in recent years in cereals in some countries, assuming no change in root:shoot ratio or water-use efficiency, could result in yield under favourable conditions being increasingly limited by ability to access water and N in future years. Therefore, some attention should be focused on optimising rooting systems for most efficient water and nutrient capture, and reduced root partitioning may not be helpful in this respect. Deeper root distribution could help to increase water and/or N capture and boost biomass production under favourable conditions, since root length density (root length per unit volume of soil) of small-grain cereals is often below a critical threshold for potential water and N capture of about 1 cm cm^{-3} (Barraclough et al., 1989; Gregory and Brown, 1989) at lower depths in the rooting profile (Ford et al., 2006; Reynolds et al., 2007). A quantitative model examining the effects of altering rooting traits in cereals on water and N uptake was proposed by King et al. (2003). A sensitivity analysis of water and N capture to changes in root traits showed that a parameter 'β', describing the cumulative root distribution with depth, had a profound effect on water capture; more uniform root distribution with depth conferring greater water and N capture. In this respect, synthetic wheat derivatives, incorporating genes from the diploid wild species *T. tauschii* (D genome), may be useful since they have a similar RDW compared to check cultivars in Mexico, although roots were distributed relatively deeper in the rooting profile.

In rice under flooded conditions, breeding attempts to optimise the root system must additionally allow for the complicated interplay between adaptations for internal aeration and those for efficient nutrient acquisition. A model developed by Kirk (2003) provides a coherent representation of the rice root system in submerged soil and predicted that a system of coarse, aerenchymatous primary roots with gas-impermeable walls conducting O_2 down to short, fine, gas-permeable laterals provided the best compromise between the need for internal aeration and the need for the largest possible absorbing surface per unit root mass. In summary, it seems there is likely only a limited capacity to reduce root partitioning roots below current values of approximately 10% at anthesis in cereals in high yield potential ideotypes, due to the trade-off with water and N capture required for future biomass gains. However, a deeper relative distribution of roots while maintain RDW could comprise part of an ideotype to maximise yield in future breeding programs. Chapter 13 (Section 4) analyses in detail the role of root vigour for improved capture of water and nitrogen.

5.1.3.2. Structural and non-structural carbohydrate components of stem

The stem DM in small-grain cereals is partitioned between structural stem DM in the stem cell walls and the NSC stored in the pith. Reducing partitioning of DM to these components would potentially favour ear or panicle partitioning. The study by Beed et al. (2007) of winter wheat in the UK demonstrated shading from flag-leaf emergence to heading reduced stem NSC proportionately more than the ear or stem structural DM, implying that stem NSC does not compete strongly with these components for assimilate. So selecting for low stem NSC may be less useful as a mechanism to raise ear or panicle index than selecting for low stem structural DM. Equivalent shading studies have not been reported in rice, barley or maize.

To reduce partitioning to the structural stem DM one avenue might be further reductions in plant height below current height ≈70–90 cm in small-grain cereals. However, this was related with reductions in grain yield due to lower biomass (Miralles and Slafer, 1995; Flintham et al., 1997), presumably associated with suboptimal source:sink balance and/or light distribution within the canopy. Alternatively, ear or panicle index could be increased by reducing the peduncle length, while maintaining the height of the leaf canopy (Richards, 1996). The peduncle, the upper internode between the flag-leaf node and the collar of the ear or panicle, competes most strongly with the growing ear. Strategies to reduce structural stem DM must be jointly optimised with those for improving lodging resistance, for example with regard to potential trade-offs with stem width and material strength (Berry et al., 2003).

Another strategy to favour partitioning to the ear over the structural stem DM may be lower tillering. In favourable environments with adequate water supply, non-surviving shoots are considered to be detrimental to crop performance, that is there is no net re-distribution of assimilate to surviving shoots after their death (Berry et al., 2003; Simons, 1982). The effects of the tiller inhibition (*tin*) gene located on chromosome 1A (Spielmeyer and Richards, 2004) were investigated by Duggan et al. (2005) examining +*tin*/ −*tin* isolines in the field in south-eastern Australia. They observed greater tiller mortality in +*tin* isolines, and that these lines increased grains per ear by 9%. In barley, the proposed use of uniculms (Donald, 1968) has had limited success. Some yield increases have been reported (Donald, 1979), but results have been inconsistent because compared to conventional-tillering lines ears per square metre tends to be reduced at all seeding rates, and reduced grains per ear are observed at high seeding rates (Dofing, 1996). Novel 'large-ear phenotype' lines with moderately restricted tillering and spikes with a longer rachis and more spikelets have recently been developed at CIMMYT involving crosses with *Triticum polonicum* L., *Triticum aestivum* L. variety Morocco and *A. elongatum* L. Larger spike index and spike biomass were observed for a novel F7+ advanced line containing the *tin* gene compared to a check cultivar Bacanora (Gaju, 2007). However, larger spike biomass was countered by a more than proportional increase in chaff weight so that grain number overall was not increased. The development of new plant type (NPT) rice at IRRI was inspired by Donald's (1968) ideotype breeding approach. The NPT was designed based on the results of simulation modelling and had a low tillering capacity (three to four tillers) (Peng et al., 1994). The first-generation NPT lines based on tropical japonicas did not yield well because excessive reduction in tillering capacity resulted in low biomass production (Peng and Khush, 2003). A second-generation of NPT lines was developed by crossing the first-generation tropical japonica NPT lines with elite indica parents. This effectively increased tillering capacity and reduced panicle size, but the second-generation NPTs did not show yield advantage over indica inbreds and demonstrated lower yield than hybrids, mainly because of fewer spikelets per panicle and per square meter. It can be concluded that reducing tillering to boost ear or panicle size in many cases worldwide did not increase grains per unit area due to a large degree of plasticity amongst yield components. So for future breeding programs attempts should be made to identify genes, likely from wide relatives, associated with large ears or panicles where the physiological basis of the large ear does not depend on tillering. In this respect the exploitation of 'earliness *per se*' genes associated with spikelet primordia production in barley and wheat may deserve further in-depth study (Gaju, 2007).

As mentioned above, evidence from shading studies in the UK indicates that stem NSC may have a lower intrinsic sink strength than the ear or panicle. This suggests that NSC tends to accumulate mainly once the sink demand of the ear and structural stem has been satisfied at least in the conditions of temperate north-west Europe. So selecting for large stem NSC may not be detrimental to ear partitioning and yield potential. Indeed, there is gathering evidence that selecting for low stem NSC may actually be detrimental to yield potential in wheat and rice in some countries (Horie et al., 2003; Shearman et al., 2005). Ruuska et al. (2006) reported large broad-sense heritability ($H = 0.90 \pm 0.12$) for stem NSC in wheat, indicating that breeding for high/low stem NSC should be possible. Practically there are prospects to develop molecular markers for stem NSC content for marker-assisted selection, using complementary knowledge on the major synthetic (fructosyltransferases) and degradative enzymes (exohydrolases) involved in fructan accumulation in barley and wheat (Van den Ende et al., 2003, 2005). In conclusion, though, the principal target to raise ear or panicle partitioning *per se* appears to be reduced partitioning of assimilate to the structural stem DM.

5.1.4. Ratio of grain to ear or panicle dry matter at anthesis

There is relatively little information on genetic variation in the ratio of grains per gram of ear or panicle dry matter at anthesis (GEDM). In bread wheat, Abbate et al. (1998) found amongst historic Argentinean wheat cultivars differences in GEDM in the range 61–106 grains g^{-1}, and that grain number was more closely related to this ratio than to dry weight of ears at anthesis. In the UK, Shearman et al. (2005) reported a range of 73–129 grains g^{-1} but observed that this ratio was not associated with breeding progress in grain number. Reynolds et al. (2007) found no association of the trait with yield in three populations of random sister lines grown under irrigation in northwest Mexico. The *tin* gene mentioned above associated with restricted tillering decreased the ratio in durum wheat (Motzo et al., 2004). Equivalent information on this trait is not available in barley or rice.

In wheat, improved floret survival (where up to 12 florets per spikelet may be formed, of which at most 4–5 survive) would be expected to increase GEDM. The process of programmed floret death is controlled genetically, but responds to environmental cues (light, photoperiod) and the decline in sugars in ears in parallel to the accumulation of sugars in stems (Ghiglione et al., 2008). Thus, a photoperiod treatment (short days) which decelerated development and led to a higher concentration of soluble carbohydrate in slow-growing spikelets increased florets per ear in that study. Photoperiod sensitivity during the rapid ear-growth stage could therefore be used as a genetic tool to further increase grain number and prospectively GEDM, since slower development results in smoother floret development and more floret primordia achieving the fertile floret stage, capable of producing a grain (Section 5 in Chapter 12; Miralles and Slafer, 2007).

The greater photosynthetic area of awned ears in small-grain cereals can be important under source-limited conditions, for example drought (Blum, 1986). Under favourable conditions, few and inconsistent effects of awns on grain yield have been observed when awnless and awned isolines were compared (Weyhrich et al., 1994). Results of our field experiments in the UK examining awnless and awned lines in a Beaver × Soissons DH population under irrigation showed that chaff weight per grain was increased by 1.1 mg with the presence of awns (Foulkes, unpublished data), but grain yield was unaffected (Foulkes et al., 2007b). This suggested that small effects of awns on GEDM are not large enough to affect attainable yield in northwest Europe. Key to improving this trait in the future will be a better understanding of the mechanisms determining genetic variation in assimilate partitioning between the rachis, rachilla and floret components. GEDM usually shows a negative relationship to potential grain weight given unlimited source (Fischer and HillRisLambers, 1978). So traits to break this potential negative trade-off with potential grain size will be a high priority in future breeding programs.

5.2. Strategies to optimise potential grain size

The concept of potential weight per grain (PWG) invokes an understanding that grain structures are established early in grain formation which confer a maximum capacity on that grain for subsequent deposition of storage materials: carbohydrates, lipids and protein. During the later stages of grain filling, this maximum capacity may or may not be realised depending on availability of assimilates. Grains whose capacity has been met will tend to appear well-filled or 'plump', whereas a shortfall in available assimilates during late grain-filling will reduce the grain weight realised and, if the shortfall is significant, grains may appear shrunken or 'shrivelled'. Primarily, it is the storage materials rather than the grain infrastructure for which grains are valued. Hence, although the grower may have a large grain yield as his first priority, the grain user primarily seeks a maximum proportion of the grain to be partitioned to storage rather than germ, seed coat, bran or husk. Thus, in setting objectives for breeding of grain crops, a balance must be struck between sink and source limitation. The extent to which this balance has been achieved appears to differ between crop species and environments:

- wheat in temperate regions has been significantly sink limited in the past but with progress in breeding appears to be approaching to a co-limitation between the sink and source of assimilates (e.g. Slafer and Savin, 1994; Shearman et al., 2005; Reynolds et al., 2005);
- in regions having frequent terminal droughts, an appropriate balance is more difficult to specify but, for wheat, a reasonable balance has possibly been struck (Borrás et al., 2004);
- barley in temperate regions still appears to be predominantly sink limited (Bingham et al., 2007b);
- barley in regions with late stress appears to exhibit, perhaps too frequently, significant source limitation (e.g. Sharma and Anderson, 2004);
- maize shows more evidence of source limitation (Borrás et al., 2004; Borrás and Westgate, 2006);
- as with wheat, breeding of higher yielding rice varieties may have been associated with progress from sink limitation towards a closer balance with source limitation (Dingkhun and Kropff, 1996) and
- soybeans commonly show co-limitation by source and sink (Borrás et al., 2004).

The switch between determination of grain number and individual grain weight at anthesis is not absolute; individual grain weight can be affected by assimilate supply for a period before anthesis (Calderini et al., 1999), and grain number can be affected by assimilate supply for a period after anthesis (Beed et al., 2007). However, considering the whole period from sowing to harvest, variation in source before anthesis tends to be expressed largely through grain number and after anthesis it tends to be expressed largely through individual grain weight. It would clearly be disadvantageous for a total potential grain weight (GN × PWG) to be set before anthesis which differs substantially from the likely availability of assimilate for grain storage after anthesis. The consequences would be either dissatisfaction for the grower due to a low total grain yield, or dissatisfaction for the user due to low partitioning to grain storage materials. This could partly explain why we find grain number to be so well related to grain yield in most well-adapted grain crops (see earlier discussion, and the debate prompted by Sinclair and Jamieson, 2006, 2008; Fischer, 2008). A consequence of breeding cultivars with predominantly well-filled grains is that their grain yields will also tend to be predominantly sink limited, and while this will result in less yield on average than for cultivars which are predominantly source-limited and a slower rate of yield increase through breeding, sink-limited cultivars are likely to exhibit greater yield stability, as well as better grain quality.

Mechanisation of harvesting also tends to favour genotypes with relatively uniform grain size, hence a higher proportion of grains that fall within the dimensions set in the harvester (Sharma and Anderson, 2004). The total grain yield of source-limited lines may include a significant proportion of partially filled grains that are either not retained in the harvesting process (or down-grade grain quality); such lines are likely to have a relatively low measured grain yield, hence will appear at a disadvantage in any breeding program. For example, the proportion of screenings in some barley lines can be as much as 25% (Moody et al., 2001; Fox et al., 2006).

It is inherent in grain crops that the same photosynthetic tissues, in the same competitive environment (i.e. shoot density), are responsible for determination of both the sink and source capacities of an inflorescence, although ageing and senescence mean that post-anthesis activity will be relatively less than that pre-anthesis. The last stage in setting the balance between sink and subsequent source capacities of the inflorescence is in the determination of PWG. Each shoot makes a commitment in terms of cell number (Brocklehusrt, 1977) during the first part of grain growth which inherently relates to its subsequent capacity for deposition of storage materials. More endosperm cells are initiated than that eventually survive, so final cell number depends on cell loss at the end of the cell division phase (in wheat ~15 days after pollination; Gao et al., 1992). Cell expansion then continues, and although final cell volume is less important in determining PGW (Brocklehurst et al., 1978), this also can influence PWG. Thus, PGW is not fully determined until about one-third (cereals) or two-thirds (soybean) of grain DM has accumulated (Borrás et al., 2004). In general, source-sink manipulation experiments (involving de-graining or defoliation during early grain development) show PWG to be responsive to assimilate supply (Brocklehusrt, 1977; Singh and Jenner, 1984; Fischer and HillRisLambers, 1978) up to, but not beyond, a certain point (Borrás et al., 2004). This is somewhat surprising, given that the DM requirements for cell formation (as opposed to deposition of storage materials) are small, and that assimilate supplies at this stage are maximal (little senescence has occurred, redistributable reserves are at a maximum and there are few competing sinks). Possibly more subtle signals, that correlate with assimilate supply, are controlling cell division.

The challenge for future yield improvement is to devise strategies that will enhance the scope for PWG to respond to availability of assimilates without unduly enhancing the risk of incomplete grain filling. It will be important for such work to be underpinned by genetic analysis, and it is encouraging in this regard that, for a range of different wheat crosses, some QTL controlling grain yield have been found to work primarily through individual grain weight without pleiotropic effects on grain number (Snape et al., 2007). Possible physiological objectives are to reduce the DM requirements of cell division and expansion, to understand and change the signals to which cell division is responding, or to increase the concurrence of cell expansion and grain DM deposition (i.e. for cereals to become more like soybeans). This last might be achieved for each grain or, more controversially (because of increased variation in maturity), by extending the disparity between development of grains within the inflorescence.

6. USE OF PHYSIOLOGICAL TOOLS TO SELECT FOR HIGH YIELD POTENTIAL

To date breeding for yield potential has relied heavily on visual selection in segregating generations and yield testing of genetically fixed lines rather than use of physiological selection criteria to realize genetic gains (Condon et al., 2008). Nonetheless, the ability to accurately measure the physiological components of yield has clear application in breeding. Furthermore, the capacity for precise phenotyping under reliable conditions probably represents the most limiting factor for the progress of genomic studies on traits underlying yield potential. There is a need for a high precision because the differences may be small, and detailed physiological measurements (e.g. of growth rate) are difficult when large numbers of genotypes are involved. Selection traits that are either more heritable or quicker to measure than grain yield may be valuable in detecting high-yielding genotypes rapidly and efficiently from a large number of genotypes. Experimental work in wheat showed that application of physiological selection criteria alongside visual selection increased accuracy in the identification of high-yielding lines by breeders and increased the proportion of genetically high-yielding lines carried forward in comparison to visual selection alone (Van Ginkel et al., 2008). Economic analysis also lent strong support to the value of such indirect selection criteria for reducing costs, for example, by discarding physiologically substandard lines prior to extensive yield testing (Brennan et al., 2007).

Direct measurement of photosynthesis, the fundamental driving force behind yield, remains a relatively time-consuming and expensive procedure and is not conducive to the demands of high-throughput phenotyping at the breeding scale. Nonetheless, surrogates can be used such as leaf porometry, canopy temperature, carbon-isotope discrimination and spectral indices that estimate leaf conductance, canopy level conductance, integrated stomatal conductance over time and shoot biomass or photosynthetic capacity, respectively. To date, such techniques have found more application in breeding programs aimed at increasing adaptation to abiotic stress, and especially drought (Condon et al., 2008). For example, while under well-watered conditions stomatal conductance may be only loosely coupled to yield, under moisture stress traits that increase access to water will be reflected by a stronger association because stomatal opening is tightly regulated by environmental conditions. Indeed Flexas et al. (2004) showed that while stomatal conductance is severely inhibited by drought and salinity stress, the response was not a result of damage to the light or dark reactions of photosynthesis. Nonetheless, as we better define the physiological components of yield and their interaction with phenology and environment, such traits are likely to have increased application in high-throughput precision phenotyping in breeding and gene discovery.

Most studies on dynamic traits have been based on the direct use of phenotypic data measured at sequential times. One tricky aspect for these analyses is the physiological age difference at a phenotyping time among individuals of a mapping population because their flowering or maturity day differed. While differential sensitivity to, for example, photoperiod is a component of what determines yield potential, it is also self-evident that such genes of major effect must be controlled experimentally when trying to determine the more subtle influence of minor genes on complex traits such as leaf photosynthesis. A logical phenotyping should be conducted at the same physiological age for all individuals. From a practical point of view, this is impossible if phenotyping needs to be made at developmental stages that are not marked by morphological changes such as flowering (Yin et al., 2004). Alternatively, a crop development model could be used to correct the measured data for the same age.

6.1. Use of spectral reflectance indices

Spectral reflectance is a remote-sensing technique for screening genotypes for canopy light reflectance properties based on the absorption of light at specific wavelengths. Spectral characteristics are affected by canopy size (biomass and GAI), plant nutrient and water status and senescence (Chapter 19). The reflectance in the visible wavelengths (VIS, 400–700 nm) is lower than in the near-infra red wavelengths (NIR, 700–1300 nm) because of the high absorption of light energy by leaf pigments. Spectral reflectance indices, including simple ratio (SR) and normalised difference vegetation index, NDVI = (NIR − VIS)/(NIR + VIS), have proved useful in the assessment of early biomass and vigour of different wheat (Elliott and Regan, 1993; Bellairs et al., 1996) and barley genotypes (Peñuelas et al., 1993, 1997). The potential use of SRI in plant breeding to differentiate genotypes for yield has been evaluated under well-watered and/or moisture-stressed conditions in wheat (Aparicio et al., 2000; Royo et al., 2003), barley (Bort et al., 2002) and soybean (Ma et al., 2001). In general, indices correlated better with yields under moisture-stressed conditions. In a set of 25 durum wheat genotypes, Ferrio et al. (2005) in experiments conducted in low, medium and high productivity environments, with average yields of 2.5, 4.5 and 7 $t\,ha^{-1}$, respectively, measured spectral reflectance between 400 and 1000 nm at anthesis and milk-grain stages. The most reliable ranking of genotypes was attained using measurements made at milk-grain stage on medium to high productivity environments and these were sufficiently accurate to rank genotypes for breeding purposes. In wheat, Babar et al. (2006a) examined the relationship between grain yield and a range of VIS/NIR- and NIR-based indices on adapted genotypes and random F3 and derived recombinant lines under irrigated conditions in northwest Mexico. The best associations with grain yield were found for NIR-based indices and there was a higher association between grain yield and the NIR-based indices at heading and mid grain-filling than at booting. Correlation coefficients between mean yield and mean for the NIR-based indices averaged over years were 0.87–0.88 demonstrating their potential of use as a tool in breeding programs for selecting for increased genetic gains for yield potential.

Spectral reflectance may be of use in measuring components of yield potential such as senescence. As the crop loses its greenness the spectral characteristics of the canopy change and more light in total is reflected. NDVI has been correlated with senescence in cereals (Idso et al., 1980; Adamsen et al., 1999). Gupta et al. (2001) suggest that comparison of wavelengths at which chlorophyll-beta (640 nm) and chlorophyll-alpha (673 nm) have maximum absorbance may give good sensitivity to maturity. Another example would be use of spectral reflectance to rank genotypes for biomass at early crop stages; Babar et al. (2006b) showed some indices to be well correlated with fresh and dry weight of shoot tissue at a range of phenological stages.

6.2. Use of stomatal aperture traits (SATs)

Stomatal aperture-related traits include stomatal conductance (gs) itself or surrogates such as canopy temperature depression (CTD), carbon-isotope discrimination (D13C) and oxygen isotope composition (Barbour et al., 2000; Condon et al., 2007). One instrument that has been utilised with some success for the rapid indirect determination of gs is the hand-held infrared thermometer, used for instantaneous measurement of canopy temperature. Results are usually expressed as canopy minus air temperature, referred to as canopy temperature depression. This instrument is best for use on sunny cloudless days, since there is a major effect of net radiation, air temperature and wind-speed on CTD, and a major effect of vapour pressure deficit. Canopy temperature, which can be sensed remotely using infrared thermometry, has been shown to be well associated with the yield of wheat and cotton cultivars (Reynolds et al., 1994; Radin et al., 1994; Fischer et al., 1998), as well with the yield of recombinant inbred lines (RILs) and advanced breeding materials (Reynolds et al., 1998, 1999; Condon et al., 2008) in irrigated, high-radiation environments as well as under moisture-limited conditions for wheat breeding materials (Blum et al., 1982) and RILs (Olivares-Villegas et al., 2007).

Recent research on wheat to identify the extent to which physiological measurements can be used as complementary tools in the CIMMYT breeding programme in northwest Mexico (a temperate, irrigated, high-radiation environment during winter) to improve the efficiency of selection for yield (Condon et al., 2007, 2008; Van Ginkel et al., 2008) has shown considerable potential for the use of SATs in early generations to complement breeders' visual selection for high yield-potential lines. Although carbon-isotope discrimination was the trait showing most promise for realising genetic gains, both canopy temperature and leaf porometry were not far behind. However, the latter two traits are considerably cheaper and easier to measure and therefore of much greater potential application in an economic context (Brennan et al., 2007). In summary, use of SATs should lead to more effective culling of low yield-potential lines in early generations, reducing the number of such lines that advance to expensive yield testing, and thereby identifying elite materials at lower cost. Interestingly, visual selection by experienced breeders, while not more economical than application of rapid-screening tools like canopy temperature, were associated with similar levels of genetic gains. However, it was the combination of both visual and physiological tools that identified the very highest yielding lines (Van Ginkel et al., 2008).

6.3. Use of chlorophyll fluorescence

Chlorophyll fluorescence has great potential as a high-throughput screen for photosynthetic potential and therefore yield potential. Nonetheless, evidence for its association with genetic gains in yield in crops is lacking and we are not aware of its application in any crop breeding programs.

6.4. Strategic crossing

A potentially powerful physiological tool for increasing yield is the systematic characterisation of potential parents and subsequent strategic crossing to combine complementary traits in progeny. For example, the identification of a number of source and sink traits associated with yield and biomass in wheat, which both principal component analysis and multiple regression suggest as being at least partially independent of one another, supported the idea that additive gene action could be achieved by adopting a physiological trait based breeding approach (Reynolds et al., 2007); the approach has been used already with success in breeding for increased drought adaptation.

7. CONCLUSIONS

Rates of genetic gain in yield potential may be slowing in a number of grain crop species but it appears that breeding progress has not stopped. This may be associated with HI in some grain crops having reached values close to theoretical maxima and biomass gains being harder to achieve. In wheat and rice at least, there is evidence that modern cultivars may be in a closer source:sink balance than their predecessors. For the majority of grain crop species there is ample evidence for a strong association between grain number per unit area and yield; and between growth during a critical phase before and around flowering and grain number. Evidence in some species now points to the importance of increased photosynthetic activity before and around flowering for recent genetic increases in yield potential. Therefore, more attention is recommended to photosynthetic activity before and around anthesis in in-depth studies. Since photosynthesis is not conducive to high-throughput phenotyping, these studies should include the use of rapid-screening tools for surrogates of photosynthesis like canopy temperature. A deeper distribution of roots is a prospective characteristic that deserves further in-depth study since raising harvest biomass implies an increased requirement for soil water and nitrogen. Improved crop designs should also relate to optimising non-structural stem carbohydrate reserves with evidence in wheat and rice that this trait is positively correlated with yield potential in modern cultivars. Overall new ideotypes in which source and sink are more or less simultaneously increased will be key to improving yields in small-grain cereals together with increased lodging resistance. More attention to grains per unit of ear or panicle weight is also urged, as well as enhancing potential grain size. With respect to the latter, possible physiological objectives are to reduce the DM requirements of cell division and expansion and to understand and change the signals to which cell division is responding. The application of physiological principles in breeding programs to increase yields to counteract global shortages while reducing the environmental footprint can only be achieved with a multidisciplinary team, including molecular biologists. Genetic studies should focus on finding QTL that affect grain number without affecting grain size, and vice versa, or ear or panicle number without affecting grains per ear or panicle. In this context, increased understanding of the physiological processes underlying yield potential at the crop level of organisation is advocated, to exploit key traits either directly in breeding or through contributing to the development and use of molecular markers for these quantitative complex traits.

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CHAPTER 16

Management and Breeding Strategies for the Improvement of Grain and Oil Quality

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1. INTRODUCTION

The quality of a harvested organ can most simply be defined as its suitability to the intended market or processing and product manufacture. The term quality may therefore encompass many criteria, as the compositional (chemical) and textural (biomechanical) requirements may vary from one product to another. For example, for oilseed sunflower it includes the potential industrial yield, the nutritional value of the oil and its stability (Box 1). For bread wheat, it includes the milling performance, the dough rheology, the baking quality, the nutritional value for humans or animals and its suitability for storage. Moreover, for a given end product, the relative importance of quality attributes changes along the market chain from grower to consumer. For example, elevated oil or protein concentration is of economic importance for farmers where a premium is paid for these attributes, whereas high baking quality in wheat or oxidative stability in oilseeds are of economic importance to food manufacturers. Also for a given crop species, quality criteria vary depending on the product end use (Box 1). For example, high-protein flours are required for leavened bread or pasta, while their low-protein counterparts are desirable for biscuits, crackers, cakes or oriental noodles. An efficient agro-industrial production system, therefore, needs to know the year-to-year variation in composition of raw materials that can be obtained in different regions or under different management practices.

The identification of novel genes or loci with major effects on quality traits has resulted in new cultivars with improved quality (Velasco and Fernandez-Martinez, 2002; DePauw et al., 2007, Chapter 14). Nonetheless, dealing with genotype-by-environment (G × E) interactions, and with pleiotropic effects (i.e. trait-by-trait interactions) remains a major difficulty in plant breeding, especially for grain quality (de la Vega and Chapman, 2001). A physiological perspective provides useful insights into G × E, as shown in this and other chapters of this book (Section 3.1 in Chapter 11; Sections 3 and 4 in Chapter 10). Further in this chapter, we argue that grain oil and protein concentration and composition are primarily determined at the crop level, and cannot be correctly understood or predicted by extrapolating from the individual plant to the population. We will show how physiological concepts and methods classically applied to yield analysis can be used to investigate and model the genetic and environmental determinants of grain oil and protein concentration and composition, for example, identification of critical periods (Section 5 in Chapter 12; Section 3.2.2 in Chapter 15), kinetics of biomass and nitrogen accumulation and partitioning (Chapters 7 and 8). Models can range from detailed mechanistic descriptions to simple response curves to environmental variables, which are 'meta-mechanisms' at the plant or crop level (Tardieu, 2003). If models are robust enough, one set of parameters represents one genotype (Hammer et al., 2006; Chapter 10), and thus they can be used to analyse complex traits with G × E and pleitropic effects.

BOX 1 Selected properties of vegetable oil and its components

Vegetable oils are composed mainly of triglycerides (or triacylglycerol, TAG), which are formed by the esterification of three fatty acids with a glycerol. Fatty acids are usually classified based on the length of their carbon chain and the number and position of double bonds. The fatty acid composition defines the nutritional, industrial and organoleptic quality of the oil. Fatty acids are expressed as a percentage of all the fatty acids in the oil.

Saturated fatty acids, with the exception of stearic acid, increase the levels of cholesterol in humans (Velasco and Fernandez-Martinez, 2002). Polyunsaturated acids, such as linoleic acid, are essential to mammals, have a potent hypocholesterolemic effect and reduce the risk of cardiovascular diseases (Kris-Etherton and Yu, 1997). They can also be used as feed to dairy cattle yielding milk with a high level of conjugated linoleic acid (Kelly et al., 1998). On the other hand, saturated fatty acids provide the oil a higher oxidative stability than unsaturated fatty acids. Therefore, for cooking and food industry, sunflower oils with oleic acid concentration near those of mid-oleic cultivars (oleic acid concentration between 60 and 79%) are often preferred (Binkoski et al., 2005). Oils with high concentration of oleic acid also allow for margarine with less proportion of undesirable *trans* fatty acids. For biodiesel, oils containing fatty acids with low degree of unsaturation are preferable, because they decrease the iodine index (inversely related to stability), and increase biodiesel cetane number (a measure of combustion quality) (Clements, 1996).

Tocopherols (α, β, γ and δ isomers) are natural antioxidants that inhibit lipid oxidation in biological systems by stabilising hydroperoxyl and other free radicals (Bramley et al., 2000). The antioxidant activity of tocopherols increases oil stability (Martínez de la Cuesta et al., 1995; Bramley et al., 2000). Tocopherols are essential for humans, and they have been associated with delayed cellular aging (White and Xing, 1997), reduced risk of cardiovascular diseases and regression of several cancers in cell culture. At high temperatures, β- and γ-tocopherols present a higher antioxidant activity than α-tocopherol and are thus preferred for cooking oil. On the other hand, α-tocopherol has the highest vitamin E activity compared to the other three isomers (Mullor, 1968).

In this chapter, quality is restricted to the biochemical composition of grains, and the focus is on sunflower as an oilseed model and bread wheat as a cereal model. Comparisons with other species are included to emphasise similarities and differences with these model crops. The rationale for the use of these model species is threefold. First, research on model species has proven useful in other areas of knowledge, for example, *Arabidopsis thaliana* and rice as models for dicotyledonous and monocotyledonous plants in genetics, respectively. Second, grain oil and protein, major storage compounds in sunflower and wheat, are important in human and animal diets and increasingly important for non-food uses. Third, our knowledge of quality aspects in these two species is sufficient to allow for meaningful quantitative models that capture major genetic, environmental and G × E effects.

This chapter comprises three main parts. First, we briefly review the effects of environmental, genetic and G × E factors on grain oil and protein concentration and composition. Second, we outline process-based crop models accounting for grain yield in both species, and for concentration and composition of oil (sunflower) and protein (wheat). Third, we use a combination of modelling and experiments to analyse the relationships between quality traits and yield, and management and breeding strategies for the improvement of grain quality.

2. ENVIRONMENTAL AND GENETIC EFFECTS ON GRAIN OIL AND PROTEIN CONCENTRATION AND COMPOSITION

2.1. Oil concentration

Grain oil accumulates mainly in the endosperm (e.g. castor bean and oat), embryo cotyledons and axis (e.g. rapeseed and sunflower), embryo scutellum and aleurone layer (e.g. maize) or mesocarp (e.g. olive and oil palm), depending on the species (Murphy, 2001). Grain oil concentration (usually expressed in percent of grain dry mass) mainly determines the industrial yield of the grains. As a consequence, in some countries, sunflower grains with an oil concentration above a threshold are paid a premium over the regular price.

Grain oil concentration is genetically determined, and plant breeding has improved it in many crops. In sunflower, low-oil varieties and hybrids (38–47% oil) have been replaced by modern high-oil hybrids (47–53% oil; de la Vega et al., 2007; Izquierdo et al., 2008). In maize and oat, high-oil hybrids (up to 18%) have been developed, although most of currently grown hybrids have 3.9–5.8% oil (Frey and Holland, 1999). The improvement in oil concentration was mainly achieved by increasing the proportion of tissue in which oil is stored (e.g. Doehlert and Lambert, 1991, in maize; Tang et al., 2006, in sunflower) rather than by increasing the oil concentration in this tissue. In sunflower, the difference in oil concentration between low-oil and high-oil hybrids is caused by differences in the duration rather than the rate of oil accumulation (Mantese et al., 2006; Izquierdo et al., 2008).

High oil concentration is associated with a high sensitivity of oil concentration to environmental conditions, as opposed to the almost stable oil concentration of low-oil hybrids (Dosio et al., 2000; Izquierdo et al., 2008), even when genotypes differ only in a single genetic region (8.1 cM) conferring the high-oil trait (León et al., 1996). Environmentally induced variation of sunflower grain oil concentration has been largely related to variation in embryo oil concentration (Santalla et al., 2002; Izquierdo et al., 2008). Variation in grain oil concentration associated with changes in the embryo-to-pericarp ratio has been found in response to temperatures above 30 °C (Rondanini et al., 2003).

Grain oil is synthesised from carbohydrates either from current photosynthesis or from the remobilisation of storage carbohydrates (Hall et al., 1990). Therefore, grain oil accumulation greatly depends on the carbon economy of the crop during grain filling (Andrade and Ferreiro, 1996; Dosio et al., 2000). In sunflower, grain oil concentration is mainly determined by the amount of photosynthetically active radiation (PAR) intercepted per plant during the grain-filling period (Andrade and Ferreiro, 1996; Dosio et al., 2000; Izquierdo et al., 2008). Likewise, in rapeseed, Izquierdo (2007) found reductions in oil concentration from 50.3 to 36.3% when incident radiation was reduced by 80%. In contrast, Andrade and Ferreiro (1996) did not detect any effect of intercepted radiation on grain oil concentration in soybean and maize. Other authors have attempted to use the source–sink ratio as the explanatory variable, finding either no relationship (Ruiz and Maddonni, 2006) or a relationship worse than that of source alone (Izquierdo et al., 2008).

In sunflower, final grain dry mass and oil concentration are most sensitive to the amount of intercepted radiation between 250 and 450 °C day after flowering (base temperature 6 °C; Aguirrezábal et al., 2003). A linear–plateau relationship between final grain oil concentration and intercepted radiation during the mentioned period was found, with a maximum (OC_{max}) at approximately 26.3 MJ per plant for high-oil hybrids (Dosio et al., 2000; Izquierdo et al., 2008; Figure 1a). This critical period, however, has not been detected yet in other oil crops (Izquierdo, 2007).

The response of grain oil concentration to temperature during grain filling depends on the species. For flax, both the quantities of oil per grain and oil concentration decrease linearly with daily average temperature between 13 and 25 °C (Green, 1986). For soybean, grain oil concentration increases with daily average temperature up to approximately 28 °C and decreases with higher temperature (Piper and Boote, 1999; Thomas et al., 2003). In sunflower, the duration of the grain-filling stage is inversely related to temperature (Ploschuk and Hall, 1995; Villalobos et al., 1996), and thus higher temperature would shorten the time for radiation interception and therefore reduce grain oil concentration (Aguirrezábal et al., 2003). However, results from the field should be interpreted with caution, since variations in temperature and radiation are usually correlated. Under controlled conditions, where temperature and daily radiation were decoupled, oil concentration has been inversely related to temperature (Canvin, 1965; Geroudet and Aguirrezábal, unpublished results). With temperature above 30 °C, oil concentration can decrease markedly, depending on the stage of grain filling (Rondanini et al., 2003, 2006).

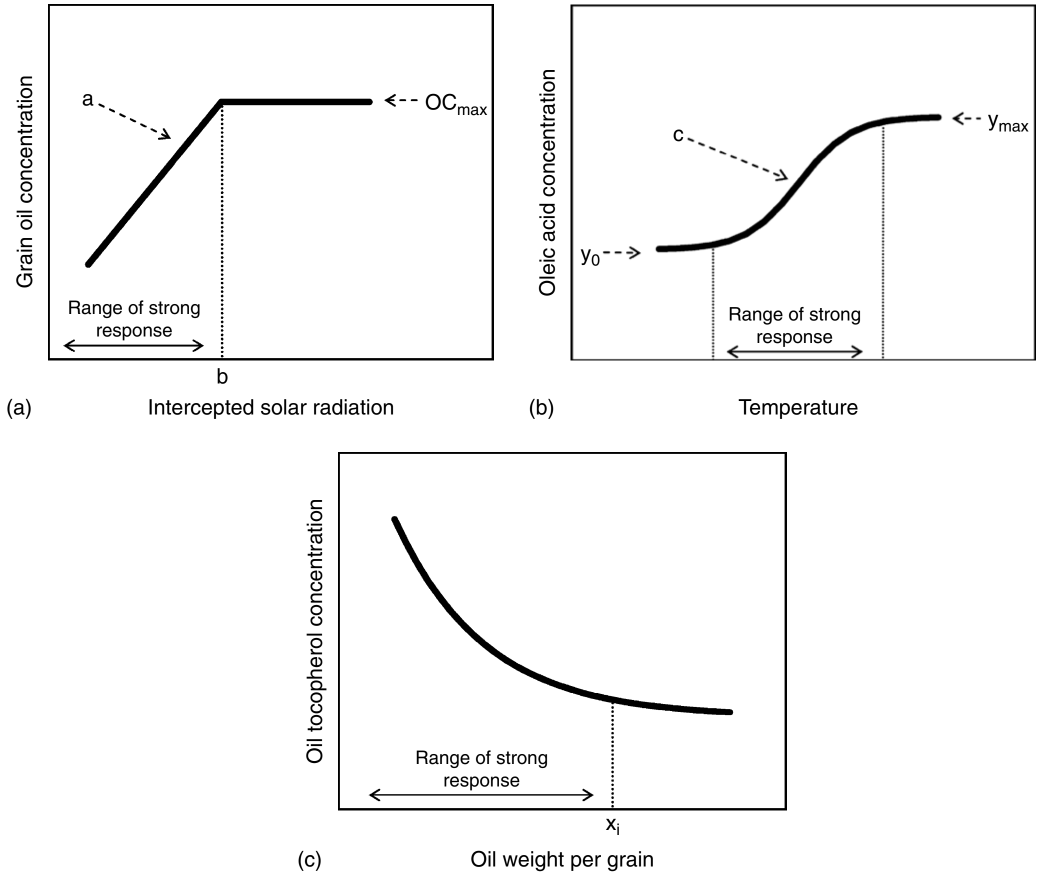

FIGURE 1

Modelling quality traits in sunflower, an oilseed model crop. (a) Linear-plateau response of grain oil concentration to intercepted solar radiation during the period 250–450°C day after flowering; parameters are the slope of the linear phase (a), the minimum intercepted radiation to obtain the maximum oil content (b), and the maximum oil concentration (OC_{max}). (b) Sigmoid function describing the relationship between oleic acid concentration and minimum night temperature during the period 100–300°C day after flowering; parameters are the maximum slope (c), the minimum oleic acid concentration (y_0) and the maximum oleic acid concentration (y_{max}). (c) Negative exponential relationship between oil tocopherol concentration and oil weight per grain; x_i is the oil weight per grain above which oil tocopherol concentration shows a stabilisation-like phase.

Water deficit during grain filling, even for a short period, can reduce grain oil concentration (Hall et al., 1985). The first effect of water shortage is the reduction of leaf expansion, which could have significant effect on radiation interception and thus on grain oil concentration. More severe water deficit can also affect leaf photosynthesis or accelerate leaf senescence, thereby reducing the availability of carbohydrate for oil synthesis. Excess nitrogen availability can also affect oil concentration, mainly through an increase in protein concentration (Steer et al., 1984, and references therein). While part of the effect of other environmental factors and management practices can be explained by their effect on intercepted radiation per plant, temperature or crop photosynthesis (e.g. foliar diseases, sowing date and sowing density), these factors can also have direct effects on grain oil concentration, as it has been shown for other oil yield components (Andrade et al., 2002). More research is needed to clarify this issue.

2.2. Oil composition

Fatty acid composition is the main determinant of oil quality, as outlined in Box 1. Fatty acid chains are built through a cycle of biochemical reactions involving the multi-enzyme fatty acid synthase FAS and the low-molecular-weight acyl carrier protein ACP. They are converted to acyl-CoA and then incorporated into TAG. The desaturation of fatty acids is mediated mainly by the enzymes stearoyl-ACP desaturase, oleoil-ACP desaturase and linoleoil-ACP desaturase. Although our knowledge of the enzymes involved in the synthesis and the desaturation of oil fatty acids, the genes that code for these enzymes and their environmental regulation has increased over the past years, our understanding of the regulation of oil synthesis and storage is still far from complete.

Oil fatty acid composition is genetically controlled. The fatty acid composition of oil varies largely among species, and also within species (Figure 2). The oil composition of traditional high-linoleic cultivars of sunflower has been modified, mostly by altering the function of major genes through mutagenesis (Lagravere et al., 1998; Fernández-Martínez et al., 1989; Lacombe and Bervillé, 2000). High-oleic cultivars have over 80% oleic acid resulting from a reduced activity of oleoil-ACP desaturase (Garcés and Mancha, 1991; Kabbaj et al., 1996). Mid-oleic sunflower oil (60–79% oleic acid) is usually produced by crossing a high oleic and a traditional line. Sunflower lines with increased concentrations of saturated fatty acids (high stearic or high palmitic) were also developed (Osorio et al., 1995; Fernández-Martínez et al., 1997). High-stearic sunflower cultivars are the result of low activity of the enzyme stearoyl-ACP desaturase or of high activity of the enzymes FATA and FATB, which increase the accumulation of stearic acid in the endoplasmic reticulum and thus reduce its desaturation.

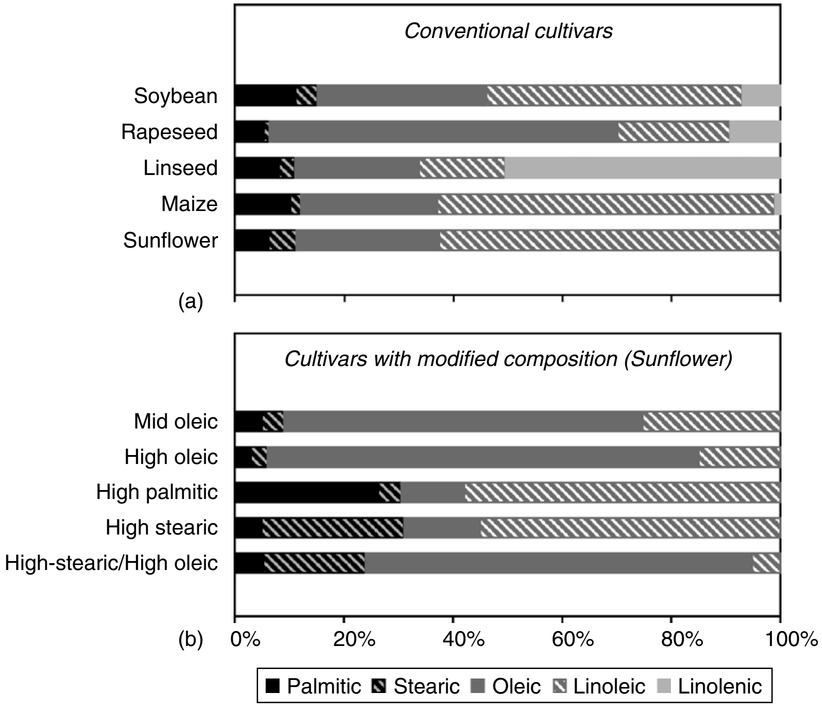

FIGURE 2

Typical oil fatty acid composition for (a) conventional cultivars of soybean, rapeseed, linseed, maize and sunflower and (b) sunflower cultivars with modified fatty acid composition: mid oleic, high oleic, high palmitic, high stearic and high stearic/high oleic. (Source: Data from Velasco and Fernandez-Martinez, 2002; Aguirrezábal and Pereyra, 1998; Izquierdo, unpublished.)

Inbred lines combining the high-stearic trait with the high-oleic trait (high stearic or high oleic) have also been obtained (Serrano-Vega et al., 2005). High-oleic, high-linoleic and high-stearic cultivars of soybean have been developed (Schnebly et al., 1996; Stojšin et al., 1998; Primomo et al., 2002; Serrano-Vega et al., 2005), but they have not been released to the seed market yet. In rape, a species with erucic acid in its oil, cultivars with low (for human consumption) or high (for industrial uses) concentrations of this fatty acid have also been developed (Velasco et al., 1999).

Oil fatty acid composition varies according to the environmental conditions (Strecker et al., 1997; Pritchard et al., 2000; Roche et al., 2006). It has long been known that an increase in temperature increases the oleic-to-linoleic acid ratio in the oil of several oilseed crops (Canvin, 1965) by affecting the total activity of the desaturase enzymes (e.g. oleoil-ACP desaturase in sunflower; Garcés et al., 1992; Kabbaj et al., 1996). The accumulation of saturated fatty acids is also affected by environmental factors (Roche et al., 2006; Izquierdo and Aguirrezábal, 2008).

Several authors observed that oleic acid concentration in sunflower oil was decreased by low temperatures (e.g. Harris et al., 1978; Rochester and Silver, 1983; Izquierdo et al., 2002). Oleic acid concentration was better related to night minimum temperature than to other temperature descriptors (Izquierdo et al., 2006). The circadian rhythm of the oleoil-ACP desaturase activity seems to be associated with this effect of temperature during the dark period (Pleite et al., 2008). In soybean and maize, however, a clear relationship between oleic acid concentration and night-time or minimum temperatures could not be detected. Rather, it has been related to daily average temperature, probably because of a lower effect of temperature on fatty acid composition in these species (Izquierdo, 2007). As found for oil concentration, very high daytime temperatures (>30°C) also affect fatty acid composition in sunflower (Rondanini et al., 2003), but probably through different (and possibly interacting) mechanisms than moderately high temperatures.

Environmental factors other than temperature, such as solar radiation (Santalla et al., 1995), rainfall (Pritchard et al., 2000), nitrogen availability (Steer and Seiler, 1990), soil salinity (Irving et al., 1988) and crop health (Zimmer and Zimmerman, 1972), can also affect fatty acid composition. However, these factors generally produce small variations in fatty acid composition than those driven by temperature (e.g. 10 vs. 40% oleic acid for sunflower). However, variations in oleic acid concentration through changes in intercepted radiation in soybean and maize (Izquierdo, 2007) were similar to those driven by latitude, extreme sowing dates and temperature (Muratorio et al., 2001; Izquierdo and Aguirrezábal, 2005; Izquierdo, 2007).

The total activity of the enzyme oleoil-ACP desaturase is maximum early during grain filling (Garcés et al., 1992; Kabbaj et al., 1996); therefore, the effect of temperature in this period could be stronger than during the rest of the grain-filling stage. Correspondingly, minimum night temperature between 100 and 300°C day after flowering (base temperature 6°C) accounted for most of the variability in the concentration of oleic and linoleic acids in two traditional hybrids and a high-oleic hybrid (Izquierdo et al., 2006; Izquierdo and Aguirrezábal, 2008). This supports the idea (usually assumed in crop simulation models; e.g. Villalobos et al., 1996; Stöckle et al., 2003) that the timing of a critical period is the same for different genotypes, provided that it is expressed in relation to developmental events and in thermal time. Such a critical period, however, could not be found in maize or soybean (Izquierdo, 2007).

The knowledge on the effects of the environment on fatty acids other than oleic and linoleic acids is more limited. Izquierdo and Aguirrezábal (2008) found a relationship to describe the response of other fatty acids to temperature in different sunflower hybrids. With increased temperature, the proportion of saturated fatty acids was reduced, mainly due to a reduction in the concentration of stearic acid (the concentration of palmitic acid remained fairly constant), indicating that there is also a temperature effect on stearoyl-ACP desaturase, as reported by Kabbaj et al. (1996). The synthesis of stearoyl-ACP desaturase peaks earlier during grain filling than that of the oleoil-ACP desaturase (12 vs. 20 days after flowering; Kabbaj et al., 1996), suggesting that the critical period for saturated fatty acids precedes the critical period for oleic-to-linoleic ratio (Izquierdo et al., 2006).

Izquierdo and Aguirrezábal (2008) investigated the response of oleic and linoleic acids to temperature in sunflower hybrids, using the empirically based relationship established by Izquierdo et al. (2006).

The concentration of oleic acid showed a sigmoidal response to minimum night temperature between 100 and 300 °C day after flowering, increasing almost linearly within a given range of temperatures (Figure 1b). Outside this range, the concentration of this fatty acid remained almost constant. The same mathematical expression characterised the response of oleic acid concentration to temperature in both traditional and high-oleic hybrids; as it could be expected, relationships between linoleic acid concentration and temperature showed inverse trends. However, the parameters of the response curves showed significant genetic variability. Differences among traditional hybrids were observed for the minimum and maximum concentrations of oleic acid and also for the maximum slope and the range of the response; differences were particularly high for the minimum concentration of this fatty acid, which ranged between 15 and 32%. The low sensitivity to the environment of a high-oleic hybrid was evidenced by the small difference between the parameters for minimum and maximum oleic acid concentrations (6.9%), as compared to traditional hybrids (16.3–43.9%). Since the same function characterised the response of several hybrids, it is possible to easily incorporate the estimation of oil fatty acid composition in crop simulation models using hybrid-specific parameters. Finally, the analysis of the variability of these parameters gives important information on the nature of the observed G × E interactions and provides new traits (parameters) that are independent of the environment. This can be used to obtain new genotypes with specific responses to environmental variables, as proposed by Tardieu (2003) and discussed further in Section 4.4.

2.3. Oil tocopherol concentration

Tocopherols (Box 1) are synthesised from specific precursors, via the isoprenoid pathway or the homogentisic acid pathway (Bramley et al., 2000). Their synthesis is regulated by the availability of these precursors. In plants, four isomers of tocopherol have been identified (α-, β-, γ- and δ-tocopherols), which differ in the position of the methyl group in the molecule, and also in their in vitro and in vivo antioxidant activities (Kamal-Eldin and Appelqvist, 1996). The relative quantities of these isomers are controlled by the enzymes catalysing the methylations. In sunflower, α-tocopherol accounts for 91–97% of the total tocopherol, with little genetic variation (Nolasco et al., 2006).

The tocopherol concentration in sunflower grain is very responsive to environmental conditions (Kandil et al., 1990; Marquard, 1990; Velasco et al., 2002). The amount of intercepted radiation per plant during grain filling was negatively correlated to tocopherol concentration in the oil in sunflower (Nolasco et al., 2004), soybean, maize and rape (Izquierdo, 2007). The effect of temperature on tocopherol concentration, however, is unclear, with many contradictory reports (Dolde et al., 1999; Almonor et al., 1998; Izquierdo et al., 2007).

Tocopherols are present in the grain in a small quantity diluted in oil (typically 500–1200 $\mu g\, g^{-1}$; Marquard, 1990; Nolasco et al., 2004), and their concentration depends on the amount of both tocopherol and oil. Nolasco et al. (2004) found that the variation in oil weight per grain accounted for 73% of the variation in total tocopherol concentration in sunflower oil. The relationship between tocopherol concentration in oil and oil weight per grain showed a dilution-like shape (Figure 1c), independently of location, the hybrid and its maximum oil concentration, or the intercepted radiation during grain filling (Nolasco et al., 2004). Oil weight per grain also accounted for much of the variation in oil tocopherol concentration in traditional varieties of soybean and rape but not in maize, a species with a low grain oil concentration (Izquierdo, 2007). The simple relationship between tocopherol concentration in oil and oil weight per grain can be easily incorporated into crop simulation models and used to identify management practices useful to obtain grains with greater quantity of tocopherols. Also, these relationships could be useful for commercialisation and grain processing, to estimate the tocopherol concentration of a grain lot from weight per grain and oil concentration, which are simpler, faster and less expensive to measure than tocopherol concentration.

2.4. Protein concentration

Grain protein concentration, usually expressed in percent of grain dry mass, is the main determinant of the end-use value of most cereal and grain legume species. This is particularly true for wheat, which is mostly consumed by humans after processing. Cereal grains contain a relatively small concentration of protein, typically between 8 and 18%, but the large dependence on maize, wheat and rice as main sources of carbohydrates and energy means these species account for 85% of dietary proteins for humans (Shewry, 2007).

In the field, variations in grain protein concentration induced by weather, water and nitrogen availability, especially during the grain-filling period, are much larger than variations due to genotype (Cooper et al., 2001). For wheat, variations in grain protein concentration in response to temperature, solar radiation, CO_2 or soil water availability are mainly related to variation in the quantity of carbon compounds (i.e. starch and oil) per grain, while the quantity of nitrogen compounds (i.e. proteins) per grain is relatively stable (Panozzo and Eagles, 1999; Triboi and Triboi-Blondel, 2002; Triboi et al., 2006). In oil crops, an increase in oil concentration is generally associated with a decrease in protein concentration (López Pereira et al., 2000; Morrison et al., 2000; Uribelarrea et al., 2004), as a result of a dilution effect (Connor and Sadras, 1992).

The interplay between carbon and nitrogen compounds leading to a final concentration of protein in grain can most simply be explained by the effects of environmental factors during the filling period on the rate and duration of accumulation of starch, oil and protein. Starch, oil and protein depositions in the grain are relatively independent from each other and are controlled differently (Jenner et al., 1991). The synthesis of grain starch and oil mostly relies on current photosynthesis. Therefore, the quantity of starch and oil per grain is mainly determined by the duration in days of the grain-filling period. The rate of accumulation of carbon compounds per day is little modified by post-anthesis environmental factors, while the duration of grain filling in thermal time shows little variation (Triboi et al., 2003; DuPont et al., 2006b). This explains why, usually, grain dry mass is closely correlated with the rate of accumulation of grain dry mass per degree-day or with the duration of grain filling in days. In contrast, under most conditions, the synthesis of grain protein relies mostly on nitrogen remobilisation from the vegetative organs. Chapter 8 (Section 3.1) discussed the relative contribution of current assimilation and reserves to the carbon and nitrogen economy of grains, and emphasised differences between wheat and rice, for which 60–95% of the harvested grain nitrogen derives from remobilisation of stored N, and maize where this proportion is only 45–65%.

The rate of grain nitrogen accumulation per degree-day is little modified by temperature or water supply (Triboi et al., 2003; DuPont et al., 2006b), which means that any temperature-driven decrease in the duration in days of the grain-filling period is compensated by an increase in the rate of accumulation of grain nitrogen per day. Under water deficit or high temperature, the higher rate per day of nitrogen remobilisation of pre-flowering nitrogen from the plant to the grain results in an acceleration of canopy senescence and a reduced remobilisation of pre-anthesis carbon (Palta et al., 1994; Triboi and Triboi-Blondel, 2002). Under very high temperature (maximum daily temperature higher than 30–35 °C, depending on the species), this compensation phenomenon decreases and the quantity of nitrogen per grain may decrease. If environmental constraints are applied during the early phase of grain development (i.e. during the phase of endosperm or cotyledon cell division), then the rate of accumulation of carbon may be reduced, which accentuates the increases of grain protein concentration (Gooding et al., 2003). The effects of these environmental factors before anthesis on grain protein concentration depend mainly on their effect on the sink-to-source ratio, but the processes described above still drive grain protein concentration (Chapter 8).

In contrast with the effects of post-flowering temperature, radiation or water supply, the effects of nitrogen supply on grain protein concentration are mostly due to changes in the amount of nitrogen per grain, which for most crop species is regulated by nitrogen availability in the vegetative organs and in the soil during the grain-filling period (e.g. Lhuillier-Soundele et al., 1999; Martre et al., 2003). The number of grains set usually matches the growth capacity of the canopy during the grain-filling period (Sinclair and Jamieson, 2006), and as a consequence, average grain dry mass is little modified (or increases slightly) under pre- and/or post-flowering soil nitrogen shortage (Triboi et al., 2003; Uribelarrea et al., 2004).

To model the effects of the environment on protein concentration, it is necessary to take into account the dynamics of carbon and nitrogen accumulation in the grain. This has been successfully achieved in the wheat model *SiriusQuality*1 (Martre et al., 2006), which is described in Section 3.2. In this model, the accumulation of structural proteins and carbon, which occurs during the stage of endosperm cell division and DNA endoreduplication, is assumed to be sink regulated and is driven by temperature. In contrast, the accumulation of storage proteins and starch, which occurs after the endosperm-cell-division period, is assumed to be source regulated (i.e. independent of the number of grains per unit ground area) and is set daily to be proportional to the current amount of vegetative non-structural nitrogen.

2.5. Protein composition

Storage proteins account for 70–80% of the total quantity of reduced nitrogen in mature grains of cereals and grain legumes, and their composition greatly influences their processing and nutritional quality (Wieser and Zimmermann, 2000; Gras et al., 2001; Khatkar et al., 2002). It is important to note that grain protein concentration in wheat has decreased linearly with the year of cultivar release, but flour functionality has increased significantly (Ortiz-Monasterio et al., 1997; Fufa et al., 2005). This trend is partly associated with the selection of favourable storage protein alleles after the mid-1980s (Branlard et al., 2001). Although the qualitative protein composition of grain depends on the genotype, its quantitative composition is largely determined by environmental factors, including nitrogen and sulphur availability (Graybosch et al., 1996; Huebner et al., 1997; Panozzo and Eagles, 2000; Zhu and Khan, 2001).

Wheat storage proteins are encoded by over 100 genes located at different loci (Shewry and Halford, 2003), coding for high-molecular-weight glutenin subunits (HMW-GS), low-molecular-weight glutenin subunits (LMW-GS), α/β-gliadins, γ-gliadins and ω-gliadins. Gliadins and glutenins are collectively referred to as prolamins. Glutenins are polymeric proteins that form very large macro-polymers with viscoelastic properties (responsible for the unique rheological properties of wheat flours; Don et al., 2003), while gliadins are important in conferring extensibility to dough (Branlard et al., 2001). Grain storage proteins accumulate mainly during the linear phase of grain filling. For wheat, during the desiccation phase after physiological maturity (Box 1 in Chapter 12), glutenin proteins form very large polymers (Carceller and Aussenac, 2001) whose size distribution plays a central role in determining wheat flour functionality (Don et al., 2003).

Environmentally induced changes in grain protein composition are associated with the altered expression of genes encoding storage proteins, in response to signals that indicate the relative availability of nitrogen and sulphur (Bevan et al., 1993; Peak et al., 1997; Chiaiese et al., 2004; Hernandez-Sebastia et al., 2005). These signals trigger transduction pathways in developing grains that, in general, balance the storage of nitrogen and sulphur to maintain homoeostasis of the total amount of protein per grain (Tabe et al., 2002; Islam et al., 2005). Emergent properties of these regulation networks, which are still poorly understood at the molecular level, are allometric relations between the amount of nitrogen per grain and the amount of the different storage protein fractions (Sexton et al., 1998b, for soybean; Landry, 2002, for maize; Triboi et al., 2003, for wheat). These relations are independent of the causes of variations of the quantity of nitrogen per grain and are similar for developing and mature grains (Figure 3a–c, compare main panels and insets; Daniel and Triboi, 2001; Triboi et al., 2003), meaning that environmental factors, including supply of water and nitrogen, do not directly influence grain protein accumulation, but only indirectly through their effect on grain nitrogen accumulation. It thus appears that the gene regulatory network involved in the control of the synthesis of storage proteins is coordinated in such a way that the grain reacts in a predictable manner to nitrogen availability, yielding a meta-mechanism at the grain level (Martre et al., 2003).

A consequence of this meta-mechanism is that grain protein composition is closely related to the total quantity of proteins per grain, independently of the cause of its variation. For wheat, the proportion of total glutenin in grain protein, as well as the proportion of each HMW-GS in the total HMW-GS (Wieser and Zimmermann, 2000; DuPont et al., 2007), appears to be independent of the quantity of nitrogen per grain; in contrast, the proportion of gliadin in grain protein shows significant environmental variation (Figure 3c). Changes in the proportion of gliadin are directly related to the variation in the quantity of nitrogen per grain and are compensated by a proportional decrease of non-prolamin protein. These variations in grain protein composition are accompanied by changes in amino acid composition with the total quantity of nitrogen per grain

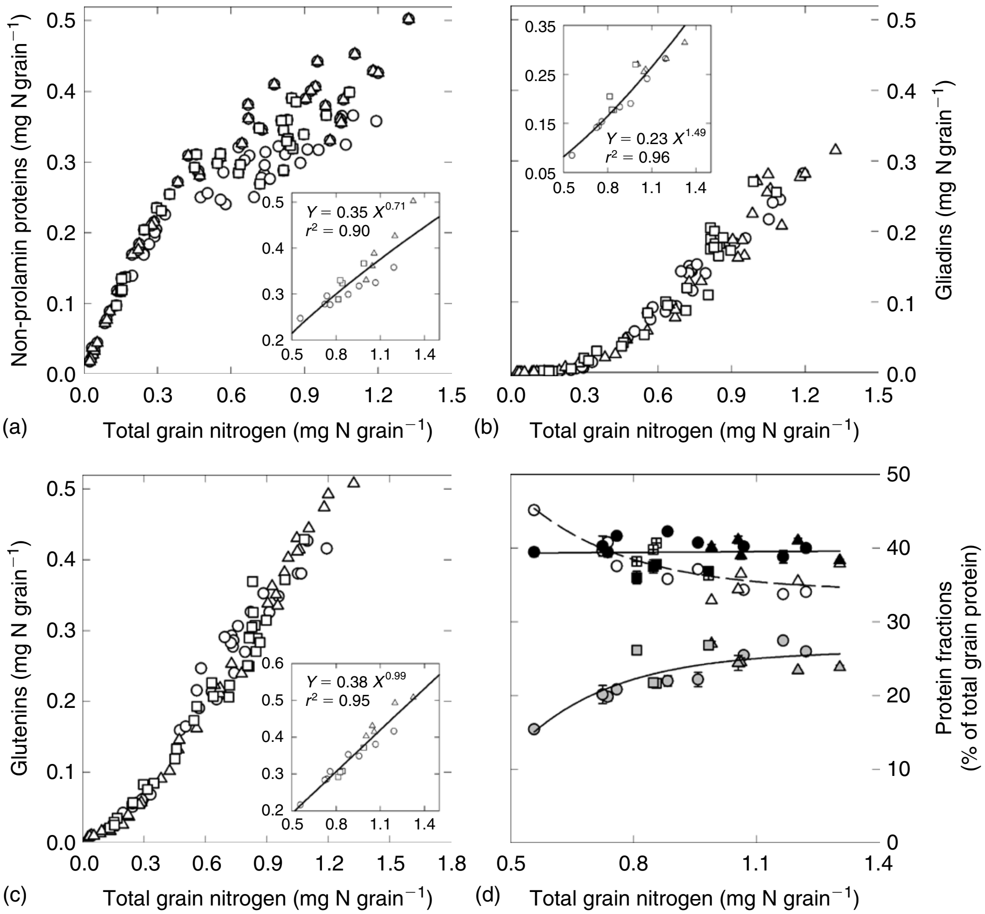

FIGURE 3

Quantities of (a) non-prolamin proteins, (b) gliadins, (c) and glutenins per grain versus the total quantity of nitrogen per grain for developing and mature grains of bread wheat. Insets show the allometric relations between the quantity of each protein fraction and the total quantity of nitrogen for mature grains only. (d) Percentages of non-prolamin proteins (open symbols), gliadins (grey symbols), and glutenins (closed symbols) versus the total quantity of nitrogen per grain for mature grains. Crops were grown in semi-controlled environments with different post-anthesis temperatures (triangles) and water supplies (rectangles), and in the field with different rates and times of nitrogen fertilisation (circles). (Source: Redrawn with permission from Triboi et al., 2003.)

(Eppendorfer, 1978; Mossé et al., 1985). A practical implication of these relations is that grain protein and amino acid composition can be calculated directly from the quantity of nitrogen per grain, independently of the growing conditions. Analysis of the genetic variations of the allocation coefficients of nitrogen in bread wheat showed that, even though there are some statistically significant variations among genotypes, genotypic differences in grain protein composition are primarily driven by variations in the total quantity of nitrogen per grain (Martre and Samoil, unpublished results).

Nitrogen supply determines the level of protein accumulation in the grain and its gross allocation between storage protein fractions, but, at a given level of nitrogen supply, sulphur supply fine-tunes the composition of the protein fractions by regulating the expression of individual storage protein genes (Hagan et al., 2003;

Chiaiese et al., 2004). Interestingly, DuPont et al. (2006a) noted that any factor that increases the amount of nitrogen per grain also increases the proportion of sulphur-poor (ω-gliadins and HMW-GS) storage protein at the expense of sulphur-rich (α/β-gliadins, γ-gliadins and LMW-GS) storage protein. These authors proposed a putative molecular mechanism by which nitrogen activates the synthesis of glutamine and proline, thus favouring the synthesis of sulphur-poor proteins rich in these amino acids. An alternative hypothesis is that the accumulation of sulphur-rich storage proteins, determined by sulphur availability, generates a signal of sulphur deficiency, which increases the expression of sulphur-poor storage proteins to the extent of nitrogen available to it. The latter hypothesis is substantiated by reported differences in temporal appearance and spatial distribution of sulphur-rich and sulphur-poor storage proteins in developing grains of maize (Lending and Larkins, 1989) and wheat (Panozzo et al., 2001).

Very high temperature, above a threshold of daily average temperature of about 30 °C, can have marked effects on wheat dough strength, and these effects are largely independent of grain protein concentration (Randall and Moss, 1990; Blumenthal et al., 1991; Wardlaw et al., 2002). Relatively small variation in the proportions of the different types of gliadin and glutenin subunits have been reported in response to chronic or short periods of very high temperature, and it is difficult to convincingly relate such variations to changes in flour functionality. Weaker dough from grains that experience one or several days of very high temperature has been related to a marked decrease in the proportion of large-molecular-size glutenin polymers (Ciaffi et al., 1996; Corbellini et al., 1998; Wardlaw et al., 2002; Don et al., 2005). The aggregation of glutenin proteins, which occurs mainly during the phase of grain desiccation after physiological maturity (Carceller and Aussenac, 2001), is likely the major process responsible for heat-shock-related dough weakening.

Extended periods of high temperature are common in many cereal-growing areas of the world, and above-optimal temperature is one of the major environmental factors affecting small grain cereal yield and composition (Randall and Moss, 1990; Borghi et al., 1995; Graybosch et al., 1995). Some results suggest that very high temperature around mid-grain filling has positive effects on wheat dough strength (Stone et al., 1997; Panozzo and Eagles, 2000), whereas very high temperature around physiological maturity has a negative effect on dough strength (Randall and Moss, 1990; Blumenthal et al., 1991; Stone and Nicolas, 1996). This difference in the response of dough properties according to the timing of heat shock may be related to different effects on the gliadin-to-glutenin ratio and the size of glutenin polymers at each developmental stage. Further experiments to identify the relative sensitivity of different development stages in terms of gliadin and glutenin accumulation and glutenin polymer formation are clearly required. Important genetic variation in the relative response of grain protein composition and flour functionality to very high temperature has been reported (Blumenthal et al., 1995; Stone et al., 1997; Spiertz et al., 2006), but the genetic and physiological bases of these differences are still largely unknown.

3. INTEGRATION OF QUALITY TRAITS INTO CROP SIMULATION MODELS

Crop simulation models for grain yield have been developed for all the major crop species (Section 4 in Chapter 20). Some sunflower models also simulate oil yield (e.g. Villalobos et al., 1996), but only recently, aspects of oil quality have been included (Pereyra-Irujo and Aguirrezábal, 2007). Most wheat models simulate crop nitrogen accumulation and partitioning (primarily because crop nitrogen status greatly affects crop biomass and grain yield); however, few models have extended the simulation of nitrogen dynamics to account for grain nitrogen concentration (Sexton et al., 1998a; Asseng et al., 2002; Martre et al., 2006). In this section, we outline simulation models for sunflower and wheat, which have integrated grain oil or protein quality modules, based on the relationships described in Section 2. In Section 4, these models will be used to explore strategies to improve quality traits through crop management or breeding.

3.1. Modelling oil concentration and composition and tocopherol concentration in sunflower

The model of Pereyra-Irujo and Aguirrezábal (2007) integrates empirical relationships (Section 2) as shown in Figure 4a. The model includes a temperature-driven phenology module that allows for the critical periods of determination of yield and quality components to be estimated. Fatty acid composition is predicted through its relationship with temperature during its critical period (Figure 1b). Grain oil concentration (Figure 1a) and yield components are estimated taking into account intercepted radiation per plant, which is calculated at the population level. Leaf growth is predicted through its relationship with temperature and plant density. Radiation interception depends, on the one hand, on plant density and individual plant leaf area (which determines the leaf area index) and, on the other hand, on incident solar radiation at the top of the canopy. Then, oil tocopherol concentration is calculated from oil weight per grain (Figure 1c), which in turn depends on grain weight and grain oil concentration.

The original model (Pereyra-Irujo and Aguirrezábal, 2007) was expanded to simulate quality traits for biodiesel (i.e. density, kinematic viscosity, heating value, cetane number and iodine value), using validated empirical relationships with oil fatty acid composition (Pereyra-Irujo et al., 2009). The model provided estimations of potential grain yield similar to those of a more complex model, and good estimates of oil quality and intermediate variables (e.g. phenology, intercepted radiation during different critical periods) over a wide range of environmental conditions (Pereyra-Irujo and Aguirrezábal, 2007; Pereyra-Irujo et al., 2009).

3.2. Modelling grain protein concentration and composition in wheat

Simulation of grain nitrogen content requires first simulating the uptake of nitrogen into the vegetative tissues of the plant, followed by a step where nitrogen is transferred to the grains from vegetative tissues. A mechanistic approach to simulate crop nitrogen accumulation and partitioning has been implemented in the wheat simulation model Sirius (Jamieson and Semenov, 2000; Martre et al., 2006). Figure 4b summarises this model. Nitrogen is distributed to leaf and stem tissues separately, with simplifying assumptions that nitrogen per unit leaf area is constant at the canopy level (Grindlay, 1997), but that the stem could store nitrogen. The effect of nitrogen shortage is to reduce first stem nitrogen concentration and then leaf expansion to maintain specific leaf nitrogen concentration. One advantage of this approach is that it reduces the number of parameters and the need to define stress factors, compared with the demand-driven approaches based on nitrogen dilution (e.g. van Keulen and Seligman, 1987; Stöckle and Debaeke, 1997; Brisson et al., 1998). This approach also provides more plasticity in the response of the crop to nitrogen availability.

The latest version of Sirius (*SiriusQuality*1; Martre et al., 2006) models nitrogen transfer to the grain more mechanistically than previous models (Sinclair and Amir, 1992; Sinclair and Muchow, 1995; Gabrielle et al., 1998; Bouman and van Laar, 2006). Accumulations of structural proteins and carbon, during the stages of endosperm cell division and DNA endoreduplication, and of storage proteins and starch, after the period of endosperm cell division, are explicitly considered. The accumulation of structural proteins and carbon per grain is assumed to be sink regulated and is driven by temperature. On the other hand, the accumulation of storage proteins and starch is assumed to be source regulated (i.e. independent of the number of grains per unit ground area), and is set daily to be proportional to the current amount of vegetative non-structural nitrogen. Sirius and *SiriusQuality*1 successfully simulated yield and protein concentration for contrasting pre- and post-flowering N supplies, post-anthesis temperature and water supply in France (Martre et al., 2006), under the dry climates of Arizona and Australia, across variations in air CO_2 concentration, water and nitrogen supplies and cultivars (Jamieson et al., 2000; Ewert et al., 2002; Jamieson et al., 2009), and under the cooler climate of New Zealand for a range of rates and patterns of water and nitrogen availabilities, locations and cultivars (Jamieson and Semenov, 2000; Armour et al., 2004).

The allometric relations between the total amount of nitrogen per grain and the amount of storage protein fractions presented in Section 2.5 have been used to model gliadin and glutenin accumulation in developing wheat grain (Martre et al., 2003). This model has been implemented in *SiriusQuality*1 and has been evaluated

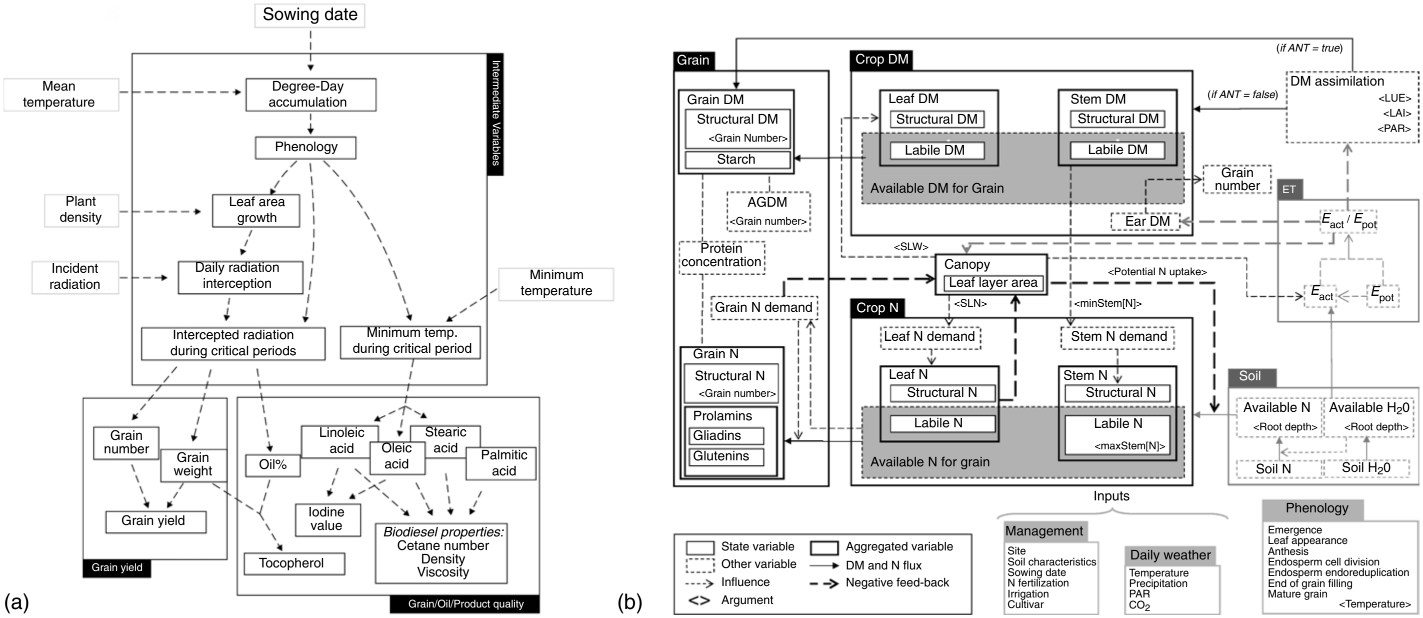

FIGURE 4

(a) Schematic representation of the sunflower simulation model from Pereyra-Irujo and Aguirrezábal (2007) and Pereyra-Irujo et al. (2009) showing the relationships between input variables (outside boxes), intermediate variables and output variables (yield and quality). (Adapted from Pereyra-Irujo and Aguirrezábal, 2007.)

(b) Schematic representation of the wheat simulation model SiriusQuality*1 (Martre et al., 2006) showing the main variables, influences and feedbacks. AGDM, average grain dry mass; ANT, anthesis; DM, dry matter; N, nitrogen;* E_{act}, *actual transpiration;* E_{pot}, *potential transpiration; LAI, leaf area index; LUE, light use efficiency; maxStem[N], maximum stem nitrogen concentration; minStem[N], minimum stem nitrogen concentration; PAR, photosynthetically active radiation; SLN, leaf nitrogen mass per unit of leaf surface area; SLW, leaf dry mass per unit of leaf surface area.*

against a wide range of nitrogen supply and post-anthesis temperature and water supply (Martre et al., 2006). The existence of environment-independent relations of nitrogen allocation for different cereals species (but with different parameter values) suggests that the model developed for wheat can be used to analyse and simulate the allocation of storage proteins for other cereals. The next step would be to model the effect of sulphur availability on the allocation of storage proteins and its interaction with nitrogen availability.

4. APPLYING CROP PHYSIOLOGY TO OBTAIN A SPECIFIC QUALITY AND HIGH YIELDS

In many agronomically relevant conditions, the trade-off between yield and quality is an obstacle to achieve the dual objective of high yield and high quality. This section thus presents a physiological viewpoint of the relationships between yield and oil attributes in sunflower and between yield and protein in wheat, and outlines the physiological concepts of potential value for management and breeding aimed at improving grain quality while obtaining high yields.

4.1. Sunflower yield and oil composition

The interactions between yield and quality in sunflower were analysed for a traditional and a high-oleic sunflower hybrid, using the model presented in Section 3.1 (Figure 4a). Quality attributes were estimated for a wide range of sowing dates and three plant densities, using 35 years of weather data from three locations in Argentina with contrasting radiation and temperature regimes. The same interactions were analysed experimentally in a trial network where five hybrids were sown in 11 locations between 26.7 and 38.6 °S (Peper et al., 2007). Large variation in observed and simulated yield and grain and oil quality traits were obtained both among and within locations.

Positive or negative associations between yield and quality traits depend on the nature of the quality trait. For most of the situations, grain oil concentration and linoleic acid concentration were positively correlated with yield, while the concentration of oleic acid (Figure 5a) and oil tocopherol concentration were negatively correlated with yield. Results for the traditional hybrids in the trial network showed a similar pattern of negative correlation between oleic acid concentration and yield (Peper et al., 2007), which suggests that it might be possible to infer the physiological causes of these correlations from the mechanisms operating in the model.

Simulations showed that temperature differences among locations were the main cause of the negative correlations between yield and oleic acid. Oleic acid concentration increases with temperature between 100 and 300 °C day after flowering, whereas grain yield decreases with temperature around flowering (Cantagallo et al., 1997) and during early grain filling (between 250 and 450 °C day after flowering; Aguirrezábal et al., 2003), when the grain number and grain dry mass are determined, respectively. Because of this overlap of the critical periods for oleic acid concentration and yield, it is not easy to avoid this negative correlation when sowing a traditional sunflower hybrid. However, because this overlap was only partial, in a given year and location, temperature fluctuations over the reproductive period can reverse the general tendencies. So, despite the average negative correlation, it is possible to calculate, from model outputs, the probability of obtaining relatively high product quality (in this case oleic acid concentration) with a high yield at a given location. For instance, the probability of obtaining oil with more than 35% oleic acid in Paraná is 50% if yield potential is lower than 2.5 $\mathrm{t\,ha^{-1}}$, and decreases to 27% for higher yields (Pereyra-Irujo and Aguirrezábal, unpublished results).

In some cases, genetic improvement can break negative correlations between quality traits and yield. This is easiest when quality traits depend on relatively few genes (as for high-oleic trait in sunflower, Section 2.2). For instance, simulated and experimental data showed that oleic acid concentration for sunflower cultivars with high-oleic genes was almost independent of yield (Figure 5b; Peper et al., 2007).

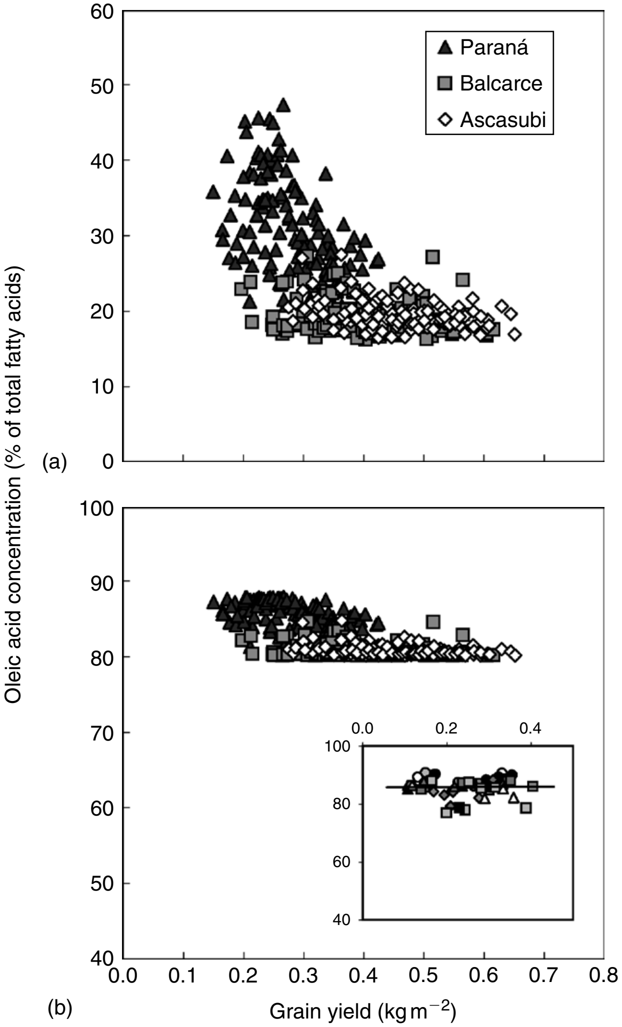

FIGURE 5

Relationship between simulated oleic acid concentration and crop grain yield for (a) a traditional hybrid and (b) a high-oleic hybrid, for three contrasting locations in Argentina. Inset: relationship between measured oleic acid concentration and grain yield for 15 high-oleic sunflower hybrids sown in different locations in Argentina (Source: Pereyra-Irujo and Aguirrezábal, unpublished).

In sunflower, oil tocopherol concentration was negatively correlated with yield (Pereyra-Irujo and Aguirrezábal, 2007). In this case, the response was the same at all locations, but depended strongly on the sowing density. This was because, at higher densities, the same yield can be obtained with a higher number of smaller grains, for which the response curve of tocopherol concentration to variations in oil concentration is steepest (Figure 1c). The negative correlation between oil tocopherol concentration and yield results from the relationship between oil tocopherol concentration and oil weight per grain. This relationship follows a dilution-like curve, with a steeper slope for grains with less than 15 μg oil (Figure 1c). Within this range, oil tocopherol is therefore inversely correlated with weight per grain, which is the main driving component of oil weight per grain, and also one of the two components of yield. However, it is well known that yield is mainly driven by the number of grain per square metre and that the correlation between grain number and weight per grain is weak for sunflower (Cantagallo et al., 1997). Therefore, it could be expected that high oil tocopherol concentration could be obtained together with high yield, provided that this yield results mainly from a high grain number per square metre with small grains. This deduction, based on simulations and application of physiological principles was confirmed in a trial network (Peper et al., 2007), where oil tocopherol concentration was negatively related with oil weight per grain, but no clear correlation was found with yield. For hybrids genetically producing small grains, oil tocopherol concentration higher than $800\,\mu g\,g\,oil^{-1}$ and yield higher than $3100\,kg\,ha^{-1}$ were obtained when grain number was higher than 6700 grains m^{-2} (A. Peper, personal communication), i.e. close to the maximum number of grains per square metre observed under normal field conditions (López Pereira et al., 1999).

4.2. Wheat yield and protein concentration

Negative relationships between yield and grain protein concentration in wheat have been known for more than 70 years (Waldron, 1933; Metzger, 1935; Neatby and McCalla, 1938; Grant and McCalla, 1949), and crop physiologists have analysed the effect of environmental factors on this relation for over 40 years (Terman et al., 1969). Since the pioneer works on wheat, this negative grain yield–protein concentration relation has been reported for all the major crops, including maize (Dubley et al., 1977), sunflower (López Pereira et al., 2000), soybean (Wilcox and Cavins, 1995) and cowpea (Olusola Bayo, 1997). This correlation is observed when comparing different genotypes and also for a given genotype in response to environmental conditions or management practices.

Several putative physiological causes of the relationship between yield and protein concentration have been proposed, but the picture is still incomplete (reviewed in Feil, 1997). It has been hypothesised that the energetic cost of protein synthesis limits crop nitrogen assimilation and protein synthesis in the grain (Bhatia and Rabson, 1976; Munier-Jolain and Salon, 2005). However, nitrogen uptake during the pre- and/or post-flowering periods and/or the efficiency of nitrogen translocation from vegetative organs to grains are more likely to explain this correlation (Kade et al., 2005). Consistently with this hypothesis, late (between heading and flowering) application of nitrogen fertiliser often increases grain protein concentration, without reducing yield (Triboi and Triboi-Blondel, 2002). It has also been suggested that the observed genetic correlation between grain yield and protein concentration is at least in part due to the increase in dry matter harvest index (i.e. grain-to-straw dry mass ratio), which has accompanied most of the genetic progresses in yield over the last 50 years, resulting in a reduction of the storage capacity of the crop for nitrogen (Kramer and Kozlowski, 1979). There is contradicting evidence concerning this issue (Cox et al., 1985; Slafer et al., 1990; Bänziger et al., 1992; Calderini et al., 1995; Uribelarrea et al., 2004; Abeledo et al., 2008), which possibly results from different patterns of spatial and temporal availability of soil nitrogen (taking into account soil moisture) throughout the growing season. Some authors (e.g. Feil, 1997) argued that the seemingly universal genetic negative correlation between grain yield and protein concentration is an artefact of inadequate availability of soil nitrogen in most experiments. However, several reports showed significant variations of crop nitrogen yield independently of yield, suggesting that a significant part of the negative relation is under genetic control (e.g. Monaghan et al., 2001; Laperche et al., 2007).

The effects of weather and specific environmental factors on the grain yield–protein concentration relation were studied using *SiriusQuality*1 (Martre et al., 2006). The model was run for a wide range of nitrogen availabilities, using 100 years of synthetic daily weather data representing typical conditions in France, as well as scenarios where conditions were modified by increasing or decreasing temperature or radiation.

At medium nitrogen supply, a unique relationship was observed, independently of the causes of yield and grain protein concentration variation (Figure 6a). The simulated effects of post-flowering temperature, radiation and water supply were very similar to those observed experimentally (Terman et al., 1969; Pushman and Bingham, 1976; Terman, 1979; Triboi et al., 2006). Interestingly, for a large range of simulated yield, the relationship with protein concentration was non-linear. The analysis of the few experimental results

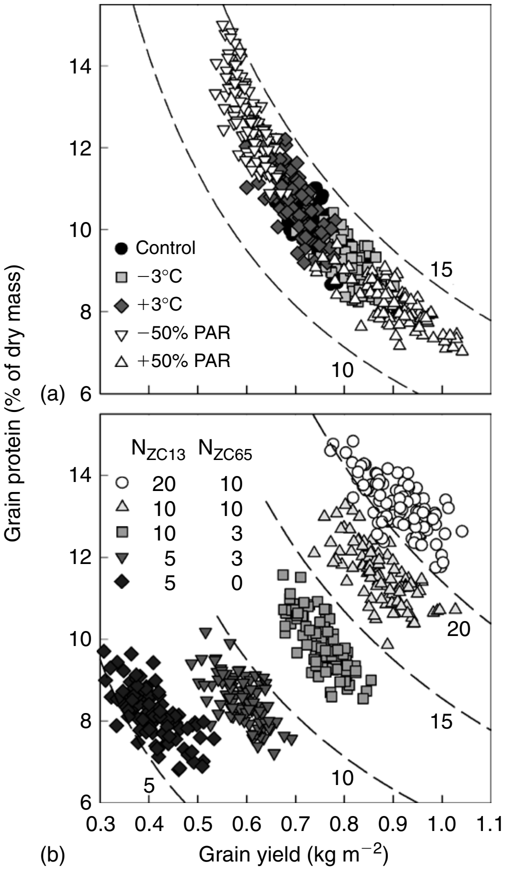

FIGURE 6

Simulated grain protein concentration versus grain yield for wheat crops in response to variations (a) of the post-flowering temperature (average daily temperature increased or decreased by 3°C) or solar radiation (daily cumulated radiation increased or decreased by 50%) and (b) of nitrogen fertilisation (indicated rates in g N m^{-2}) were applied when the crops had three leaves [N_{ZC13}] or at anthesis [N_{ZC65}]). In (a) the crops received 10 g N m^{-2} at three leaves and 10 g N m^{-2} at anthesis. Simulations were performed with the wheat simulation model SiriusQuality*1 (Martre et al., 2006) for 100 years of daily synthetic weather generated with the LARS-WG stochastic weather generator (Semenov and Brooks, 1999) for Clermont-Ferrand, France. Dashed lines are grain nitrogen yield isopleths (g N m^{-2}). Details of the soil and cultivar characteristics are given in Martre et al. (2007).*

with significant ranges of grain yield also clearly indicates that the relation deviates from linearity (Metzger, 1935; Simmonds, 1995; Rharrabti et al., 2001). The non-linearity is due to the dilution of a roughly constant amount of nitrogen in an increasing amount of carbon components. The negative relation also tends to deviate slightly from the grain nitrogen yield isopleths showing decreases of the simulated crop grain nitrogen yield for the higher yielding conditions. This was associated with a decrease in the total crop N yield rather than with a systematic effect on the nitrogen harvest index (data not shown). These high-yielding conditions were associated with long growth cycles (when simulation was performed considering that average daily temperature was increased by 3 °C), with late grain filling occurring under water-limited conditions, thus limiting crop nitrogen accumulation. This phenomenon probably reflected an interaction between the simulated treatment and the climate structure of the study site rather than an absolute outcome of the model. More generally, it is interesting to note that, in *SiriusQuality*1, the dynamics of nitrogen and dry matter are mostly independent from each other. This relation is therefore an emergent property of the model. The model was thus able to simulate the observed effects of temperature, radiation and water and nitrogen supplies on the negative relation, although it was not part of the model assumptions. These results give confidence for using *SiriusQuality*1 to analyse environmentally induced variation of grain yield and protein concentration, and the interactions between carbon and nitrogen metabolisms at the crop level.

At low nitrogen availability, grain yield increases linearly with the amount of nitrogen available, and a constant grain protein concentration is expected. For higher availability of nitrogen, the rate of increase of grain yield with soil nitrogen availability decreases (nitrogen use efficiency decreases), grain protein concentration increases faster than grain yield and a positive correlation between grain yield and grain protein concentration is expected (Fowler et al., 1990); Section 4.3 in Chapter 8 further discusses the trade-offs between nitrogen use efficiency and protein content. Similarly, the simulated effect of nitrogen fertiliser on the grain yield–protein concentration relation (Figure 6b) is in agreement with the existing literature (Pushman and Bingham, 1976; Oury et al., 2003; Triboi et al., 2006). Some experimental data suggest possible weaker correlation with very high or low nitrogen supplies (Kramer, 1979; Fowler et al., 1990). Such effects were not observed in the present simulations, but extreme treatments would probably have more drastic effects on the grain yield–protein concentration relationship in an environment with a more marked inter-annual variability for water stress during the growth cycle.

Figure 7 summarises the effects of environmental variables on grain yield and protein concentration. At a given nitrogen supply and sink-to-source ratio, environmental factors modify grain yield and protein concentration symmetrically, and a close negative correlation between grain yield and protein concentration is observed (Terman et al., 1969; Terman, 1979; Triboi et al., 2006). If environmental conditions reduce the sink-to-source ratio, then a partial compensation may occur; the grain yield–protein concentration relation is then shifted. If the sink capacity (number of grains) is limited by early drought, by high temperature or genetically, then the duration of grain filling can be shortened. In this case, yield decreases despite

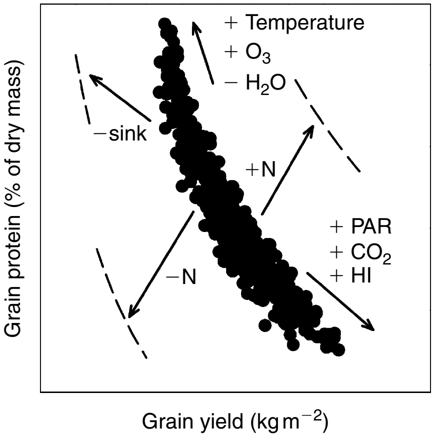

FIGURE 7

Summary of the effects of temperature, CO_2, O_3, radiation, supply of nitrogen and water, and ecophysiological traits (-sink: low sink-to-source ratio; +HI: increased dry mass harvest index) on the relationship between grain yield and protein concentration. Genetic progress has continuously increased grain yield while grain N concentration has decreased linearly with yield (closed symbols). The environmental factors have contrasting effects on this relation, depending if they modify or not the sink–source ratio, and on their effects on grain yield. HI, harvest index; PAR, photosynthetically active radiation. (Source: Triboi et al., 2006.)

an increase in single grain dry mass. At the grain level, the sink-to-source ratio increases more for nitrogen than for carbon, and grain protein concentration can be higher than under conditions of non-limiting sink. Under limiting-nitrogen conditions, the slope of the genetic yield–protein concentration relationship decreased (Triboi et al., 2006), and thus grain protein concentration became slightly more sensitive to yield variation than under non-limiting-nitrogen conditions (Figure 7).

The grain yield–protein concentration relationship is often hidden by environmental and management effects and, on average, can often be non-existent (Simmonds, 1995; Oury et al., 2003; Munier-Jolain and Salon, 2005). As shown here, this is explained by the different effects of environmental factors and management practices on crop dry mass and nitrogen dynamics, but these effects can be successfully analysed through simulation models.

4.3. Management strategies for obtaining a target grain and oil composition

4.3.1. Grain oil concentration

Grain oil concentration in sunflower depends on intercepted radiation per plant during a critical period (Figure 1a). High oil concentration would therefore require adjustment of management practices (e.g. sowing date, choice of cultivar, sowing density and fertilisation) to enhance intercepted radiation during such period. For instance, late sowing decreases not only grain yield but also grain oil concentration in high-oil sunflower hybrids. For three locations in Argentina, simulated grain oil concentration decreased when sowing date was delayed (Pereyra-Irujo and Aguirrezábal, 2007). This was due to the fact that, on average, radiation decreases more rapidly than temperature after the summer solstice, causing a steady decline in the amount of radiation intercepted per plant. Delaying sowing decreased grain oil concentration at 1–2% per month, but with a different magnitude, according to the location. When a low intercepted radiation during grain filling is expected (e.g. late sowing), the oil yield of low-oil hybrids is similar to that of high-oil hybrids (Izquierdo et al., 2008); therefore, cultivar choice can be based on other traits.

A fine-tuning of nitrogen supply and demand is necessary to obtain high oil concentration. Excessive fertilisation can reduce grain oil concentration and therefore decrease the commercial quality of the product in sunflower and rape (e.g. Steer et al., 1984; Jeuffroy et al., 2006). In sunflower, this situation can be frequent, since sunflower nitrogen requirements are relatively low, with respect to other crops (Andrade et al., 1996). Models and spatial technologies accounting for soil variation can assist in a more precise prevision of nitrogen requirements for specific yield and grain quality targets (Section 2.2 in Chapter 19; Jeuffroy et al., 2006).

4.3.2. Oil fatty acid composition

Hybrid selection, sowing date and location are the three main management practices that can be used to obtain oils with different properties (Box 1), as illustrated in Figure 8. To obtain oil with a high proportion of oleic acid using traditional hybrids, crops should be grown in warm regions, sowing date should be adjusted so that minimum temperatures are high during grain filling and hybrids with a high maximum concentration of oleic acid should be used (about 50%, close to a mid-oleic hybrid) (Figure 8). High-oleic hybrids, on the other hand, would yield oil with low unsaturation (80% oleic acid), independently of location or sowing date (Figure 8). To obtain oils with a high proportion of linoleic acid, hybrids with a low minimum oleic acid concentration (high maximum linoleic acid concentration) should be used, and they should be sown early at high latitudes (Figure 8).

Several quality parameters of biodiesel are highly dependent on fatty acid composition (Clements, 1996). Simulated density, kinematic viscosity and heating value produced from sunflower oil were very stable, whereas simulated iodine value and cetane number were highly variable between hybrids, regions and sowing

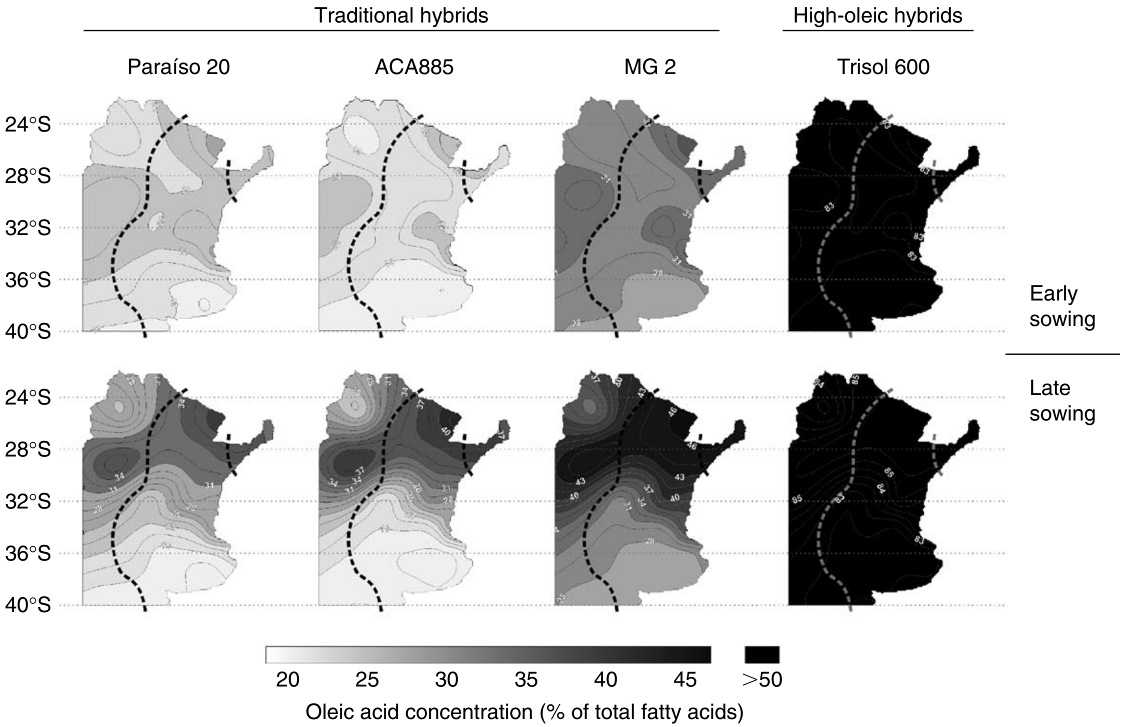

FIGURE 8

Simulated oleic acid concentration for traditional and high-oleic sunflower hybrids. Early (top maps) and late (bottom maps) sowings were used in simulations. Simulations using the optimum sowing date (not shown) yielded results intermediate between those of early and late sowings. The main sunflower growing region of Argentina is between the two dotted lines. Details of the simulations are given in Pereyra-Irujo et al. (2009).

dates. For the high-oleic sunflower cultivar, all the analysed parameters fell within the limits of the two main biodiesel standards (ASTM D6751 from the United States, and EN 14214 from Europe). For traditional cultivars, the US standard was met in almost all cases, whereas the European specifications were met only by the hybrid with the highest maximum oleic acid concentration. For a given cultivar, biodiesel quality tended to be higher at lower latitudes and in late sowings, following the degree of oil saturation (Figure 8).

4.3.3. Grain protein concentration

In most intensive cropping areas, management of nitrogen fertiliser is the main approach to obtain a targeted grain yield and protein concentration. This practice has an important economical cost for the farmer – for example, in France, it represents about 60% of the cost of growing a wheat crop – but also has a potentially deleterious environmental effect (Section 1 in Chapter 8). Until very recently, considerations of fertiliser needs have been mostly driven by yield rather than protein targets, except in crops such as barley where narrower bands of grain protein have a more marked influence on grain price. Management of nitrogen fertilisation is discussed in other parts of this book; Chapter 8 (Section 2.3) details physiological approaches for the diagnosis of nitrogen deficiency, and Chapter 19 (Section 2.2) combines physiological principles, modelling and spatial techniques to deal with the elusive nitrogen-by-water interaction driving fertiliser needs in dry land farming.

4.4. Strategies for genetic improvement of quality traits

4.4.1. *Grain oil concentration*

As mentioned earlier, genetic analyses of crosses between high-oil sunflower hybrids have identified alleles that could potentially increase grain oil concentration (Mestries et al., 1998; Mokrani et al., 2002; Bert et al., 2003). These studies, however, did not link the differences in oil concentration to anatomical or physiological characteristics. This information could be of importance to determine, for instance, whether future increases in grain oil concentration through decreased pericarp weight (and therefore decreased grain weight) could be negatively correlated to yield, if grain number is not able to compensate for a reduced grain weight (Mantese et al., 2006).

As genetic differences become smaller among modern, high-oil, sunflower hybrids, and given the relative environmental instability of their oil concentration (as compared to low-oil hybrids), the effect of the environment becomes increasingly important. However, the effect of environmental conditions and their interactions with genotype on oil concentration have received less attention than the effect of genotype. The well-known effect of radiation on grain oil concentration (Figure 1a) is probably one of the causes of the frequent co-localisation of QTLs for flowering date and grain oil concentration (Section 3.1.2 in Chapter 11; León et al., 2000). In sunflower, a critical period during grain filling has been identified (Aguirrezábal et al., 2003), during which grain oil concentration is closely associated with intercepted radiation and temperature, following a predictable response curve. Based on this relationship, two (possibly complementary) strategies for improving oil concentration can be proposed, which are represented in Figure 9a:

(i) Selecting for traits that result in increased radiation interception during this period (e.g. stay-green mutants, resistance to leaf diseases) should lead to increased oil concentration (Figure 9a). Also, care should be taken that increases in 'greenness' effectively result in increased photosynthesis, which is not always the case with stay-green mutants (Hall, 2001; see also Box 1 in Chapter 9). Likewise, visual disease symptoms are not always correlated to reductions in photosynthesis (e.g. Sadras et al., 2000).

(ii) Another strategy could be to select for higher maximum oil concentration (dotted line in Figure 9a). A simple way to measure this trait would be to thin, after flowering, crops sown at a normal density. This would result in high radiation interception per plant, without the confounding effects of high grain number per plant or high grain weight potential (Aguirrezábal et al., 2003).

4.4.2. *Oil fatty acid composition*

Crop breeding has achieved many modifications of the fatty acid profile of oil in many species, mainly through the incorporation of genes with large effects (for a review, see Velasco and Fernandez-Martinez, 2002). The effect of the environment on these genotypes with modified fatty acid composition is relatively small (e.g. up to 6.9% for high-oleic sunflower; Izquierdo and Aguirrezábal, 2008), but it can still be a concern, especially with strict market standards. The stability of improved fatty acid compositions and the achievement of a desired quality under specific environments are important breeding objectives.

The parameters of the model in Section 2.2 showed a wide variation between traditional high-linoleic sunflower hybrids (Izquierdo and Aguirrezábal, 2008). The stability of minimum and maximum oleic acid concentrations for temperatures outside the range of strong response (Figure 1b) provides a simple way to screen for high or low values of individual parameters (y_0 and y_{max}, dotted lines in Figure 9b), by sowing at locations or on dates of known temperature, or under semi-controlled conditions, for example, greenhouse. Of these two parameters, y_0 showed the highest genetic variability. Such screening could be simpler and less expensive than direct screening for the trait (oleic acid percentage). Another approach could be to develop cultivars for specific environments. For instance, a genotype yielding very-high-linoleic oil under low temperature could be obtained by selecting for a low y_0, irrespective of other parameters.

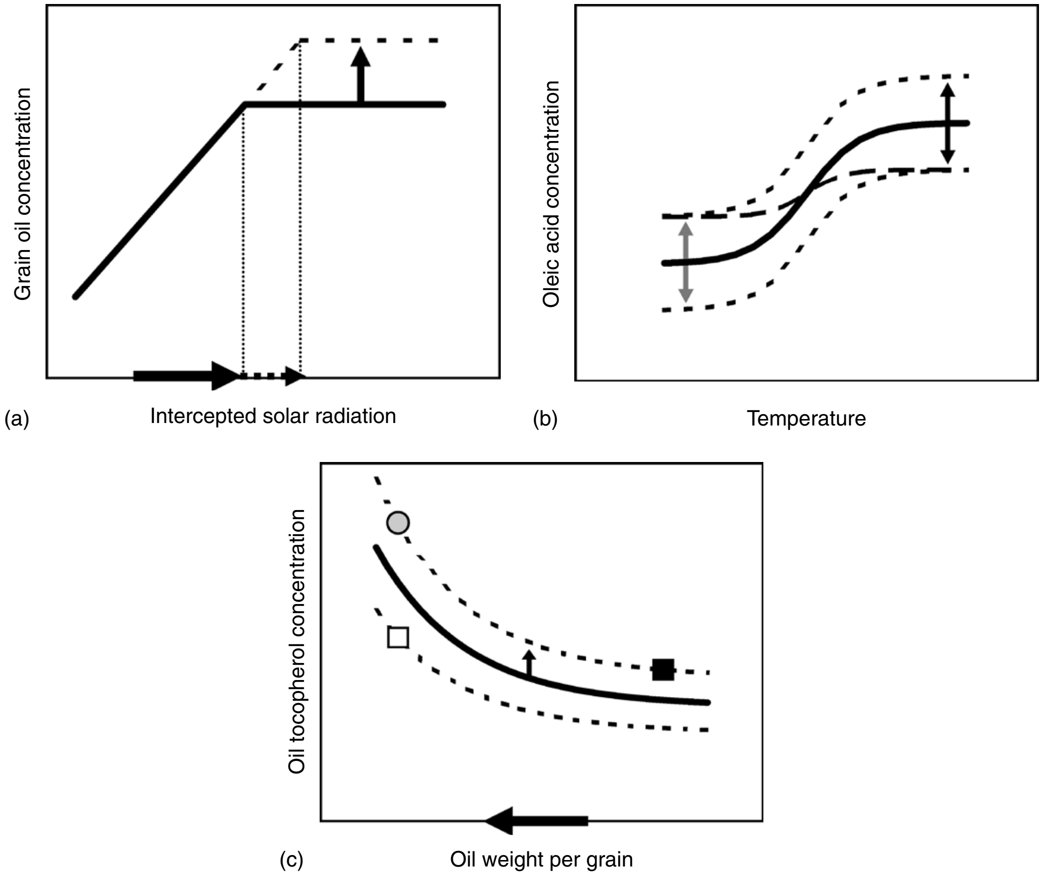

FIGURE 9

Main avenues proposed for the genetic modification of sunflower quality traits, based on relationships presented in Figure 1: (a) grain oil concentration: increased radiation interception during the critical period (arrows along the x-axis), and higher maximum oil concentration (dotted line); (b) oleic acid concentration: changes in the plateau values for minimum (grey arrows) and maximum (black arrows) oleic acid concentrations, to obtain either higher or lower average concentration (dotted lines) or increased stability (dashed line); and (c) oil tocopherol concentration: increased tocopherol concentration relative to that expected through the dilution curve (vertical arrow), and decreased oil weight per grain (arrow along the x-axis), combined to obtain high oil tocopherol concentration (grey circle); black and white squares: see text.

This model is also valid for a high-oleic hybrid. Breeders have improved high-oleic sunflower mostly by indirectly selecting for a high y_0. There are, however, high-oleic genotypes that differ in their response to temperature, although this genetic variability has not been quantified using the approach described above. An interesting breeding goal for these genotypes would be to increase the stability of fatty acid composition by selecting for low $slope_{max}$, that is, a low difference between the minimum and maximum concentrations of oleic acid (dashed line in Figure 9b).

For other species, the lack of a robust model, and the need to take into account the effect of radiation (and possibly the interaction between temperature and radiation), could make these approaches more difficult.

4.4.3. Oil tocopherol concentration

In sunflower, an inverse relationship between tocopherol concentration and oil weight per grain (Figure 1c) accounts for most of the environmental effect; therefore, this relationship can theoretically be used to quantify the genetic variability of oil tocopherol concentration. Nolasco et al. (2006) analysed the genetic variability of tocopherol concentration among a group of sunflower hybrids, finding the effect of the environment to be larger than the genotypic effect. A re-analysis of data from Nolasco et al. (2004) through a two-way ANOVA, using the ratio between the measured and expected (according to the dilution-like curve) values (as opposed to the raw tocopherol concentration data), showed that environmental and G × E effects were reduced, the effect of the genotype was increased and differences between genotypes were detected.

Based on this relationship, two strategies for improving oil tocopherol concentration have been proposed:

(i) An ideotype for high-tocopherol concentration in the oil could be defined as a plant with a small amount of oil in each grain. Reducing oil weight per grain (solid arrow along the x-axis in Figure 9c) should preferably be achieved through smaller grains, and not through reduced grain oil concentration (which is an important quality trait per se). Therefore, to avoid negative consequences on grain yield, a smaller grain weight should be compensated by an increased grain number (see also section 4.1).

(ii) Using the relationship between tocopherol concentration and oil weight per grain, screen for genotypes with an improved tocopherol concentration, independently of genetic or environmental variations in oil concentration or grain weight. Such a genotype would be one with a positive deviation from the expected 'dilution' curve (e.g. black square in Figure 9c). A genotype with a higher absolute tocopherol concentration but with a negative value relative to the curve (e.g. white square in Figure 9c) would be expected to have a negative direct effect on tocopherol concentration. This latter genotype should, however, have a positive indirect effect through a decreased oil weight per grain, according to strategy (i). Provided the independence of these two effects, the two strategies presented here could hypothetically be applied simultaneously (grey circle in Figure 9c).

4.4.4. Grain protein concentration

The yield–protein concentration correlation and the large genotype-by-management and G × E interaction components of variance relative to the genotypic component (Cooper et al., 2001) have significantly restrained genetic improvements of grain protein concentration. Breaking this negative relationship remains a major challenge for cereal breeders (DePauw et al., 2007; Oury and Godin, 2007).

Both grain yield and protein concentration are genetically determined by a large number of independent loci. On this basis, some authors have concluded that genetic restrictions caused by linkage or pleiotropy are not sufficient to simultaneously hinder the improvement of both traits (Kibite and Evans, 1984; Monaghan et al., 2001); several breeding programmes have been successful in breaking or shifting this correlation, demonstrating that there is no physiological or genetic barriers to breeding high-yielding, high-protein genotypes. Cober and Voldeng (2000) developed high-protein soybean populations exhibiting a very low or no association between grain yield and protein concentration. Similarly, high-protein and low-protein maize strains resulting from long-term divergent recurrent selection allowed to shift the negative grain yield–protein concentration relation (Uribelarrea et al., 2004). More recently, the transfer of a chromosomic region from an accession of emmer wheat (*Triticum turgidum* L. var. *dicoccoides*) associated with high grain protein concentration into high-yielding bread wheat (DePauw et al., 2007) and durum wheat (Chee et al., 2001) cultivars also allowed to shift the correlation.

Crop simulation models can be used to assess the link between physiological traits (model parameter) and grain yield or protein concentration (Boote et al., 2001; Hammer et al., 2006). The wheat simulation models Sirius and *SiriusQuality*1 (Martre et al., 2007; Semenov et al., 2007) and APSIM-Nwheat (Asseng and Milroy, 2006) have been used to analyse the effect of single-plant or crop traits on both grain yield and protein concentration. These simulations showed that variations in weather and nitrogen treatments induced larger variations in grain yield and protein concentration than most of the physiological traits considered, and revealed strong trait-by-nitrogen and trait-by-water interactions.

Monaghan et al. (2001) showed that under western European conditions, positive departures from the grain yield–protein concentration relation were associated with the amount of nitrogen accumulated by the crop after flowering. The sensitivity analysis of *SiriusQuality*1 was consistent with this finding: for high nitrogen supply, increasing the maximum rate of nitrogen uptake during grain filling allowed to shift the negative grain yield–protein concentration correlation (Figure 10b). To analyse the effect of the rate of nitrogen remobilisation from leaves and stems to grains on crop dry matter and nitrogen dynamics, a scaling parameter (β) changing proportionally the daily rate of accumulation of grain nitrogen was introduced in *SiriusQuality*1 (Martre et al., 2007). For both low and high nitrogen supply, simulated grain yield increased significantly when the rate of grain nitrogen accumulation was decreased, whereas grain nitrogen yield, post-flowering nitrogen uptake and nitrogen harvest index were very similar, even for high nitrogen supply (Figure 10c and d). Therefore, increasing in the model the daily rate of grain nitrogen accumulation leads to a dilution of grain nitrogen. Surprisingly, about 75% of the increase in grain yield was due to the increase in dry matter harvest index, which increased by about 6% when β was decreased from 1 to 0.7. In good agreement with this result, pot-grown stay-green mutants of durum wheat in a greenhouse had a higher grain yield per plant than the wild type, but the grain nitrogen yield was the same for the mutants and the wild type; therefore, the grain protein concentration was lower in the mutants than in the wild type (Spano et al., 2003). In contrast, Uauy et al. (2006a, b) reported that acceleration of canopy senescence in transgenic wheat plants under-expressing a NAC transcription factor located at a QTL for high grain protein concentration paralleled acceleration of nutrient remobilisation from leaves to grains, leading to higher grain protein concentration; however, grain yield was not reported in these studies.

A survey of UK winter wheat cultivars revealed a positive association between grain yield and stem nitrogen concentration at flowering (Shearman et al., 2005). In the sensitivity analysis of *SiriusQuality*1, the nitrogen storage capacity of both leaves and stems was considered. Under limiting nitrogen supply, increasing the storage capacity of the leaves or stems did not shift the negative correlation between grain yield and protein concentration (Figure 10e and g). The increase in leaf nitrogen mass per unit leaf surface area was associated with a reduction in grain yield because of reduced leaf expansion due to nitrogen shortage. In contrast, under high nitrogen supply, increasing maximum stem nitrogen concentration or leaf nitrogen mass per unit of leaf surface increased both grain yield and grain protein concentration (Figure 10f and h). Similar trends in grain yield and protein concentration were observed when the efficiency of nitrogen remobilisation was modified, but changes in grain yield and protein concentration were much more limited. This simulation analysis shows that, under high nitrogen inputs, increasing the nitrogen storage capacity of the leaves and stem and/or the efficiency of nitrogen remobilisation may significantly shift the negative grain yield–protein concentration correlation. Moreover, it may also reduce the risk of nitrogen losses by leaching and volatilisation.

5. CONCLUDING REMARKS

Diverse industries require grains with high and reliable quality for specific uses, and breeders have responded by tailoring new cultivars to these demands (DePauw et al., 2007; Velasco and Fernandez-Martinez, 2002). There is therefore an increasing need for knowledge of the physiology of quality traits, in support of both breeding and crop management aimed at the dual objective of high yield and high quality. While breeding for crop yield has been always performed at the population (crop) level, the improvement of quality traits has mostly focused on individual plants or plant parts (i.e. grain). Combining experiments and simulations, we demonstrated that most quality traits, and certainly quality–yield interactions, cannot be correctly understood or predicted by extrapolating from individual plants to the population. The determination of quality traits – such as that of yield components – should be analysed at the crop level, and crop physiology concepts and methods classically applied to yield analysis can be powerful tools.

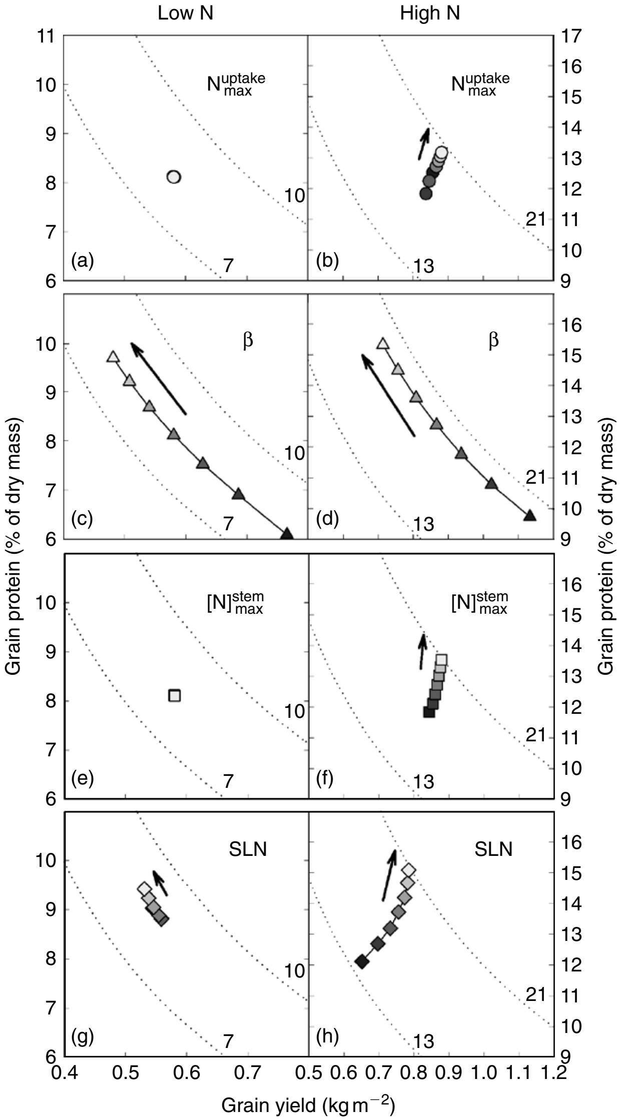

FIGURE 10

Simulated grain protein concentration versus grain yield for wheat crops in response to (a, b) variations of the maximum rate of nitrogen uptake at anthesis (N_{max}^{uptake} , default value 4 g N m^{-2} ground day^{-1}), (c, d) a scaling parameter modifying the daily rate of grain nitrogen accumulation (β, default value 1), (e, f) the nitrogen storage capacity of the stem ($[N]_{max}^{stem}$, default value 10 mg N g^{-1} DM) and (g, h) leaf nitrogen mass per unit of leaf surface area (SLN, default value 1.5 g N m^{-2} leaf). Simulations were performed with the wheat simulation model SiriusQuality*1 (Martre et al., 2006). Data are means for 32 years at Clermont-Ferrand at low (8 g N m^{-2} applied in two splits; a, c, d and g) and high (25 g N m^{-2} applied in four splits; b, d, f and h) nitrogen supplies. The grey intensity of the symbols decreases as the parameters increase by 10% increments from −30% to +30% of their default value. Arrows indicate the way of the increase of the parameter values. Dotted lines are grain nitrogen yield (g N m^{-2}) isopleths. Details of the soil and cultivar characteristics are given in Martre et al. (2007). (Source: Martre et al., 2007.)*

Much of our current knowledge about the physiology of grain quality in oilseed crops and cereals has been obtained in sunflower and bread wheat, and hence the value of these species as models for quality studies illustrated in this chapter. Examples were presented where relationships (and underlying processes) between a given quality trait and its predictor, first identified in model crops, were then found to be common to other crops. This research strategy seems promising for further insights into the physiology of quality traits in several crops.

Mathematical crop models have incorporated quality modules that allow for the simultaneous simulation of grain yield and quality (Section 3). Several cases were presented to illustrate how, by means of these models, crop physiology can be used for designing better management and breeding strategies for improving quality in oil crops and cereals. Interestingly, these models are more than a means to gather physiological knowledge; they also help creating new knowledge by highlighting emergent properties that arise from the combination of different processes. For example, crop models realistically reproduced relationships between yield and quality traits (Section 4), which are assumed to be independent processes in the models.

Dealing with G × E interactions is still one of the major challenges for plant breeders. As a complement to classical approaches, quantitative relationships between quality traits and environmental drivers in this chapter are a more robust means of quantifying G × E interactions, and of generating new 'traits' (model parameters) that are largely independent of the environment. These relationships represent meta-mechanisms at the plant or crop level and, therefore, could help to fill the current gap between genotype and phenotype, specially for complex traits (see also Chapter 10). Coupling physiological and genetic approaches to improve quality traits, we argue, represents one of the next challenges for crop physiology and breeding.

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Dynamics of Crop–Pathogen Interactions: From Gene to Continental Scale

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1. INTRODUCTION

Pathogens (viruses, bacteria, fungi, Oomycetes and nematodes) are among the major biotic stresses affecting plants, impacting on crop production principally by reducing yield and quality. Table 1 in Chapter 18 summarises the potential and actual yield losses caused by pathogens in field crops.

One of the most graphic historical accounts of the impact of a pathogen on crop production is that of the Irish potato famine (1846–1850), precipitated by the destruction of potato crops by *Phytophthora infestans* (Large, 2003). While the net result of the famine can be simply stated as "about one million deaths from starvation and the emigration of more than one million people", the suffering experienced and the resulting upheaval caused by this Oomycete pathogen defy imagination.

Farmers devised and practiced strategies to help reduce the impact of these stresses on their valuable crops long before the aetiology of plant disease was understood. Despite not knowing that diseases were caused by pathogens, early agronomic practices to reduce disease impacts included the eradication of alternate hosts such as barberry (*Berberis vulgaris*) to control stem rust in wheat in the 1700s (Walker, 1976) and the removal of dew from crops with a net or rope in the 1800s (Zadoks and Bouwman, 1985). Theophrastus (370–286 B.C.) noted the different abilities of plants to resist disease, and the selective harvest and the retention of seed of superior plants for future crops by early farmers can be considered a genetic approach to disease control belonging to the second phase of crop evolution outlined in Chapter 14 (Section 1), well before Mendel's laws of inheritance were discovered.

Many studies have examined the physiological effects of pathogens in plants, the genetic basis of resistance in plants to pathogens, and more recently, the physiological processes controlled and switched on by resistance genes that lead to resistance. The application of knowledge gained from these studies to controlling pathogens in crops was an important ingredient in the increases in crop yields seen during the twentieth century, including the Green Revolution in which higher yielding semi-dwarf cereals were developed with genetic resistance to diseases (Perkins, 1997).

While the focus of this chapter is to examine the dynamics of pathogen–crop interactions from a genetic perspective, it should be noted that considerable work has targeted modelling of the crop–pathogen interface and approaches to measure yield losses attributable to disease. The integration of crop and pathogen models was pioneered by Boote et al. (1983) and Johnson (1987), who proposed "linkage points" between crop and pest models; Table 3 in Chapter 5 illustrates these linkage points for pathogens of crops in farming systems of Asia. While most of these studies have utilised susceptible host genotypes (e.g. Lopes and Berger, 2001; Robert et al., 2004), some have used host genotypes with different agronomic traits (e.g. Bancal et al., 2007) or disease susceptibility (Bassanezi et al., 2001). These important topics related to crop diseases are beyond the scope of this chapter, which reviews the genetic basis of plant:pathogen interactions, explores the extension of these genetic principles to the interface between crops and pathogens and examines implications for disease control at the level of the crop and beyond.

2. PATHOGEN BIOLOGY

The many pathogens that attack plants make a living from their hosts either by killing host cells and then feeding on the dead substrate (necrotrophs) or by colonising and feeding on living host cells (biotrophs). Some necrotrophic pathogens produce host-specific toxins (e.g. *Cochliobolus heterostrophus* race T, which produces a T-toxin that induces cell death specifically in maize varieties based on Texas cytoplasmic male sterility, enabling necrotrophic colonisation [Leonard, 1987]). Other necrotrophs use toxins with much broader activity, and these species tend to have wide host ranges (e.g. *Sclerotinia sclerotiorum*; Hegedus and Rimmer, 2005). Rusts and powdery mildews are examples of biotrophs. The establishment of a compatible host–pathogen interaction is necessary in order for these pathogens to reproduce. Because of the intimate cellular relationship required for compatibility, biotrophic pathogens often have a complex race structure based on gene-for-gene regulation of resistance.

Depending on the plant part targeted and/or disease epidemiology, pathogens are also broadly classified as soil-borne or air-borne. Rusts and powdery mildews are disseminated as air-borne spores that infect leaf tissue, colonise and sporulate (Walker, 1976). *Gauemannomyces graminis*, the take-all pathogen of cereals, is a soil-borne pathogen that survives as hyphae in infected roots and root debris in soils and completes its disease cycle in the soil (Parberry and Morgan, 1980). The rice blast pathogen, *Magnaporthe oryzae*, long regarded as a foliar pathogen, is also capable of infecting roots, using different infection pathways for each organ (Dufresne and Osbourn, 2001).

Clearly, the terms used in defining pathogen biology are somewhat arbitrary, representing the extremes of a spectrum across which most pathogens exhibit both biotrophy and necrotrophy (hemibiotrophs) and pathogens having both soil-borne and air-borne phases. Pathogen biology has nonetheless a profound impact on the success or failure of genetic approaches to plant disease management.

3. THE GENETIC BASIS OF RESISTANCE TO PATHOGENS

Formal genetic analysis of disease resistance in plants began over 100 years ago when Biffin (1905) demonstrated that resistance to stripe rust in wheat (caused by the biotrophic pathogen *Puccinia striiformis* f. sp. *tritici*) was inherited as a single recessive Mendelian trait. This work also demonstrated independence of the resistance from other traits and established that lines breeding true for the resistance phenotype could be obtained (Knott, 1989). Since this initial work, many genes conferring resistance to pathogens in crop plants have been characterised, and the genetic basis of pathogenicity (virulence/avirulence) has been studied in many plant pathogens. This knowledge culminated in the development of the gene-for-gene hypothesis by Flor (1955) based on genetic studies of the interaction between flax and the flax rust pathogen, which has provided a framework for much if not all of the work on disease resistance in the years since.

Resistance is “any genetically determined characteristic of a host plant that in any way limits damage produced by disease” (Browder, 1985). The responses of plants to pathogens are relative and may vary between apparent immunity (sometimes regarded as indicative of non-host resistance [NHR]) and extreme susceptibility. For practical purposes, the most important features of resistance are the level of protection from economic damage afforded and durability. Durable resistance was defined by Johnson (1978) as "resistance that remains effective when a cultivar is grown widely in environments favouring disease development". The concept of durable resistance makes no assumptions concerning the mechanisms or genetic control of resistance, and has proved a very useful concept in disease resistance breeding.

In the experimental context, resistance is often defined in terms of function or genetics (Day, 1974). In functional terms, resistance is defined based on epidemiological (e.g. slow rusting, rate reducing) or developmental (e.g. seedling versus adult plant resistance [APR]) criteria. In genetic terms, resistance is generally defined by mode of inheritance, with broad distinctions drawn between oligogenic (controlled by one or few genes of major effect) and polygenic (controlled by many genes of individually small phenotypic effect) resistances.

3.1. Oligogenic resistance

Although usually race specific, oligogenic resistance (including single gene resistance) has in some cases proven durable (Eenink, 1977). While most characterised resistance genes are dominant in action, some recessive resistance genes have proven to be important sources of durable resistance (e.g. gene *Sr2* conferring resistance in wheat to stem rust [McIntosh et al., 1995]; gene *mlo* for mildew resistance in barley [Jørgensen, 1994]). There are also many examples of resistance genes that display partial dominance (gene dosage dependence; e.g. the resistance gene *Lr9* in wheat to *P. triticina*, Samborski, 1963). Dominance or recessiveness of resistance genes is, however, not absolute and can even be governed by the attribute used to measure the disease phenotype (Johnson, 1992), genetic background, pathogen isolate or environment. In discussing resistance in *Phaseolus vulgaris* to bean common mosaic virus, Fraser (1992) described how resistance could be classified as either recessive or dominant, depending on whether symptoms in heterozygous F_1 plants were classified on the basis of symptom expression or on virus multiplication, respectively.

Examples of oligogenic resistance in which additive and non-additive interaction occurs between genes at separate loci are known. The genes *Lr13* and *Lr34* in wheat interact in an additive manner to confer resistance to leaf rust, not only with each other, but also with other genes for resistance to leaf rust (German and Kolmer, 1991; Kolmer, 1992). Non-additive gene interaction occurs when two genes in the host are only effective when present together. In such cases, the genes in the host are referred as complementary. Baker (1966) demonstrated complementary action of the genes *Pc3* and *Pc4* conferring resistance to *Puccinia coronata* in the oat cultivar Bond.

3.2. Polygenic resistance

Polygenic resistance is controlled by many genes, which, although of individually small phenotypic effect, can be combined to produce progeny with effective resistance. The genes involved are often referred as minor genes and show additive effects. The progeny from a cross between a plant with polygenic resistance and a susceptible plant display a continuous range of disease response between and sometimes beyond those of the parents. Resistance expressed on a continuous scale in segregating populations is referred as quantitative resistance, and the individual loci that control polygenic quantitative traits are referred as polygenes or quantitative trait loci (QTL) (Tanksley, 1993).

It should be noted that not all quantitative resistance is polygenically inherited (Geiger and Heun, 1989). Young (1996) presented examples where quantitative resistance appeared to be under the control of relatively few loci, including several instances where only one or two loci were inferred. Quantitative resistances slow down the rates of epidemic development, resulting in reduced disease severity (Geiger and Heun, 1989). The components of such resistance that contribute to slowing the rate of epidemic development include reduced infection efficiency, increased latent period, reduced spore production and a shorter infectious period (Parlevliet, 1979). In viral diseases, components of quantitative resistance also include a reduction in the number of plants infected or showing symptoms, milder symptoms, decreased virus accumulation and incomplete virus invasion (Kegler and Meyer, 1987).

3.3. Resistance to toxin-producing necrotrophic fungal pathogens

The diseases Victoria blight of oats (caused by certain isolates of the fungus *Cochliobolus victoriae*) and southern leaf blight of maize (caused by *C. heterostrophus*, anamorph *Bipolaris maydis*) are examples of host–pathogen interactions in which a susceptible response results only when a toxin-producing isolate of the necrotrophic pathogen interacts with a host plant carrying a dominant gene for toxin sensitivity (Ellingboe, 1976; Leonard, 1993). The inheritance of disease response in maize to race T of the southern maize leaf blight pathogen is under cytoplasmic control because sensitivity to the T-toxin produced by this race is controlled by a protein encoded by Tcms mitochondrial DNA (Levings and Siedow, 1992). In both southern leaf blight and Victoria blight, the resistant phenotype results from toxin insensitivity in the plant, an inability of an isolate to produce a toxin or both, and hence does not result from a recognition event as postulated to occur in classic gene-for-gene interactions. In both cases, resistance is recessive, resulting from the presumed absence of a toxin receptor in the host (Pryor and Ellis, 1993). Faris et al. (1996) also reported recessive inheritance of insensitivity in wheat to a necrosis-inducing toxin produced by *Pyrenophora tritici-repentis*, causal agent of tan or yellow spot.

While the genetics of these host–pathogen interactions are relatively simple, with only one gene for resistance corresponding to a single toxin product by a gene family in the pathogen, several independent dominant genes have been identified in barley for resistance to the toxin-producing pathogen *Rhynchosporium secalis* (e.g. Jørgensen, 1992). Detailed studies of the interaction of host lines with the resistance gene *Rrs1* with isolates possessing avirulence for this gene have indicated that the corresponding avirulence gene produces a secreted protein, NIP1. This protein acts as a toxin in plants lacking the *Rrs1* resistance gene, and as an elicitor of the resistance response in lines possessing *Rrs1* (Rohe et al., 1995).

4. LINKING GENETICS OF RESISTANCE WITH CELLULAR AND PLANT PHYSIOLOGY

In physiological terms, resistance results from pre-formed and induced defences that restrict pathogen development. Chapter 9 (Section 2) discusses constitutive and induced defences in terms of trade-offs between allocation of resources to protection and other functions with consequences for plant fitness and crop yield. Plants protect themselves passively using a combination of constitutive morphological and biochemical defences. A basal defence response is induced upon microbial challenge, while the recognition of an avirulent pathogen elicits an impressive arsenal of active responses, including reactive oxygen release, hypersensitive cell death, phytoalexin accumulation and cell wall reinforcement (Dangl and Jones, 2001; Greenberg and Yao, 2004). These responses execute the resistance conditioned by resistance genes upon pathogen recognition.

4.1. Colonisation of the plant host

Successful pathogen colonisation of plant hosts requires several layers of plant defence to be overcome. The first line of defence is essentially passive and involves pre-formed physical and chemical barriers (Heath, 2000). The second line of defence is an active recognition process. Animals and plants contain receptors that recognise common, conserved pathogen molecules known as pathogen-associated molecular patterns (PAMPs) (reviewed by Ausubel, 2005; Bittel and Robatzek, 2007; Schwessinger and Zipfel, 2008). In bacterial pathogens, these PAMPs molecules include bacterial flagellin proteins, cell wall lipopolysaccharides and protein elongation factors, while fungal PAMPs include β-glucan molecules and chitin. Host recognition of PAMP molecules is mediated by plasma membrane-localised receptors in some instances, leading to activation of a defence response called PAMP-triggered immunity, or PTI (Jones and Dangl, 2006). The PTI response includes callose-mediated cell wall fortification, ion fluxes, production of reactive oxygen species, MAP kinase signalling cascades and defence gene induction (Asai et al., 2002; Zipfel et al., 2004, 2006). Mechanistically, this response shows features common to the plant defence response initiated by R genes; however, it is considered slower and "weaker" and often does not involve programmed plant cell death (Jones and Dangl, 2006). PTI contributes to the resistance of plants to most potential microbial infections and is a major component of NHR.

An adapted pathogen of a plant host has the ability to circumvent the PAMP-triggered immune response by the transfer of pathogen molecules, called effectors, directly into plant cells. These effectors specifically target and inactivate PTI components thereby enabling successful colonisation by the pathogen (reviewed by Bent and Mackey, 2007; Kamoun, 2007; Da Cunha et al., 2007). In spite of pathogen suppression of the NHR response of host plants, these plants can be made even more susceptible by mutation (Glazebrook et al., 1996). This observation suggests that plant NHR is only partially suppressed by the pathogen or alternatively argues for the existence of an additional resistance mechanism termed basal resistance. NHR and basal resistance share common molecular cascades and may be the same response and central to both resistance responses is PAMP recognition leading to PTI (Jones and Dangl, 2006).

The host range of a pathogen species is delineated by the ability of the pathogen to circumvent the PAMP-triggered NHR and basal defences of potential hosts with an appropriate or adapted set of effector molecules. A pathogen is therefore described as an adapted pathogen of its target host(s) and a non-adapted pathogen of immune plant species, that is, non-hosts. A great deal of host specialisation is apparent among plant pathogens indicating that NHR/basal host defence mechanisms and/or the host molecules that regulate them are not invariant. Several NHR genes (*pen1*–*pen3*) have recently been isolated from Arabidopsis that provide protection against epidermal penetration of this plant by powdery mildew pathogens for which Arabidopsis is a non-host. These genes encode a syntaxin protein involved in vesicle targeting, an ABC transporter and a glucosyl transferase, respectively (reviewed by Lipka et al., 2008). When the *pen3* gene is combined with a second Arabidopsis mutant gene, *eds1*, the double mutant plant becomes a virtual host of pea powdery mildew (*Erysiphe pisi*) by allowing growth and sporulation of the fungus (Stein et al., 2006). These observations demonstrate that NHR is not as genetically intractable as previously thought.

Mechanistically, pathogen effector molecules have been demonstrated to inhibit plant callose deposition (Hauck et al., 2003; Kim et al., 2005), suppress plant defences and increase plant susceptibility (Da Cunha et al., 2007). The molecular function of these effector molecules has been determined in some instances and includes protease inhibitors, proteases, kinase inhibitors, ubiquitin ligases, phosphotases, chitin-binding proteins and transcription activators (van den Burg et al., 2006; Kamoun, 2007; Da Cunha et al., 2007; Block et al., 2008; van Esse et al., 2008). The genomes of the Oomycete pathogen *Phytophthora* contain several hundred genes with conserved motifs present in known effectors raising the possibility that large numbers of effector molecules are introduced into the plant host and further suggests redundancy in function (reviewed by Kamoun, 2007; Birch et al., 2008). The host molecules targeted by pathogen effectors have also been elucidated in some cases and include kinases, RNA-binding proteins and components of the ubiquination pathway (reviewed by Da Cunha et al., 2007; Block et al., 2008).

To circumvent pathogen suppression of PTI, host plants in turn have evolved R proteins that recognise, either directly or indirectly, a specific effector molecule produced by an adapted pathogen whereupon a defence response is initiated leading to effector-triggered immunity, or ETI (Jones and Dangl, 2006). ETI may not function solely against adapted plant pathogens but may also contribute to NHR/basal responses (Jones and Dangl, 2006; Lin and Martin, 2007). Pathogen effector molecules that are recognised by R proteins have historically been called avirulence gene products. A large number of diverse avirulence proteins have been reported from viral (Erickson et al., 1999; Pfitzner and Pfitzner, 1992; Bendahmane et al., 1995; Weber and Pfitzner, 1998), bacterial (reviewed by Block et al., 2008) and fungal pathogens (reviewed by Rivas and Thomas, 2005; Kamoun, 2007; Catanzariti et al., 2007). The molecular structure of the R proteins that recognise these avirulence proteins is described below using specific examples. A comprehensive catalogue of over 70 cloned plant R genes is reported by Liu et al. (2007).

4.2. The structure of resistance genes

The first molecular characterisation of a resistance gene that confers resistance by pathogen recognition and subsequent activation of ETI was the tomato *Pto* gene, which provides resistance to *Pseudomonas syringae* pv. *tomato* (Martin et al., 1993). An ever increasing number of oligogenic resistance genes involved in pathogen recognition and defence activation have been cloned from both monocot and dicot plant species, and the deduced proteins encoded by these resistance genes fall into a variety of different structural classes. By far, the largest class of resistance genes described to date encodes proteins containing an amino terminal nucleotide binding site domain (NBS domain, also known as an NB-ARC domain [van der Beizen and Jones, 1998]) that binds ATP (Tameling et al., 2002), and a carboxyl terminal domain consisting of a series of degenerate leucine rich repeats (LRR). This class of R protein has been shown to recognise viral (e.g. tobacco mosaic virus in *Nicotiana tabacum*; Whitham et al., 1994), bacterial, fungal (e.g. *Fusarium oxysporum* f. sp. *lycopersici* in tomato; Ori et al., 1997), nematode (e.g. root knot nematode in tomato; Milligan et al., 1998) and insect (e.g. the aphid *Macrosiphum euphorbiae* in *Lycopersicon*; Vos et al., 1998) pathogens.

Mechanistically, the LRR domain is believed to be involved in pathogen recognition, while the NBS domain is believed to alter the activation state of the molecule enabling signal transduction. However, subsequent experiments have demonstrated that this molecular model is overly simplistic with intramolecular interactions occurring between domains (Warren et al., 1998; Luck et al., 2000; Bendahamane et al., 2002; Hwang and Williamson, 2003; Rairdan et al., 2008). Another feature of NBS-LRR genes is that the proteins they encode contain highly variable regions in the LRR domain that occur on the predicted exposed surface of the molecule and are likely to be involved in pathogen effector recognition (Parniske et al., 1997; Meyers et al., 1998). Unlike the vast majority of genes that are under positive selection for sequence conservation, these regions of NBS-LRR genes actually show selection for sequence divergence, as evidenced by the presence of a high frequency of non-synonymous mutations (Parniske et al., 1997; Meyers et al., 1998). This selection for sequence divergence coupled with recombination between othologous and paralogous R genes enables evolution of new R gene specificities in the face of rapidly evolving pathogen populations (Michelmore and Meyers, 1998).

The NBS-LRR class of R genes can be further divided into two major subgroups. The first subgroup contains an extreme amino terminal region with homology to the *Drosophila* Toll protein (involved in defining embryonic polarity) and the human interleukin 1 receptor (TIR domain). The second subgroup of NBS-LRR proteins lack a TIR domain and often have this domain replaced by a coiled-coil (CC) domain that is implicated in protein–protein interactions (i.e. CC-NBS-LRR proteins). A major distinction between monocot and dicot plant species is that no TIR-NBS-LRR encoding genes have been identified to date in monocots. In contrast, the TIR-NBS-LRR class is the most abundant form in dicots, with the possible exception of sugar beet where no TIR-NBS-LRR genes have been identified (Tian et al., 2004). Approximately three quarters of the estimated 150 NBS-LRR genes in *Arabidopsis* are of the TIR-NBS-LRR class (Meyers et al., 2003). In contrast, the 600 NBS-LRR genes encoded in the rice genome are all of the non-TIR class (Goff et al., 2002). Apart from the *csa1* mutant of Arabidopsis which encodes a NBS-LRR protein implicated in photomorphological development (Faigon-Soverna et al., 2006), no other function has been ascribed to these proteins apart from disease resistance, suggesting that most functional versions of these genes within the plant genome are defence related. NBS-LRR genes with demonstrated resistance gene function were initially identified in dicot species due to the experimental amenability of these species, but an ever increasing number of cereal NBS-LRR genes have been demonstrated to confer disease resistance, for example, the maize *Rp*1 rust resistance gene, the rice *Pi-ta* blast resistance gene, the barley *Mla* powdery mildew resistance gene and wheat *Lr1*, *Lr10* and *Lr21* leaf rust resistance genes (described with further examples in Ayliffe and Lagudah, 2004; Liu et al., 2007).

In an interesting evolutionary twist, NBS-LRR genes that characteristically provide resistance against biotrophic pathogens have been shown to act as targets for nectotrophic pathogen toxins. “Recognition” of the pathogen toxin by a specific NBS-LRR gene leads to activation of a plant defence response and cell death. The death of this host tissue is thought to facilitate colonisation by these nectotrophic pathogens. Examples include the *LOV1* gene from Arabidopsis which is the target of the *C. victoriae* victorin toxin (Lorang et al., 2007) and the *Pc* locus of sorghum which is the target of the fungus *Periconia circinata* peritoxin (Nagy and Bennetzen, 2008).

The second class of oligogenic resistance genes identified in plants encodes protein kinases. Protein kinases have been shown to confer disease resistance in tomato against the bacterial pathogen *P. syringae* (Martin et al., 1993) and in barley against the stem rust pathogen *Puccinia graminis* (Brueggeman et al., 2002). In the tomato example, the protein kinase encoded by the *Pto* gene also requires an NBS-LRR protein for function, implicating these two molecules in a common signal transduction cascade leading to a defence response (Salmeron et al., 1996). A third class of R gene, first identified in tomato as conferring resistance against the fungal pathogen *Cladosporium fulvum*, encodes an extracellular membrane-anchored protein containing a series of LRRs (Jones et al., 1994; Dixon et al., 1996, 1998; Thomas et al., 1997). The fourth class of R gene, typified by the *Xa21* and *Xa26* genes of rice that confer resistance against the bacterial pathogen *Xanthomonas oryzae*, encodes transmembrane proteins containing an extracellular LRR domain joined to an intracellular protein kinase domain and is a member of the receptor kinase class of plant proteins (Song et al., 1995; Sun et al., 2004). This latter receptor kinase protein class therefore appears structurally as a chimera between the extracellular LRR protein class and the intracellular protein kinase class. While NBS-LRR proteins appear to be defence related only, protein kinases and receptor kinases have been implicated in other plant processes. Determining which of the numerous protein kinases and receptor kinases encoded in the plant genome are involved in disease resistance is therefore not a straightforward process.

The above examples highlight the structures of most characterised R proteins; however, several other R genes have been identified that do not encode members of the above protein classes. The Hs1$^{pro\text{-}1}$ nematode resistance gene from sugar beet (Cai et al., 1997) encodes a protein that does not readily fit the NBS-LRR protein structure (Ellis and Jones, 1998). Similarly, the broad spectrum *Erysiphe cruciferarum* and *E. cichoracearum* resistance genes of *Arabidopsis*, *RPW8.1* and *RPW8.2* encode structurally unique R proteins. An interesting R protein from *Arabidopsis*, *RRS1-R*, which confers broad spectrum resistance to *Ralstonia solanacearum*, is a TIR-NBS-LRR protein that also contains a WRKY motif that is characteristic of some plant transcriptional factors (Deslandes et al., 2002). Several other structurally atypical R proteins are described by Liu et al. (2007). Additional types of R gene products are likely to be identified from future molecular analyses.

These molecular data are consistent with the evolution of multiple strategies for pathogen recognition. In some cases, this may be a consequence of differences in modes of pathogenesis. For example, the tomato fungal pathogen *C. fulvum* infects the plant apoplast and does not penetrate host cells. The evolution of extracellular membrane-anchored proteins for recognition of this pathogen is therefore not unexpected. Similarly, the probable intracellular location of the NBS-LRR encoding tobacco *N* gene, which provides resistance to tobacco mosaic virus, is consistent with the intracellular replication strategy of this virus. However, the physical location of the pathogen does not account for all R gene structural diversity and the intrahost cell localisation of pathogen effectors accounts for the cytoplasmic localisation of NBS-LRR proteins (Jones and Dangl, 2006). The diversity in R protein structure and localisation therefore appears to arise from the site of effector product accumulation rather than the pathogen infection site.

4.3. The function of resistance genes

All the R proteins described above recognise biotrophic and hemibiotrophic pathogens. They do not provide resistance per se, but act by recognising pathogen effector molecules leading to activation of ETI (Jones and Dangl, 2006). The cloning of host resistance genes and pathogen effector genes has permitted critical examination of the models that were advanced to explain how resistance genes activate the physiological processes that lead to stopping or reducing pathogen invasion. In some instances, this recognition involves a direct physical interaction between the host R protein and the pathogen avirulence effector (the "receptor–ligand" model). Such an interaction has been observed for the tomato Pto protein kinase and the corresponding avrPto bacterial avirulence protein of *P. syringae* (Tang et al., 1996), the rice NBS-LRR Pi-ta protein that directly interacts with the corresponding AVR-Pita protein of the rice blast fungus *Magnaporthe grisea* (Jia et al., 2000) and the TIR-NBS-LRR-WRKY protein, RRS1-R, of *Arabidopsis* and the corresponding Pop2 avirulence protein of *R. solanacearum* (Deslandes et al., 2003), and a number of flax NBS-LRR resistance proteins and their cognate flax rust (*Melampsora lini*) effector ligands (Dodds et al., 2006; Ellis et al., 2007).

However, there are numerous other examples where both the plant R gene and corresponding pathogen avirulence gene have been cloned and direct physical interaction between their products cannot be shown experimentally. R protein recognition of these pathogen effectors is indirect and recognition occurs by detecting modification of the host targets of these effectors or effector/target complexes rather than the effector itself. This recognition is summarised by the "guard hypothesis" whereby the R protein guards the host target molecule from effector modification (Bogdanove, 2002). This situation has been shown to occur for several *Arabidopsis* R protein/effector protein interactions (Mackey et al., 2002, 2003; Axtell and Staskawicz, 2003; Kim et al., 2005). The guard hypothesis has been further modified to the "decoy hypothesis" where it is suggested that some host proteins have evolved solely to be modified by pathogen effectors and thereby act as signals for R protein recognition (van der Hoorn and Kamoun, 2008).

Following effector recognition, the defence response of plants is regulated by either the salicylic acid-dependent pathway or by jasmonic acid and ethylene signalling. While the salicylic acid pathway seems to be primarily associated with resistance to biotrophs and jasmonic acid/ethylene signalling appears to be more often associated with defence responses to necrotrophs, there are exceptions to this and all three signalling pathways also interact extensively in regulating gene expression (Glazebrook, 2005). Salicylate and jasmonate signalling also provide a physiological explanation for resistance induced in multilines and cultivar mixtures, through the release of their volatile methyl derivatives.

4.4. The barley *Mlo* gene links basal resistance and non-host resistance

The barley *mlo* gene was first identified in mutagenised barley although naturally occurring alleles were subsequently identified, is genetically recessive and confers resistance to the powdery mildew pathogen *Blumeria graminis* (Jørgensen, 1994). Molecular studies have shown that the dominant *Mlo* susceptibility allele encodes a cytoplasmic membrane, localised protein containing seven transmembrane domains (Buschges et al., 1997). The wild-type susceptibility protein functions in a calmodulin-dependent manner and is thought to encode a dominant suppressor of a basal defence response and possibly acts via intracellular and extracellular signal recognition (Kim et al., 2002). Mutations in this protein result in an up-regulated basal defence response that occurs in a pathogen-independent fashion, with resistance being recessively inherited. Hence, the Mlo protein is a regulatory component of basal plant resistance and not an R gene involved in effector recognition. Interestingly, while *mlo* plants show resistance to barley powdery mildew, these lines paradoxically show increased susceptibility to the hemibiotroph *M. grisea* (Jarosch et al., 2003) and necrotroph *Cochliobolus sativus* (Kumar et al., 2001).

An additional gene required for *mlo* resistance, *Ror2*, has been cloned and shown to encode a syntaxin protein (Collins et al., 2003). Syntaxin proteins are members of a superfamily of proteins called SNAREs. These proteins reside on membrane surfaces and are involved in targeting vesicles to the appropriate membrane surface by forming transcomplexes with other SNARE proteins located on the target membrane (Jahn et al., 2003). This observation coupled with the presence of hydrogen peroxide-filled vesicles at the sites of powdery mildew infection in *mlo* plants suggests that vesicle exocytosis at infection sites is an essential component of this resistance (Collins et al., 2003). Of great interest is the observation that the Arabidopsis homologue of *Ror2* is the *pen1* gene, which is a component of NHR against barley and pea powdery mildew described above (Collins et al., 2003). Subsequent mutagenesis and gene silencing of Arabidopsis *MLO* othologues demonstrated that combined inactivation of several members of this gene family conferred resistance to two adapted powdery mildew pathogens of this species. Additionally epidermal penetration of these Arabidopsis *mlo* mutants by non-adapted mildews was suppressed (Consonni et al., 2006). The basal defence regulatory role of *Mlo* is therefore conserved among dicot and monocot plants.

5. LINKING GENETICS OF RESISTANCE WITH AGRONOMY

Although the application of knowledge of the genetics of resistance in plant breeding has made a major contribution to reducing yield losses caused by pathogens, most strategies to control pathogens in crops involve the integrated use of agronomic practices and genetic resistance. Where disease control is deemed necessary, the need for genetic resistance is likely to be less if agronomic practices provide long-term sustained control. Outbreaks of pathogens with limited dispersal ability (e.g. many soil-borne pathogens) typically have little effect beyond the farm on which they occur and control at the level of the individual paddock by practices such as rotation and fallow can be effective, reducing the need for genetically resistant cultivars. In contrast, outbreaks of pathogens with high dispersal ability (e.g. many air-borne pathogens) can require regional, national and, in some cases, international coordination to achieve effective and sustained control because of their particularly high epidemic and pandemic potentials. While genetic resistance is a desirable component of control strategies in these cases, its use depends on the availability of resistance in adapted germplasm, the genetic complexity of available resistance and ease of phenotypic selection of resistance.

5.1. Controlling pathogens with high dispersal potential; the wheat rusts

The rust pathogens of wheat are among the most intensively studied plant pathogens. Long-term monitoring of pathogenic variability in some regions has provided arguably the best evidence of long-distance migration by a plant pathogen. Based on studies of pathogenicity, spore size and growth in axenic culture, Watson and de Sousa (1982) concluded that two pathotypes of the wheat stem rust pathogen *P. graminis* f. sp. *tritici* first detected in Australia in 1969 originated from central Africa, suggesting that they had reached Australia by aerial wind transport of urediniospores across the Indian Ocean. Pathogenicity surveys of wheat rust pathogens within Australasia have also provided convincing evidence of long-distance migration of pathotypes within this region. A single pathotype of the leaf rust pathogen *P. triticina*, first detected in Victoria in 1984, was detected in all wheat-growing regions of Australia and New Zealand by 1990 (Park et al., 1995). Similarly, a pathotype of the stripe rust pathogen, *P. striiformis* f. sp. *tritici*, first detected in Western Australia in 2002, was present in eastern Australia the following year (Wellings, 2007). Within North America, the existence of a "Puccinia pathway" from the southern plains states of Texas and Oklahoma to Canada, along which wheat rust urediniospores are carried on wind currents, is well documented (Kolmer, 2001).

5.1.1. Genetic control of wheat rust diseases

Because of the importance of wheat and the ability of wheat rust pathogens to migrate over large distances and to build up rapidly to epidemic levels, considerable effort has targeted the coordinated development and deployment of wheat cultivars with genetic rust resistance. At the time of his studies on the inheritance of resistance to stripe rust in wheat, Biffin was unaware of pathogenic variability in the stripe rust pathogen. The discovery of physiological races in the wheat stem rust pathogen (*P. graminis* f. sp. *tritici*) by Stakman and Piemeisel (1917) was important in demonstrating the need to monitor pathogenic variability and to use this information and the most relevant rust isolates in resistance breeding. These discoveries led to great optimism that a solution to rust diseases had been found (Watson and Butler, 1984). Early attempts to develop genetically resistant wheats, however, involved the development of cultivars with single genes for resistance, and invariably, matching virulence in the rust pathogen often followed with the cultivar being rendered susceptible in what became known as the "boom-and-bust" cycle. The first stem rust-resistant wheat released in Australia was cv Eureka (1938), protected by the single resistance gene *Sr6*. It increased in popularity and by 1945 occupied about 18% of the wheat acreage in northern New South Wales and Queensland (Watson and Luig, 1963). Virulence for *Sr6* was first detected in 1942, and its frequency in the *P. graminis* f. sp. *tritici* population in this region increased as the area sown to Eureka increased (Watson and Luig, 1963).

Despite setbacks associated with the development of matching virulence in rust pathogen populations, significant progress was made in developing wheat cultivars with useful resistance to rust, and the knowledge gained was an important ingredient of the Green Revolution, in which high-yielding rust-resistant wheat cultivars were developed and cultivated over large areas. Throughout this process, single rust resistance genes that protect individual plants have been deployed in widely grown cultivars. While many of these genes like *Sr6* have been overcome by mutation to matching virulence in rust pathogens, some have nonetheless been deployed with great success across huge areas spanning continents. A notable example is the stem rust resistance gene

Sr2, regarded by McIntosh et al. (1995) as "arguably the most important gene for stem rust resistance and one of the most important disease resistance genes to be deployed in modern plant breeding". It was an important component of the resistance of cv Selkirk (*Sr2*, *Sr6*, *Sr7b*, *Sr9d*, *Sr17*, *Sr23*), which was crucial in halting stem rust epidemics in the northern Great Plains of the USA caused by race 15B (Roelfs, 1985), and since then, has been deployed on millions of hectares over more than 30 years in North America (Roelfs, 1988) and elsewhere.

Many sources of additive polygenic resistance to leaf rust and stripe rust are known in wheat, including several that involve genetic associations between resistance to both diseases (e.g. *Lr34*/*Yr18*, *Lr46*/*Yr29*). In contrast, few sources of polygenic resistance are known to stem rust. In this case, pyramids of major oligogenic resistances have been used successfully, both in Australia (Park, 2007) and in North America (Martens and Dyck, 1989). In the latter case, Martens and Dyck (1989) concluded that for more than 30 years, relatively few major genes in various combinations, from four genetic lines (Iumillio durum, Yaroslav emmer, H44-24 emmer and McMurachy or other genes), provided complete control of stem rust in an epidemiological system comprising hundreds of millions of hectares and thousands of billions of rust propagules. Significantly, they also stated that the genetic basis of this widespread control of stem rust was not fully understood.

5.1.2. Integrating agronomic practices with genetic resistance

Because of the pathogenic variability in wheat rust pathogens, their abilities to disperse over large distances and their high epidemic potential, most success with resistance breeding has been achieved by integrating strategies based on agronomic practices, which essentially reduce the size of rust pathogen populations and thereby reduce the risk of epidemic development and resistance gene "break down".

In addition to utilising genetic resistance to control rust diseases in wheat, breeders have selected for other traits such as early maturity to reduce the risk of epidemic development. Early attempts to grow wheat in Australia were based on late maturing genotypes from other parts of the world and epidemics of stem rust were frequent. The first significant step in reducing the frequency of these epidemics came with the release of wheat cultivars bred in Australia by William Farrer, which were not necessarily resistant as such, but matured earlier and escaped stem rust infection, and had improved adaptation that allowed cultivation in drier less rust-prone regions (McIntosh, 2007). This adaptive aspect of shortening season length in Australian wheats has been overlooked in physiological studies emphasising the role of early maturity in drought escape (Section 1 in Chapter 12).

Rust pathogens are biotrophic, and require a living host on which to survive. This means that in most wheat-growing regions, where there is a non-cropping phase due to either winter (Europe, North America) or summer (Australia, South Africa and South America), rust pathogen populations undergo a severe bottleneck caused by a huge reduction in living host tissue. In regions where a bottleneck occurs over winter, and where the alternate host is no longer important, initial inoculum may be transported by wind currents from another region, as is the case with the "Puccinia pathway" in North America. In regions where over-summering is important, the rust pathogens must survive on susceptible grass species or self-sown (volunteer) wheat plants (the "green bridge"). When summer conditions favour the establishment of a "green bridge", destruction by either grazing, cultivation or herbicides is an important component of control. The green bridge is particularly critical in intensive agricultural systems such as those of Asia where two or three crops are grown in the annual cropping season (Section 3 and Table 1 in Chapter 5). Luig and Watson (1977) showed the close association between rust isolates on the "green bridge" and those contributing to epidemics of stem rust in wheat in 1973, and a close association was also shown for pathotypes of the crown rust pathogen of oats in wild oat populations and cultivated hexaploid oats in north-eastern Australia (Oates et al., 1983; Park et al., 2000). Where genetically resistant cultivars are grown, self-sown plants are also resistant and reduce the effectiveness of any "green bridge" in sustaining rust from one season to the next.

The eradication of alternate hosts has also been an important factor in allowing progress in the genetic control of diseases like stem rust. It had been known for many years that barberry was in some way connected with epidemics of stem rust, but it was not until 1865 when de Bary proved conclusively that infection on these two hosts represented two different stages of the life cycle of a single rust species, *P. graminis*, and coined the term heteroecism (Peterson, 2001). Subsequently, Craigie (1927) demonstrated the function of pycnia in *P. graminis*, and Mendelian inheritance of pathogenicity to specific cultivars was demonstrated by Newton et al. (1930). One of the largest and best documented barberry eradication campaigns was conducted in North America following a severe epidemic in 1916. By 1942, some 300 million barberry bushes had been eradicated, and according to Roelfs (1985), this altered stem rust epidemiology in four ways, all of which have been important in reducing the frequency of stem rust epidemics: delayed disease onset, reduction in initial inoculum level, decreased number of pathogen races and stabilisation of pathogen phenotypes. The reduction in the number of races present in particular allowed breeders to select for effective and durable resistance (Campbell and Long, 2001).

5.1.3. Negative effects of scaling up rust resistance breeding

The extension of genetic resistance to the development and deployment of rust-resistant wheat cultivars, and its integration with agronomic practices, has reduced the threat of rust diseases significantly. The application of traits discovered and characterised based on studies of individual plants to crops has shown that while some traits remain relevant across levels of organisation, others do not, displaying a range of buffering processes ("scale-dependent" or "buffered" traits) (Section 5 in Chapter 1) and trade-offs (Chapter 9). Simplistically, the incorporation of a single disease resistance gene in a single plant genotype and its deployment in a crop can be regarded as being "scale independent". The effective deployment of the *Bt* gene, derived from the bacterium *Bacillus thuringiensis*, in a wide range of plant species (e.g. canola, cotton, maize, potato, tomato, rice, chickpea, walnut and Japanese persimmon) is an example of such a scale-independent trait. There are, however, other factors that need to be considered in determining the effectiveness of resistance genes at the crop level and their effects on the interaction between a given pathogen and the crop species, particularly with air-borne diseases. Unlike physiological traits such as photosynthesis and respiration, genetic resistance can be ephemeral (Chapter 9) and the longevity of resistance can at least in part be determined on how genes are managed at the regional or continental levels.

In addition to the benefits of protecting crops from rust diseases, some alien derived rust resistances in wheat are also believed to be associated with improved adaptation (e.g. *Lr26*/*Yr9*/*Sr31* from *Secale cereale*, McIntosh et al., 1995) and yield (e.g. *Lr19* from *Thinopyrum ponticum*, under disease-free irrigated conditions; Singh et al., 1998; Monneveux et al., 2003). Some alien derived rust resistances are, however, known to be associated with negative traits, and their incorporation into hexaploid wheat has been associated with linkage drag. Using near-isogenic lines with and without *Sr26*, a stem rust resistance gene derived from *Th. ponticum*, The et al. (1988) recorded an average 9% yield depression in lines carrying *Sr26*. Despite this, many cultivars carrying *Sr26* have been widely grown in Australia, including the cultivar Currawong, which is regarded to be high yielding (McRae, 2002). It is likely in these cases that the negative or positive effects associated with the alien derived resistances are due to other genes on the translocated segments on which they occur, which do not recombine in the wheat genome because of lack of homology. Efforts to reduce the negative effects of such linkage drag (yield and quality) using a pairing mutant that induces homeologous recombination between the alien segment and normal wheat chromosome have been underway in Australia for the past 20 years, targeting a range of alien derived stem rust resistance genes including *Sr26*, *Sr32*, *Sr37* and *Sr40* (Dundas et al., 2007). More specifically, however, there has been debate over whether or not resistance genes per se reduce host fitness in the absence of disease. A study by Tian et al. (2003) demonstrated a 9% reduction in seed production in *Arabidopsis thaliana* associated with the resistance gene *RPM1*. In reviewing this and other studies, Brown (2003) concluded that the cost associated with *RPM1* may well not be representative of resistance genes in general. Chapters 2 (Section 4.2) and 3 (Section 3.1) discuss putative trade-offs between crop yield potential and disease resistance from a farming system perspective.

Some rust resistance genes are expressed throughout the life of the wheat plant (seedling resistance), while others are expressed only at post-seedling growth stages (APR). While yield loss studies have generally shown that APR will protect against significant yield loss (Park et al., 1988), this is not always the case. For example, studies in which the protective value of the stripe rust APR gene *Yr18* was assessed using near-isogenic paired lines with and without *Yr18* demonstrated yield losses of 74–94% in the line lacking *Yr18*, but 31–52% in the line carrying *Yr18* (Ma and Singh, 1996). Studies under controlled conditions have shown that some APR genes are expressed under certain conditions either at or soon after seedling growth stages (e.g. *Lr13*), while others do not become effective until flag leaf emergence (e.g. *Lr22b*, Park and McIntosh, 1994). Where wheat crops are to be used for grazing, resistances like *Lr22b* that are not expressed until later growth stages will not provide protection from early growth and if grazing is to occur, fungicide use is clearly undesirable. Just how and at what growth stages resistance genes are expressed, are important considerations in ensuring adequate protection from diseases. Similarly, it has been demonstrated that the genetic mechanisms underlying resistance to pathogens can differ with tissue or organ. For example, two wheat cultivars with APR to stripe rust were shown to be susceptible to spike infection (Cromey, 1989), and more recently, the gene-for-gene foliar resistance of certain rice genotypes to *M. oryzae* was shown to be ineffective in preventing root infection (Jansen et al., 2006).

5.1.4. Negative impacts of agronomic practices

Just as the control of the "green bridge" will contribute to reducing inoculum carryover in biotrophic plant pathogens like rusts, lack of "green bridge" control or continuous cropping increases pathogen populations leading to higher levels of initial inoculum and greater pathogen diversity. High diversity of the stem rust pathogen has been reported in Kenya, where wheat is cultivated throughout the year in highlands near the equator, where day length is almost constant and crops take four to seven months to mature (Martens, 1975; Luig, 1983). It is likely that these practices have contributed to the development of a stem rust pathotype carrying virulence for many resistance genes, including *Sr31*, which was detected in neighbouring Uganda in 1999 (Pretorius et al., 2000).

Some pathogens infect more than one crop species, and so practices adopted in production systems based on different crops can lead to increased disease risk. It has been known for many years that Fusarium Head Blight (FHB) is more severe in situations where maize and wheat or barley are grown in close association, a practice that increased along with the adoption of conservation tillage in the Red River Valley in North America and is believed to have contributed to the disastrous FHB epidemic in 1993 (Stack, 2003). Similarly, some pathotypes of *P. graminis* f. sp. *tritici* (causal agent of stem rust of wheat) have acquired the ability to infect triticale in Australia (McIntosh et al., 1983) and South Africa (Pretorius et al., 2007). Favourable climatic conditions, plus the occurrence of two mutant stem rust pathotypes with virulence for triticale, led to severe stem rust epidemics in triticale in Queensland (Australia) in 1982 and 1983 (McIntosh et al., 1983). Fortunately most wheat cultivars grown in this region were resistant to the two triticale-attacking pathotypes due to the presence of different resistance genes, which led in essence to separate populations of the stem rust pathogen specialised to the two crops (Zwer et al., 1992). The strategy of improving and diversifying stem rust resistance in triticale and ensuring different genes are used in each crop was viewed as important in controlling the disease in both crops (Zwer et al., 1992). An even greater challenge now exists with the recent detection in Australia of a *Pst* pathotype with added virulence for a resistance gene in the triticale cultivar Jackie (C.R. Wellings, unpublished). This pathotype is virulent on many wheat cultivars in eastern Australia, and in 2008, inoculum build up in early sown triticale crops has provided initial inoculum for later sown spring wheat crops.

Chapter 2 (Section 4.2) further discusses negative and positive interactions between crop and soil management practices (e.g. stubble retention) and diseases from a broad farming system perspective. Chapter 13 (Section 4.3) analyses in detail the interaction between wheat, fungal pathogens (*Rhizoctonia*, *Pythium*) and bacteria (*Pseudomonas*), with emphasis on root vigour as a trait that may overcome some of the negative biological effects of reduced tillage.

5.1.5. Gene deployment and minimum disease standards

Several examples exist of resistance genes that have been deployed widely, and remained effective for many years before being rendered ineffective. For example, the stem rust resistance gene *Sr31* remained effective for many years over large areas, before being rendered ineffective by a pathotype first detected in Uganda in 1999 (Pretorius et al., 2000). Similarly, the stem rust resistance gene *Rpg1* in barley was deployed widely in North America, and remained effective for 60 years until a mutant pathotype with matching virulence was detected in 1988 (McCallum et al., 2007). The reasons why these resistance genes remained effective for so long before succumbing to virulent pathotypes are unclear.

Although the frequency of mutation in cereal rust fungi is low (e.g. about 1.6 per 100,000–200,000 urediniospores in *Pst*; Gassner and Straib, cited by Chester, 1946), and cereal rusts are dikaryotic (i.e. double mutations may be required to generate a virulent isolate), huge numbers of urediniospores can be produced even at relatively low levels of disease. In *Puccinia recondita*, for example, a single uredinium can produce some 2000 urediniospores per day for two weeks or more (Park, 2000). The longevity of a resistance gene may therefore depend on the amount of rust present; the more rust, the more mutants and the greater probability of development of virulence for a given resistance gene. In the case of the leaf rust resistance gene *Lr24* in Australia, there is evidence to suggest that the gene remained effective because it was initially deployed in a region with low inoculum levels (Park et al., 2000). At least 28 cultivars with *Lr24* were released in Australia following the release of Torres in 1983, and by 1993, the area sown to cultivars with *Lr24* was about 45% in Queensland and 35% in New South Wales (Brown, 1994). Despite this, the gene remained effective from 1983 until virulence was detected in a single pathotype in South Australia in 2000 (Park et al., 2002). In contrast, *Lr24* was either ineffective or overcome not long after the deployment of cultivars with this gene in the USA (Long and Leonard, 2000), Canada (Kolmer, 1998) and South Africa in 1967 (Pretorius et al., 1987). The reason(s) why virulence for *Lr24* was not detected in Australia for 17 years after the gene was first deployed, although not entirely clear, likely relate to its initial deployment in northern NSW and Queensland where leaf rust inoculum levels were low, the result of strict adherence to minimum rust resistance standards in this region from the 1970s onwards (Platz and Sheppard, 2007; Wallwork, 2007). In this region, fewer mutational events would be expected in situations of small pathogen population size. The initial detection of virulence for *Lr24* in southern regions is consistent with this theory, because leaf rust was at relatively high levels in this region at that time (Park et al., 2002).

The longevity of rust resistance genes once deployed can also be related to the ability of the pathogen to acquire matching virulence. Mutagenesis experiments using the chemical mutagen ethyl methane sulphonate by Luig (1978) established that avirulence genes in *P. graminis* f. sp. *tritici* vary in their mutability; for example, while mutations to virulence for the resistance genes *Sr5*, *Sr9e* and *Sr21* were relatively common, mutations to virulence for *Sr26* were never observed. Luig (1978) suggested that these differences indicated that the avirulence genes present in *Pgt* have intrinsic differences. Clearly, the effectiveness of resistance genes when deployed over large areas is complex, being determined not only by the ability of the pathogen to acquire matching virulence, but also by other traits in the pathogen. Long-term surveys of pathogenicity of wheat rust pathogens in Australia, where sexual recombination does not exist, have also provided many examples where certain pathogen genotypes seem to have greater survival ability, independent of virulence for resistance genes. A recent example is that of a pathotype of *P. striiformis* f. sp. *tritici* (*Pst*; causal agent of wheat stripe rust), first detected in Western Australia in 2002 and now present in all Australian wheat-growing regions (Wellings, 2007). This pathotype resulted in a rapid and major shift in the Australian *Pst* flora, which does not appear to be related to virulence for a specific resistance gene(s). Comparative studies have shown that this pathotype is very similar to or the same as one occurring in North America, which is now regarded as having greater aggressiveness (Milus et al., 2006).

5.2. Crop composition

Interactions between hosts and pathogens are often scale dependent. While the basic process of challenge and response that underlies evolutionary change clearly occurs at the biochemical level where products of individual pathogen and host cells within a single plant respond to each other, the probability and subsequent consequences of evolutionary change in either host or pathogen are played out on a much broader tapestry of whole populations or metapopulations. In an agricultural context, these are the interactions occurring on spatial scales that range from single fields to the entire crop of a discreet region. In natural systems, these interactions occur within and among individual patches occurring in the same local area.

Many, if not most, agricultural crops are grown at high density, under high nutrient conditions in large homeogeneous populations. This situation is a long way from the situation typical for most host–pathogen interactions including those that the ancestors of our crop plants faced before domestication. Indeed, most natural plant populations occur in discrete patches or populations separated from other patches of the same species by varying distances of metres to kilometres, while the size of individual populations varies from a few to tens of thousands of individuals. This spatial distance and population size variability in host populations imposes a similar pattern of diversity on associated pathogen species. Thus, the genetic structure and evolutionary trajectory of collections of more or less discrete pathogen populations ("metapopulations") are potentially quite different to the equivalent-sized population occurring as a single homogeneous body.

This becomes particularly apparent in pathogens that typically go through "boom-and-bust" cycles as is the case for many rust and mildew species. In these instances, the genetic structure of individual rust populations in a metapopulation may show distinct and persistent differences between one another as a consequence of the effects of local drift and selection (Burdon and Thrall, 1999). Therefore, pathogen populations that occur in a metapopulation structure typically show a greater diversity in traits under positive selection pressure (e.g. virulence) than do homogeneous pathogen populations of an equivalent total size.

5.2.1. *Epidemiological effects of population size and patchiness*

The extent to which epidemics of disease develop within individual host populations is dependent on a broad range of host, pathogen and environmentally related factors. Notwithstanding this complexity though, inter-host proximity (equating to host density; Burdon and Chilvers, 1982) and overall population size are two broad host demographic features that typically show significant positive correlations with disease prevalence and severity. At the small population sizes often found in nature, disease occurrence is patchy as the spread of the pathogen from one patch to another is highly unpredictable. Moreover, even when present, the rate of increase is generally lower as most inoculum produced is dispersed beyond the bounds of the population into areas where the host is absent. As population sizes increase, disease incidence becomes more reliable and less inoculum is lost (Burdon et al., 1995; Smith et al., 2003).

The same sort of relationship between host and pathogen population size holds in an agricultural context although there, small host populations are not usually encountered. However, these effects are seen in much of the early work associated with the use of mixtures to control disease. Thus, small plot sizes typically underestimate the level of disease that would occur in single varietal stands (due to loss of inoculum beyond the plot edge) while simultaneously over-estimate the level in adjacent mixed stands as a consequence of a local swamping effect (Wolfe, 1985). Figure 6 in Chapter 5 illustrates how mixtures of wheat varieties outyielded pure crops in small-plot (1.5 m × 5 m) experiments in Nepal, against a background of spot blotch (*Bipolaris sorokiniana*) and rusts (*P. recondita*). As mixture experiments became more ambitious in size, the confounding effect of plot size (and hence host population size) became clearer (Wolfe, 1985).

5.2.2. *Genetic effects of population size and patchiness*

The probability of a novel virulence allele occurring in a pathogen population through random mutation (essentially the ultimate source of novel variation) is directly correlated with the size of the pathogen population. However, the chances that such a "spark of evolution" actually becomes established are dependent on the selective advantage that the mutation confers the novel pathotype in the pathogen population as well as stochastic forces associated with random drift as the pathogen goes through environmentally driven surges and abrupt declines in population size.

In agricultural crops, the deployment of resistance genes – the number and their combination – is determined by breeders, but with the exception of mixture strategies, individual stands are largely monocultures of near-identical individuals. In these circumstances, mutations that confer no selective advantage are only likely to become apparent if associated with others that confer advantage. On the other hand, mutations that enable a pathogen to overcome resistances widely deployed in a crop will ensure access of the mutant pathotype to large areas of the crop that were previously free of disease.

The situation in natural host–pathogen metapopulations is potentially distinctly different. There, host and pathogen variability in resistance and virulence drive one another directly and host populations often contain many different resistance genes (Bevan et al., 1993; Laine, 2004). A diverse resistance structure within an individual host population also has both epidemiological and evolutionary implications. While this might seem largely irrelevant to major field crop situations, the underlying implications are seen in mixture strategies – most obviously in random varietal mixtures but also to a lesser extent in on-farm pure stand varietal diversification (Finckh et al., 2000).

The presence of hosts with a range of different resistance phenotypes will reduce the effective host population size for all pathogen isolates other than those carrying a combination of virulence traits capable of overcoming the resistance phenotypes present in the population. As a consequence, one would expect more diverse host populations to incur lower disease incidence and severity than less diverse ones. This expectation is borne out in both natural and agricultural populations. Thus, the severity of rust caused by *M. lini* in natural populations of *Linum marginale* was significantly, inversely correlated with the diversity of resistance phenotypes present in the population (Thrall and Burdon, 2000). This pattern reflects the large body of evidence that shows that the use of cultivar mixtures or multilines reduces the severity of diseases in a wide range of agricultural circumstances (Wolfe, 1985). Similarly, in mixtures of three barley varieties, Chin and Wolfe (1984) found that after an initial early season tendency for a "super-race" to dominate, as epidemics developed, there was a greater diversity of pathotypes in the varietial mixtures than in the pure-line controls. A mirroring pattern appears to occur in the *M. lini*–*L. marginale* interaction where a near significant ($P = 0.08$) correlation between host diversity and pathogen diversity was detected.

Chin and Wolfe (1984) also reported that the pathogen isolates that dominated pathogen populations attacking their varietal mixtures later in the epidemic, while restricted in their virulence spectrum, were more fecund (produced more spores) than the super-race line. The universality of this trade-off between fecundity and virulence has been confirmed in the *M. lini*–*L. marginale* interaction where pathotypes with multiple virulence combinations were significantly less fecund (Thrall and Burdon, 2003).

5.2.3. Interplay of epidemiology and genetics in agricultural situations

As already indicated, evolution is essentially a numbers game and by effective application of this knowledge it is possible to reduce the rate of evolution in agricultural pathogen populations. Practices that reduce the size of the pathogen population reduce the number of random mutations in the population, as well as the chance that any potentially beneficial mutation (from the pathogen's perspective) for virulence encounters the conditions needed to ensure its increase in the population. Thus, it has long been recognised in cereal breeding that the use of single gene protection is extremely vulnerable to rapid failure – indeed, it was the repeated cycles of single gene deployment followed by rapid pathogen evolution in cereal breeding in the first half of the twentieth century that led to many classic boom-and-bust cycles and coining of the phrase "man-guided evolution of the rusts" (Johnson, 1961). Clearly, presenting a pathogen with two novel resistances simultaneously very significantly decreases the probability of appearance of a mutant pathotype capable of overcoming both simultaneously. In the case of two resistance genes that require two truly independent mutations, if the probability of mutation for any one gene is $1/10^6$, then for both genes simultaneously it would be $1/10^{12}$! The successful application of such a strategy thus has the potential to reduce the total pathogen population very substantially and can lead to a marked increase in the durability of individual resistance genes.

However, the effectiveness of such strategies is highly dependent on ensuring minimum disease standards, the rapid withdrawal of cultivars with insufficient or defeated resistances and appropriate phytosanitation to minimise "green bridges". Agronomic practices of this kind can have very significant impacts on pathogen population sizes. Two contrasting examples of such impacts are found in changing cropping practices, and in the extent to which pathogens move between crops and associated weedy plant communities.

In the former case, apparently innocuous changes in tilling practices, in particular the upsurge in minimum till, can lead to major changes in off-season pathogen survival and subsequent increased disease problems. A similar outcome may result from weedy species that act as a "reservoir" of inoculum providing a "green bridge" between the maturity of one crop and the appearance of susceptible material in the next. There are numerous examples of such phenomena involving both soil-borne pathogens such as *Fusarium* spp. (Hennessy et al., 2005) and aerial dispersed ones like the cereal rusts *P. coronata* and *P. striiformis*. A case in point is provided by introduced weedy *Hordeum* species that have been implicated together with volunteer wheat plants as off-season (over-summering) hosts for *P. striiformis* (Wellings, 2007).

6. FROM GENE TO CONTINENT: CONCLUSIONS AND FUTURE PROSPECTS

Fundamental research on the genetic bases of disease resistance in plants and of host–pathogen interactions has greatly improved the efficiency of manipulating disease resistance genes in practical breeding programmes and resulted in the deployment of high-yielding genetically resistant crop cultivars that in some cases have occupied vast areas. The integration of genetic resistance with agronomic practices has often been particularly important in improving the effectiveness of resistance in reducing yield losses, and in minimising the chance of pathogens overcoming resistance.

One of the greatest challenges in protecting crops from pathogens has come from exotic pathogen incursions, and significant crop losses have occurred as a result of accidental intercontinental movements of plant pathogens (Finckh, 2008). It is quite feasible that in future, such long-distance movements of plant pathogens may become more frequent due to changes in climate and increased international movement of people and goods, necessitating even greater coordination in the control of plant diseases at the continental or even global levels. Scherm and Coakley (2003) noted that the rate of exotic pathogen invasion in the USA during the 1990s had increased threefold from the prevalent rate (about five instances per decade) between 1940 and 1970. A similar situation has been observed in Australia with incursions of exotic wheat rust isolates, four instances of which were detected in the 45 years from 1925 to 1970, four over the 30 years from 1970 to 2000, and three over the past seven years (R.F. Park, unpublished). The increases noted by Scherm and Coakley (2003) were attributed to increased global trade in plant produce, a trend that may continue with global climate change. Instead, the increased frequency of wheat rust incursions in Australia is likely associated with increased international travel and contaminated clothing (e.g. Wellings, 2007). Changes in concentration of key atmospheric gases and global warming may also affect disease incidence (see Section 4.2 in Chapter 5). Retrospective studies of the annual incidences of the two wheat pathogens *Phaeosphaeria nodorum* and *Mycosphaerella graminicola* in grain since 1843 at Rothamstead, UK, established that they were positively and negatively associated with atmospheric concentration of SO_2 (Shaw et al., 2007). While the concentration of SO_2 has declined in Europe and North America over the past 20 years, these results nonetheless illustrate a potential cause and effect connection between atmospheric gas concentration and pathogen incidence. According to Coakley et al. (1999), predicted increases in CO_2 concentration could either favour or hinder plant pathogens, making precise predictions difficult.

While a great deal of knowledge now exists from how individual host and pathogen genes interact and how resistance genes function in plants to ecologically based studies of host–pathogen interactions, much remains to be learnt at the interface of the genetics of resistance and crop physiology. The cloning of resistance genes and corresponding avirulence genes have indicated considerable complexity not only in structure but also in the way in which gene products interact and trigger resistance. At the crop level and beyond, few large-scale studies have addressed in detail the effects of genetic diversity in crops in reducing disease incidence. In one such study, in which the control of *M. grisea* was examined in 3342 ha of rice crops in China, the benefits of genetic diversity were very clear, with varietal mixtures resulting in an 89% yield increase in susceptible varieties (Zhu et al., 2000). Clearly, genetic diversity is important in sustained control of plant diseases, and it has been argued that even in cases where specific or major resistance genes are used, genetic diversity can be used as insurance against lack of durability and hence as a means of reducing genetic vulnerability (McIntosh, 1988). The durability of some single gene resistances, despite extensive use, and the preferential survival of some pathogen genotypes in the absence of no obvious advantage in terms of virulence that has been well documented with wheat rust pathogens in Australia, indicates that the interaction of hosts and pathogens is indeed complex.

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CHAPTER 18

Improving Crop Competitiveness with Weeds: Adaptations and Trade-offs

Glenn K. McDonald and Gurjeet S. Gill

> … But soon the cornfields
> Themselves become a labour: blighting mildew
> Devoured the haulm; slothful in the ploughland
> The thistle reared its prickles. Crops are choked,
> A shaggy growth comes up, of burrs and caltrops,
> And amid the shining tilth the sorry darnel
> And barren wild oats reign.
> Virgil "The Georgics" Book 1, Lines 150–154

1. INTRODUCTION

Weeds are a pervasive feature of cropping systems throughout the world and if poorly managed can cause significant losses in yield and reduce the quality of grain crops (Oerke and Dehne, 2004). Managing weeds to minimise their impact on crop production is therefore a major activity in crop production (Section 4.1 in Chapter 2). Effective weed control can be a problem for many reasons depending on the production system used, ranging from the development of herbicide-resistant weeds in highly mechanised broadacre production systems to the inability to afford herbicides in subsistence farming systems. Despite the diverse array of farming practices and environments in which crops grow, weed management relies to varying degrees on vigorous crop growth. A benefit of improving the competitive ability of crops is that it is a low-cost, low-risk strategy which complements other weed management practices. This can be important where other methods of weed management are difficult, ineffective or expensive.

This chapter will examine the importance of crop competition to weed management. Improvements in the competitive ability of crops can be achieved both by breeding and by crop management (Lemerle et al., 2001a) and often crop management has a larger effect on weed management than crop genotype (Blackshaw et al., 2006; Carlson and Hill, 1986; Lemerle et al., 2001b; McDonald et al., 2007; Zhao et al., 2007). However, this review will concentrate on genetic aspects of competitive ability, the traits that enhance competitive ability and their influence on grain yield. The relationship between competitive ability and fitness will also be discussed, with an emphasis on how plants compete for the limited resources that sustain crop growth and yield when challenged by weeds. The influence of the environment and the importance of genotype by environment (G × E) interactions to competitive ability will be examined. Allelopathy, which can also play a role in weed suppression and competitive ability (Lemerle et al., 2001a; Bertholdsson, 2005; Schenk, 2006), will not be considered explicitly, although there may be certain cases where allelopathic effects are important in understanding the interactions between neighbouring plants.

2. INTERACTIONS BETWEEN PLANTS

Whether in natural or managed systems, plants rarely grow in isolation: they are members of a community of plants and each individual interacts with its neighbours. Plant growth requires a limited number of resources, which are light, nutrients and water. Whenever two plants grow near to one another, they interact by altering their immediate environment, which influences their acquisition of these resources. Changes in the environment may be qualitative, such as changes in the ratio of red:far red light, or they may be quantitative, such as the depletion of water and nutrients or a reduction in light intensity by shading, but in both cases the environmental changes can alter production, morphology and partitioning of dry matter. It is generally considered that plants do not compete for space, but for the resources that are contained within the space (Donald, 1963, 1968; Aldrich, 1984a). Wilson et al. (2007) recently re-examined this issue and while they found some evidence to suggest that competition for space can occur, they concluded that the effect was so small that it can be ignored in plant communities.

2.1. Agricultural and natural systems

Much of the theoretical work on competition has been based on studies of natural ecosystems (e.g. Harper, 1977; Crawley, 1986; Tilman, 1988). While many of the general principles of plant interactions are applicable to agricultural systems, there are important differences between natural and managed systems that need to be considered when extrapolating from one system to the other. Most of the world's cropping systems are highly managed and are based on annual crops grown in a specific rotation with high supplies of nutrients. Crop–weed competition often occurs between a dominant weed and one crop species within a single growing season, although management practices in the preceding years can influence the weed burden in a field. In contrast, many of the studies on the competitive relationships within natural ecosystems consider long-term succession, diversity and composition in communities that are composed of a large number of competing species. Also, much of this work is based on perennial systems. While competitive relationships within a single growing season may influence longer term trends in crop–weed interactions, often changes that occur over the short term in a plant community may be quite different to long-term changes (Tilman, 1986, p. 74). In natural systems, herbivory and plant disease can be important influences on competitive relationships and community composition (Watkinson, 1986), but in broadacre cropping systems these effects are minimised as much as possible by the use of chemicals or by growing resistant and/or tolerant crop varieties. However, there are examples where insects and pathogens have been used in biocontrol programmes to aid weed management, but these are often used in large-scale intervention programmes, rather than by individual farmers. The differences in the complexity and levels of human intervention of the two systems need to be considered when using information from one system to interpret and understand competitive relationships in the other.

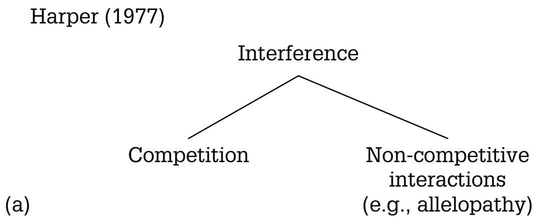
2.2. Interference and competition

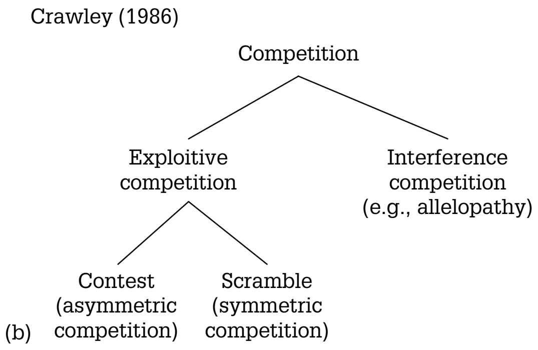
There are various terms that are used to describe the ways plants interact. The most commonly used terms are interference and competition, although they are not always used consistently and are sometimes used interchangeably (Box 1). Interference describes how plants respond to the presence of neighbouring plants. Competition refers to the relative abilities of different plants within the community to exploit a resource, which will be influenced by how effectively plants acquire resources and how efficiently they use the resources for growth and seed yield. The competitive ability of a crop species or variety describes how well it can limit the yield loss from weeds and/or suppress the growth of weeds.

Five possible types of interactions can be identified within a plant community based on whether one member causes an increase (+), a decrease (−) or has no effect (0) on the growth of another member of the community (Williamson, 1972): −+ (plant/herbivore, plant/pathogen), −− (competition), ++ (mutualism), +0 (commensalism) and − 0 (amensalism). Of these, commensalism and amensalism can be considered to be specific examples of mutualism and competition, respectively, and are generally not considered. Mutualism may be important in intercropping (Vandermeer, 1992), but is of little significance in crop–weed

BOX 1 Interference and competition

While competition is an important concept in studying interactions between plants, there is no general agreement on the best definition of the term, which is often used in a manner that can lead to some confusion (Hall, 1974; Vandermeer, 1992; Schenk, 2006). Interference has been suggested as a more appropriate term to describe the different forms of negative plant interactions (Harper, 1977), but often ‘competition’ and ‘interference’ are used interchangeably (e.g. Lemerle et al., 2001a). The two basic frameworks to describe plant interactions are exemplified by Harper (1977) and Crawley (1986):





Vandermeer (1992) considered the difference in terminology to be related to differences between British and North American schools. He highlighted the problem of the inconsistencies by observing that what was ‘competition’ to the Americans was ‘interference’ to the British, and what the Americans described as ‘exploitive competition’ was simply ‘competition’ to the British. Interference to the Americans was considered by the British as that part of interference that is not competition. However, even the definitions within each of these two frameworks for plant interactions are not used consistently. In a review of root competition, Schenk (2006) referred to resource depletion as ‘scramble or exploitation competition’ and mechanisms that inhibit resource access by roots as ‘interference or contest competition’.

Many definitions of competition (e.g. Donald, 1963; Vandermeer, 1992) echo that originally proposed by Clements (1907; quoted in Clements et al., 1929):

“Competition is purely a physical process .... Competition arises from the reaction of one plant upon the physical factors about it and the effect of the modified environment upon its competitors. In the exact sense, two plants, no matter how close, do not compete with one another so long as the water content, the nutrient material, the light and heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins.”

However, the growing recognition that plants can interact with neighbours by mechanisms other than resource depletion has meant that this concept of competition needs to be widened. While Harper’s original suggestion that ‘interference’ is a more useful genetic term to describe interplant competition was dismissed as unnecessary by Donald (1963), it now provides a useful way of clearly distinguishing between the different forms of plant interference which are based on depletion of resources (competition) and those which do not depend on the availability of resources.

Symmetric and asymmetric interactions

Plants may not be equally affected when they interact with each other. Competition has been described as symmetric when the interaction has a mutually deleterious effect on both plants and asymmetric where one plant suffers little or no reduction in fitness. Exploitation competition has been further classified according to the level of asymmetry in the competitive relationship, from contest (highly asymmetric) which results in clear winners and losers to scramble (symmetric) in which the limited resources are distributed among the competitors. There is a continuum in the level of exploitation competition between contest and scramble (Crawley, 1986).

Anticipation of competition

There is an increasing amount of evidence that plants can interact with one another independently of any changes in the availability of resources. Plants are able to sense the presence of neighbours through subtle changes in the environment or the perception of chemical signals, which induces a change in the growth or morphology of the plant

(Continued)

BOX 1 Continued

(Ballaré and Casal, 2000; Schenk, 2006). By this means, plants can anticipate competition, although this term has anthropomorphic connotations. In essence, plants respond to environmental signals to alter their pattern of growth or morphology to pre-empt competition from neighbours.

Intraspecific and interspecific competition
Competition can occur between plants of the same species (intraspecific competition) or between plants of different species (interspecific competition) and both types occur in crop–weed interaction.

competition. In cropping systems, competitive relationships are the most important to understand crop–weed interactions.

2.3. Environmental influences on competitive ability

Competitive ability is affected by the genotype of the plant, which influences traits such as seedling vigour, canopy architecture, root growth and resource use efficiency, and by the management of the crop, such as plant density, row spacing or sowing date. Apart from traits that contribute directly to the competitive ability of a crop, the adaptation of a crop or a variety to particular environmental conditions, such as climatic conditions, soil pH, nutrient deficiencies and toxicities, is also an important influence on crop–weed interactions (Lemerle et al., 2001a). This is no less true for weeds, but there is an important difference between crop and weed species. Weeds often show a high variation in growth traits across environments, whereas crops are generally bred to show a high uniformity in important agronomic characteristics over a range of environments. After their initial introduction, weeds can evolve in response to the environmental limitations of the site or region. The management of the crop imposes additional selection pressure on the weed. As a result of these pressures, weed ecotypes develop. In contrast, in broad-scale, mechanised cropping systems, a particular crop variety can be grown over a wide geographic area under a variety of climatic and edaphic conditions, which can influence its vigour. Thus, there are environmental influences on weed–crop interactions that may be manifested as G × E interactions in competitive ability of crops. Describing and understanding the bases of G × E interactions is an important aspect of crop improvement that has received little attention in studies on competitive abilities of crops. This will be considered in more detail below.

3. CROP YIELD LOSSES FROM WEEDS

Yield losses from weed competition have a greater potential than disease or insect pest to reduce yields of the major food and industrial crops (Table 1). However, current weed management practices in many production systems are generally effective in reducing these losses and the efficacy of weed control is the highest among the different pest groups (Oerke and Dehne, 2004). Weeds can also reduce the quality of the harvested product by contaminating grain (Aldrich, 1984b). The severity of the yield loss from weeds is variable and depends on a number of different characteristics of the weed, the crop and the environment in which they grow.

3.1. Weed density

The density of weeds is one of the major determinants of yield loss. All available evidence indicates that the relationship between weed density and crop yield loss is hyperbolic or exponential in shape (Gill and Davidson, 2000). Absolute yield or the relative yield (yield in the presence of weeds:weed-free yield) decreases asymptotically with increasing density of weeds and the type of weed affects the rate of yield loss.

The variation in the rate of yield loss among weed species is due to several factors intrinsic to the weed species, including initial seedling size and vigour, relative growth rate, leaf area, canopy architecture, root growth and distribution, allelopathic effects as well as the competitiveness of the crop. A comparison of the

Table 1 Summary of the Potential and Actual Yield Losses (%) due to Fungal and Bacterial Pathogens, Viruses, Animal Pests and Weeds and the Efficacy of the Control Measures in Wheat, Rice, Maize, Barley, Potatoes, Soybean, Sugar Beet and Cotton

	Pest Group				
	Fungi and Bacteria	**Viruses**	**Animal Pests**	**Weeds**	**Total**
Potential loss	14.9	3.1	17.6	31.8	67.4
Actual loss	9.9	2.7	10.1	9.4	32.0
Efficacy	33.8	12.9	42.4	70.6	52.5

Potential yield loss is the loss without any physical, chemical or biological intervention, while actual yield loss is the loss incurred despite the use of crop protection practices. Efficacy is the proportion of potential yield loss prevented by crop protection practices.
Source: Oerke and Dehne (2004).

impact of different weed species on wheat yield loss showed more than a 100-fold difference in percentage yield loss per weed plant (Gill and Davidson, 2000).

Most agricultural weeds have a capacity to cause large reductions in crop grain yield if present at high densities, but it is remarkable that substantial losses in yield can occur with very few weeds. For example, Carlson and Hill (1986) measured yield losses in wheat (*Triticum aestivum*) of 40–50% with only 8–16 wild oat (*Avena fatua*) plants m^{-2}. Similarly, Anderson (1993) showed that 18 plants m^{-2} of jointed goatgrass (*Aegilops cylindrica*) reduced wheat grain yield by 27% in eastern Colorado. Yield losses can be even greater in less competitive crops, such as pulses. In chickpea (*Cicer arietnum*), yields were reduced by 40% at 5 plants m^{-2} of turnip weed (*Rapistrum rugosum*) and by 25% at 5 plants m^{-2} of wild oat (*Avena sterilis* ssp. *ludoviciana*) (Whish et al., 2002) while 10 plants m^{-2} of wild radish (*Raphanus raphanistrum*) caused a 28% loss in yield in lupin (*Lupinus angustifolius*) (Hashem and Wilkins, 2002) and 10 canola plants m^{-2} (used as a weed mimic) reduced lentil (*Lens culinaris*) yields by 15–26% (McDonald et al., 2007).

The sensitivity of crop yield to small weed populations suggests that many weed species are very effective in the capture and/or the efficient use of resources, or they have other attributes, such as allelopathy, which help to suppress crop growth. Plant populations of wheat crops are commonly 100–200 plants m^{-2}, suggesting the yield losses cited above can occur with a weed population 10–20% that of the wheat crop. In contrast, increasing the plant population of cereals by 10–20% above the standard rate generally has little impact on yield.

The competitive nature of some weeds is shown by the relative competitive ability (RCA), which measures growth or yield of a weed relative to the crop in which it is growing. Values for RCA can be high: Eslami (2006), for example, measured RCA of 5–8 for wild radish when growing in a wheat crop, indicating one wild radish plant was equivalent to five to eight wheat plants. Similarly, Pantone et al. (1991) concluded that in terms of its competitive ability, one weedy rice (*Oryza sativa*) plant was equivalent to three 'Mars' rice plants.

3.2. Spatial distribution of weeds

In contrast to most experiments on crop–weed interactions which use uniform weed populations, weeds are generally not uniformly distributed in crops, growing either as an isolated weed among crop plants or in clumps of weeds. Consequently, the level of interference and competition is not uniform within a crop. Computer simulations suggest non-uniform spatial distribution of weeds may result in a lower yield loss than that expected from uniformly distributed weeds (Thornton et al., 1990). The modelling predicted that 10 plants m^{-2} of wild oats (*A. fatua*) would reduce the yield of wheat by 15% if uniformly distributed, but this would fall to 5% if the plants were clumped into 10% of the area. This apparently occurs because the

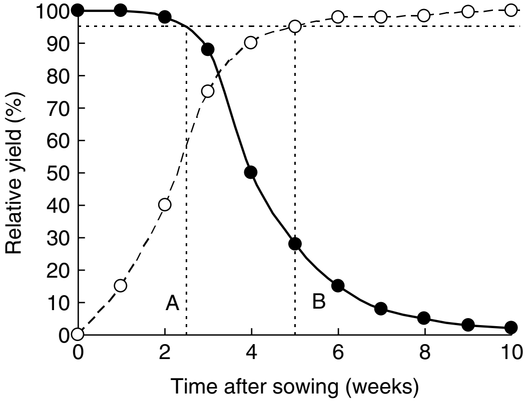


FIGURE 1

Hypothetical responses in crop yield to (A) the time when weeds are present (●) and (B) the weed-free period (○). Weeds are removed at different times after sowing to determine the period of crop growth over which weeds are tolerated or crops are maintained weed-free for different lengths of time after sowing to determine the weed-free period. Critical times are generally defined by the time when a 5% yield reduction occurs. In this example, A is the critical time of weed tolerance and B is the critical weed-free time. The period B–A is the critical period of weed–crop competition as before and after this weed interference will reduce yields by no more than 5%.

effect of weed competition is compressed into small, discrete areas. The importance of spatial variability in weeds within a crop and its effect on yield loss has received relatively little attention to date, but the advent of variable rate technology and precision agriculture will make this aspect of crop–weed interactions more important in future.

3.3. Timing of crop–weed interactions

Yield losses are also influenced by the timing of the crop–weed interaction. This effect is commonly measured by weed removal studies and it is examined in two ways: (i) the period of time during which weeds are tolerated and (ii) the period of time that the crops needs to be weed-free before there is a significant reduction in yield (Figure 1). The period of crop tolerance measures the effects of early weed interference as weeds are removed at successively later growth stages. In effect, it measures the competitiveness of the weed against the crop. The weed-free period measures the effect of progressively later weed interference on the crop and this measures the competitiveness of the crop against weeds. The critical time for weed tolerance (A in Figure 1) and the critical weed-free period (B) define the early and late boundaries of the critical period of crop–weed competition. During this period, the presence of weeds has the greatest effect on crop growth and yield and weed competition during this period should be minimised to reduce losses in yield.

Weed removal studies demonstrate that crops often have a short period during which they can tolerate weed interference, but many crops become competitive early (Table 2). However, there is considerable variation in the values, which is related to factors such as weed density and the germination and growth patterns of the weeds in relation to the crop. In an analysis of yield losses in crop–weed interactions from a large number of different experiments, van Heemst (1985) found that the relative yield of crops was significantly correlated with the end of the critical time of competition ($r = -0.82$, $P < 0.001$, $n = 14$); there was no correlation with the start of the critical period ($r = -0.19$, $n = 14$) and the correlation with the duration of the critical period, while significant, was weaker ($r = -0.65$, $P < 0.01$, $n = 14$). The greater importance of the end of the critical period of weed competition may reflect the greater importance of weed competition later in the

Table 2 Periods (Weeks after Sowing) during which Weeds will be Tolerated without Significantly Reducing Yields and the Length of the Weed-Free Period needed before Yield Losses occur

Crop	Weed	Location	Period		Reference
			When Weeds Tolerated	To be Weed Free	
Bean	Mixed annuals	WA, USA	8	5	Aldrich (1984b)
Cabbage	Mixed annuals	England	3–4	2	
Lettuce	Mixed annuals	England	3	3	
Soybean	Giant foxtail	IL, USA	8–9	3	
Sugar beet	Barnyard grass	WA, USA	12	10	
Winter wheat	Downy brome	OR, USA	22		
		NE, USA		2	
Peanut	Mixed annuals	NC, USA	3	9	Everman et al. (2008)
Maize	Mixed annuals	Mexico	3	5	
Maize	Mixed annuals	NY, USA	5		Cox et al. (2006)
Canola	Mixed annuals	Manitoba, Canada	2.5-maturity	0–6	Martin et al. (2001)

growing season when demand and competition for resources becomes more intense and which coincides with the determination of important yield components. For example, Cox et al. (2006) found that maize (*Zea mays*) yields were reduced by about 25% if weeds were present during the first six weeks of growth. Yield was reduced mainly by fewer kernels per plant rather than ears per plant and rows per ear, suggesting early interference affected the development of yield components determined at later stages of growth. While early interference may occur, at this stage there may be little or no competition for resources as the crops and weeds are small and yields are not greatly affected by the presence of weeds, as long as the weeds do not persist. The agronomic implication of this is that to be most effective, weeds need to be controlled early, before significant levels of competition develop.

While weed removal studies provide guidelines for the most appropriate time for weed management, they provide little understanding of the underlying causes of the responses. Few, if any, studies have examined this, or have made detailed measurements of resource allocation and partitioning as competition between the crop and the weed develops. There is a need to understand the effects of timing of crop–weed interactions on the yield reductions.

In the past, weed removal studies were particularly useful for formulating advice for the timing of manual weeding in crops in developing countries. With widespread adoption of herbicides even in most developing countries, the importance of such studies has diminished as the timing of weed control is often determined by available herbicides. However, recent adoption of genetically modified, herbicide-tolerant crops has renewed interest in the timing of weed control among researchers. For example, in a study with glyphosate-resistant maize, Cox et al. (2006) found that early post-emergence application of glyphosate (3–4 leaf stage of maize) prevented loss in grain yield from weed competition, but delaying herbicide application until mid (5–6 leaf stage) or late-post-emergence (7–8 leaf stage) resulted in 25 and 42% reduction in grain yield, respectively. Such studies have practical importance because glyphosate can effectively kill weeds even at very late stages of crop development; however, if the herbicide is used after its optimal timing, the yield potential of the crop would have been already reduced. Based on this study, it was recommended that the growers in north-eastern USA should apply glyphosate by the 3–4 leaf stage of maize to avoid yield losses from early season weed competition.

4. THE ROLE OF COMPETITIVE CROPS IN WEED MANAGEMENT

With the large potential losses in yield from weeds, the development of cheap, selective herbicides has been one of the most important advances in agriculture and a major reason for the increase in the productivity of broadacre crops over the past 50 years. Improvements in spray technology have further enhanced the efficacy of herbicides. With the exception of subsistence and organic farming systems, herbicides are the dominant method of weed control in grain production. For example, herbicides comprise 20–30% of input costs in North American cropping systems (Derksen et al., 2002), which would be typical of broadacre, mechanised farming systems worldwide. In Australia, the combination of large cropping areas, expensive labour, short growing seasons, fragile soils and the imperative to minimise production costs have all contributed towards herbicides remaining a vital component of cropping systems (Walsh and Powles, 2004).

One of the negative consequences of the widespread use of herbicides for weed control has been the development of herbicide resistance in weed species. The rise of herbicide resistance has necessitated a re-evaluation of weed management strategies and the management of herbicides. Since the first report of a herbicide-resistant weed (Ryan, 1970), the number of resistant biotypes has increased rapidly and there is little evidence of the trend easing. According to Heap (2008), there are now 319 unique herbicide-resistant weed biotypes belonging to 185 species around the world. For a long time, the prospect of evolution of resistance to glyphosate in weed populations was considered remote, but glyphosate resistance has now been confirmed in 14 weed species worldwide (Heap, 2008). There is no doubt the problem of herbicide resistance in weeds is truly global and is relevant to all cropping systems. The incidence of herbicide resistance is increasing at a rapid rate and as cropping intensity increases worldwide in response to growing human population, selection for herbicide resistance will continue unabated.

In response to this trend, the concept of integrated weed management (IWM) has been promoted. This is a systems approach to weed management, which uses an ecological framework to combine a range of weed management practices. Although a suite of control methods is employed, they aim to do one of the following three things: (i) reduce the weed burden in a field by limiting the size of the weed seed bank; (ii) reduce the weed population by minimising weed seed germination and seedling establishment; and (iii) reduce the competitiveness of established weeds by increasing the competitive ability of the crop or eliminating weeds within the crop by chemical or physical control. An important component of IWM is the use of competitive cultivars (Lemerle et al., 2001a), which can contribute to each of these aims.

The benefits of competitive cultivars derive from the reductions in growth and fecundity of the weed species as well as interactions with other practices. More competitive cultivars may also provide an opportunity to use lower rates of herbicides to achieve an acceptable weed suppression (Christensen, 1994; Blackshaw et al., 2006; Williams et al., 2008). The corollary of this is that if herbicide efficacy is reduced for some reason, a high competitiveness will still limit yield losses from weed competition and reduce weed seed production.

5. COMPETITIVE ABILITY OF CROPS

As a plant grows, it will affect the quantity of a resource and neighbouring plants will respond to the change in the availability of the resource. In the case of light, the quality of the resource may also be important (Rajcan and Swanton, 2001). Implicit in this description when applied to crop–weed interactions is the recognition that both crop and weed species are involved in a competitive relationship, not just the weed. The presence of weeds does not necessarily mean it will compete with the crop plant for resources (Aldrich, 1984a). For example, the use of a soil resource may not be correlated with competitive ability if there is partitioning within the habitat. This may happen when shallow and deep-rooted species grow together and water is utilised from different parts of the profile (Casper and Jackson, 1997). The other factor that may influence competitive ability is the efficiency with which plants use the resource (nutrient, radiation and water use efficiency [WUE]), which may affect plant growth rates even in the absence of marked differences in the acquisition of resources.

In weedy crops, there are two types of competition relevant to crop yield: the interspecific competition between the crop and the weed and the intraspecific competition between the individuals of the crop (Box 1). There may be a trade-off between competitiveness and yield because traits that suppress growth of weeds (i.e. interspecific competition) may not necessarily be conducive to high yields in monoculture (i.e. intraspecific competition) (Donald, 1968; Donald and Hamblin, 1976; Jannink et al., 2000). Based on the principles of competition for resources, Donald (1968, 1981) developed the concept of the 'communal ideotype' in which yield of the community is enhanced by reducing intraspecific competition. He argued that a high yield potential could be achieved by a more equitable allocation of resources among members of the community and the traits that would enable this to occur would also lead to a reduction in competitiveness. Subsequent experiments in which the effects of shoot and root competition were assessed in varieties differing in yield potential have supported Donald's original ideas (Reynolds et al., 1994; Sadras et al., 2000; Waines and Ehdaie, 2007). It has been suggested that the pursuit of high yields by plant breeders has reduced the competitive ability of modern cereal crop varieties, making grain yields more sensitive to weed competition (Lemerle et al., 2001a; Murphy et al., 2008). This has important implications when considering genetic improvements to competitive ability.

Competitiveness in crops has two facets: the ability to yield well in the presence of weeds (tolerance to weed pressure) and the ability to effectively reduce weed growth (weed suppression) (Goldberg, 1990). Crop tolerance is generally measured as yield loss and weed suppression is measured as either weed biomass or weed seed yield. While the two may be positively related (Lemerle et al., 2001a, 2006), they may also show no or weak correlations (McDonald, 2003; Vandeleur and Gill, 2004; Lemerle et al., 2006). Crop tolerance will allow economic returns in the face of competition from weeds, but may not reduce the weed burden in the field, and conversely, weed suppression can reduce seed set by the weed but may not affect yield losses from weed competition. Ideally, a competitive crop variety will have a high tolerance and high suppressive ability.

6. ENVIRONMENTAL INFLUENCES ON COMPETITIVE ABILITY

The ability of a crop to compete against weeds will depend on the relative responses of the crop and weed species to the environmental conditions in which they grow (Patterson, 1995). This will depend on how well they exploit the resources through better acquisition and/or use efficiency. Consequently, the competitive relationships between a crop and weed may vary considerably depending on environmental conditions.

6.1. Resource availability

Competition occurs when the availability of one or more resources becomes limiting. An important issue that has been the basis of much discussion in ecological studies of competition is whether competition increases or deceases as the availability of resources declines (Craine, 2005). Tilman (1980, 1985, 1986, 1988) examined the effects of the environment on community structure over time and argued that species diversity will be greatest in environments with a low to moderate availability of resources. The importance of nutrient availability on community composition was illustrated by the effect of fertiliser applications on the Rothamsted Park Grass experiment. The greatest number of species, and lowest productivity, was found in the unfertilised plots, whereas adding fertiliser increased biomass and reduced the number of species. There was a strong negative correlation between species richness and biomass within this experiment. However, in this case, species diversity appears to be used synonymously with competition. Increasing the amount of available nutrients led to dominance by one or two species of grass, which suggests that most of the species that were present under low fertility were eliminated as the availability of nutrients increased. While the diversity of species had declined, the remaining species showed the greatest competitive ability. Although there may have been competition among more species at low fertility, the replacement of most of these with a small number of species suggests that competition intensified as fertility increased. Schenk (2006) concluded that the intensity of root competition was generally greater when the availability of resources was low. This is not inconsistent with the suggestion that the level of competition increased with nutrient supply, but may reflect a shift from a greater importance of root competition under low nutrient supply to increasing importance for shoot competition at high nutrient supplies (Casper and Jackson, 1997).

The different arguments about the effect of resource availability on competition have been based largely on understanding the structure of communities over time or along productivity gradients. There is a tendency to view the relationship between resource availability and interspecific competitiveness as a dichotomy: it is either greater at low levels of fertility or greatest at high levels of fertility. The experimental data for crop–weed interactions in response to nutrient availability show a more complex and less predictable relationship. Rather than consistently increasing or decreasing the competitiveness of weeds, adding nutrients can increase, reduce or have no effect on the competitiveness of weeds (Lemerle et al., 2001a).

Figure 2 illustrates the contrasting effects of resource availability on the competitiveness of weeds and crop. When grown with and without annual ryegrass (*Lolium rigidum*), the relative yield loss of wheat was greatest

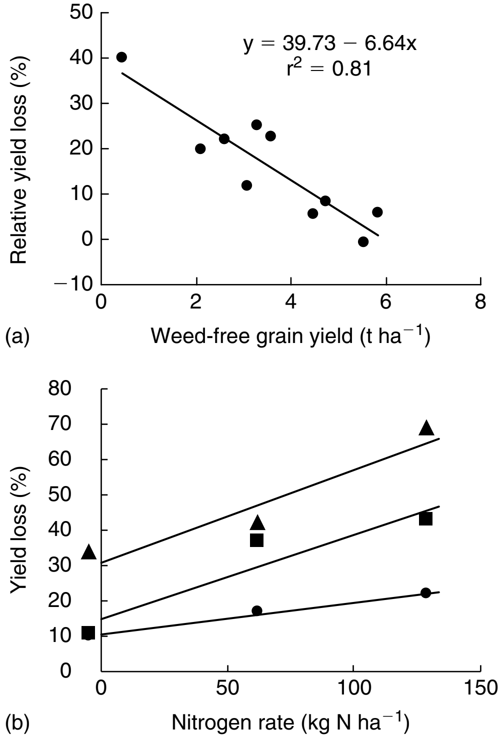


FIGURE 2

*(a) Relationship between the site mean weed-free grain yield and the mean loss in grain yield from weed competition in experiments conducted at 10 sites over three years. Each point is the average of 12 cultivars of bread wheat. Wheat was grown in plots oversown with annual ryegrass (*Lolium rigidum*) or maintained free of weeds. Yield loss is the percentage reduction in yield. Data from Lemerle et al. (2001a). (b) The effect of nitrogen fertiliser rate on the yield loss in wheat from competition from wild oat (*Avena fatua*). Wheat was grown with three different densities of wild oats, 4 plants m^{-2} (●), 16 plants m^{-2} (■) and 32 plants m^{-2} (▲). (Source: Carlson and Hill, 1986.)*

at the low yielding sites (Figure 2a), even though weed biomass production was also reduced. However, no yield loss occurred in a high yielding year, most likely because the better growing conditions favoured early and prolonged canopy development in the wheat crops, which shaded out competing weeds. In this case, the wheat crop appeared to be more responsive to the environment and was more competitive under favourable conditions: weed competition was apparently greatest at lower levels of available resources. In contrast, there will be cases where the weed is more responsive to the availability of a limiting resource and becomes increasingly competitive as the supply increases. For example, in a study on the interaction between wild oat (*A. fatua*) and wheat, the addition of nitrogen fertiliser promoted the growth of wild oat more than wheat and as a result yield losses were increased at higher nitrogen rates (Figure 2b) (Carlson and Hill, 1986). In this case, the competitive effects on wheat increased as the availability of the limiting resource (nitrogen) increased, presumably due to intensification of competition for a different resource (e.g. light).

The environmental effects on crop–weed interactions are complex and difficult to predict. However, part of the problem appears to be that there is often no clear definition of how competition intensity is measured or a clear distinction between root and shoot competition. Competition is often quantified using a single parameter, such as plant biomass or yield, which may overlook the dynamics of the competitive relationship that determines this final value. Wilson (2007) derived two indices to measure the components of competition: (i) 'relative crowding', which describes the effect of the abundance of neighbouring plants on the productivity of the target plant and is calculated as the ratio of the number of neighbouring plants to the biomass of the target plant, and (ii) 'intensity strength' which describes the level of suppression of the target plant relative to the growth of the neighbouring plant. By partitioning competition into these two components, it was found that changes in resource availability can alter the indices independently, and as a consequence competitiveness showed either no response or a positive response to increased resource availability. This approach has not been applied to crop–weed interactions but may provide a better insight into interspecific and intraspecific competition within crops.

The severity of competition will not only depend on the availability of resources, it will also be tempered by the sensitivity of the crop and the weed species to the environmental conditions in which they grow. This reflects the general adaptation of the crop and weeds species to the environment: a poorly adapted crop variety may be less competitive irrespective of resource availability. In crop species, this interaction can be large and may dominate genetic differences in crop–weed interactions (Lemerle et al., 2001a). The consequence of this is that the magnitude of yield losses from weeds may vary considerably between seasons and across sites (Lemerle et al., 2001b; McDonald, 2003; Watson et al., 2006).

6.2. Responses to environmental change: signals

Reductions in growth can occur when there is competition for resources, but there may also be alterations in growth patterns caused by the presence of neighbouring plants that are unrelated to resource competition. Changes in the red:far red ratio associated with transmission and reflection of light by the plant canopy can alter height, leaf size and the root:shoot ratio (Box 1). Such changes may help prepare the plant for the imminent onset of competition. Similarly, there is evidence that roots can respond to the presence of neighbouring roots (Raper and Barber, 1970) and can distinguish roots from the same plant from roots of neighbouring plants (described as 'self' vs. 'non-self' recognition) (Schenk, 2006; Dudley and File, 2007; Murphy and Dudley, 2007). These responses occur independently of resource availability and are initiated by as yet unidentified signals from the roots or by the release of allelochemicals. Understanding the roles of these signals and toxins in the interactions between plants is still poor.

6.3. Resource use efficiency

Crop growth depends on how effectively plants acquire resources and how efficiently they utilise these resources, that is, their resource use efficiency. A reduction in the availability of a resource from competition may be compensated to some extent by an increase in the efficiency with which it is used, or greater resource use efficiency may amplify the competitive advantage of greater resource acquisition. Much of the work on competition has considered only the effect of resource availability and acquisition and there is little information on resource use efficiency. An important reason for this is the difficulty in estimating the partitioning of resource use between two or more species growing together and hence estimating resource use efficiency among individual species within the community.

6.3.1. Radiation use efficiency

As there is often strong competition for light in crop–weed interactions, differences in radiation use efficiency (RUE) may be important in explaining differences in competitiveness among species. The RUE of mixed communities has been reported to be intermediate between the RUE of the component species (Kiniry, 1994; Cavero et al., 1999). In the case of maize infested with Johnson grass (*Sorghum halepense*), the RUE of the mixture was found to be similar to the weighted RUE of the monocultures of the two species. These studies were not able to estimate the RUE of the two species individually within the mixed community, but the agreement between the measured RUE when the two species were grown together and the weighted average RUE suggests that in this case the RUE of each of the species in the mixed community was similar to the values in monoculture (Kiniry, 1994). However, Gramig et al. (2006) estimated the RUE of weeds in monoculture and in a crop–weed mixture and found that the RUE of the weed species was higher in the mixtures than when grown as a monoculture. Over four different weed species, the average pure stand RUE was $1.85 \pm 0.13\,\mathrm{g\,MJ^{-1}}$ compared with $3.66 \pm 0.19\,\mathrm{g\,MJ^{-1}}$ when they grew in competition with maize. The greater RUE in the weedy maize crop was attributed to the more diffuse light environment within the maize canopy and less light saturation of individual leaves of the weeds. The biomass and yield of this experiment was not reported, so the effect of this improved RUE on the competitive relationship between the two species is not known.

Plant height, a trait that can contribute to competitive ability (see below), may also influence RUE. Miralles and Slafer (1997) compared the RUE of near isogenic lines of bread wheat that differed in height. The double dwarf lines had significantly lower pre-anthesis RUE ($1.09\,\mathrm{g\,MJ^{-1}}$) than the semi-dwarf and standard height isolines ($1.34\,\mathrm{g\,MJ^{-1}}$). Short wheat genotypes may therefore be at a competitive disadvantage when grown with taller weeds for two reasons: greater shading which reduces the amount of incident light reaching the leaves and their inherently lower RUE. However, the results of Gramig et al. (2006) suggest that reduction in growth due to increased level of shading may be partly compensated by improved RUE under shading.

6.3.2. Water use efficiency

It is widely acknowledged that the presence of weeds can reduce the WUE of crops (Massinga et al., 2003; Turner and Asseng, 2005; Passioura, 2006), yet there are relatively little experimental data on patterns of water use or the WUE of weeds growing in competition with crops. The depth of water extraction and the pattern of water use by weeds varies considerably (e.g. Jacobson et al., 1994), which will influence the ability of the weed to compete against crop species for soil water. Total water use by weedy crops is similar to or greater than the water use of weed-free crops (Massinga et al., 2003; van Wychen et al., 2004), but since crop biomass and grain yield are reduced, the WUE of a weedy crop will be lower than a weed-free crop. However, there is little information on the relative water use of crops and weeds and on WUE of weeds in weedy crops.

There does not appear to be any consistent difference in the transpiration efficiencies of crop and weedy species. Norris (1996) found the transpiration efficiencies of many weed species were similar to crop plants which have the same photosynthetic pathway (C3 or C4). There have been few studies of the WUE of individual weedy species when grown in mixed communities, but this may be important in understanding the causes of differences in competitiveness in crop and weeds. Szente et al. (1993), for example, found the WUE of fat hen (*Chenopodium album*) was significantly greater than that of sunflower (*Helianthus annuus*) when the two species were grown together under drought stress for two reasons: fat hen had a lower transpiration rate, a difference that was exaggerated in the mixed stand, and its photosynthetic rate was not affected by drought, while that of sunflower was significantly reduced. In summary, there are considerable differences in depth of water extraction, rates of water use and WUE efficiency of weeds, but the importance of these on interspecific competition has not been studied in much detail and is not well understood.

6.3.3. Nutrient use efficiency

Weeds may also show differences in the ability to utilise soil nutrients and in nutrient use efficiency. Genotypes with a high nutrient use efficiency are able to produce more biomass or yield at a given supply of a nutrient and so may be more competitive than a less efficient genotype when the nutrient supply is limited. Differences in nutrient use efficiency also mean that the competitive relationships between competing species or genotypes may change as the availability of a limiting nutrient varies.

Given that nitrogen is required by plants in relatively large amounts compared to other essential elements and it is quite mobile in the soil, it is not surprising that nitrogen has been frequently implicated as a driver of crop–weed competition. As with other resources, most studies on crop–weed competition have tended to determine the effect of nitrogen supply on competitive outcomes rather than any changes in nitrogen use efficiency (e.g. Carlson and Hill, 1986). An exception to this is a study on competition between rice and weedy rice by Burgoss et al. (2006), who combined ^{15}N and nitrogen rates to determine the impact of nitrogen supply on nitrogen use efficiency. The bulk of applied fertiliser nitrogen was taken up by the weedy rice and its competitiveness increased with nitrogen rate. As well as taking up more nitrogen, the nitrogen use efficiency of the weedy rice was higher than that of cultivated rice: weedy rice produced 42 g shoot biomass g^{-1} added nitrogen compared to 33 g g^{-1} of added nitrogen for rice variety Drew. In a previous study, Stiers (2002) showed that weedy red rice produced 1.7–1.8 times more root biomass than rice varieties. Such large investment in root system will enable weedy rice to capture greater proportion of applied nitrogen.

The focus for the majority of the work on the effects of crop nutrition on crop–weed interactions has been on nitrogen nutrition (DiTomaso, 1995) and there is relatively little information on the requirements for or responses to nutrients other than nitrogen in weedy species. However, this may be important to understand the ecological bases of competition. The interaction between the availability of nitrogen and phosphorus, for example, may alter the competitive relationships between species (Suding et al., 2004). Many agricultural weeds show positive responses to additional phosphorus, but the magnitude of the response varies considerably (Blackshaw et al., 2004) and hence the competitive relationships with crop species will change depending on the availability of phosphorus.

Very few studies have examined the importance of micronutrient nutrition to crop–weed interactions. There are a number of instances where weedy species have higher micronutrient concentrations than crop or pasture species. For example, Reddy et al. (1981) found the weedy species capeweed (*Arcotheca calendula*) and silver grass (*Vulpia* sp.) contained significantly higher concentrations of copper and molybdenum than annual ryegrass (*L. rigidum* cv *Wimmera*) or subterranean clover (*Trifolium subterraneum*). Two species of barley grass (*Hordeum leporinum* and *H. glaucum*) were found to be more tolerant of low supplies of manganese and copper than wheat (Kriedemann and Anderson, 1988). The high nutrient efficiency of barley grass was clearly demonstrated in a solution culture experiment in which it produced the same amount of biomass as wheat but on less than 4% of the manganese concentration in solution (Sweeney et al., 1989). Similarly, bromegrass (*Bromus* sp.) took up three times as much manganese as wheat from soil in which the supply of manganese was low. The greater micronutrient efficiency of these weeds would provide them with a competitive advantage in soils where the availability of micronutrients is low and conversely, fertilising with micronutrients may improve the competitiveness of the crop against weeds.

The vast majority of the work on the effects of nutrition on crop–weed interactions has focussed on nitrogen. While this has shown that competition for nitrogen uptake is important in explaining crop–weed interactions, there has been little work examining the effects of other aspects of plant nutrition and nutrient use efficiency on weed ecology in agricultural systems.

6.4. Changes over time

In annual cropping systems, there can be strong temporal effects on competitive ability. The progression of the growing season leads to changes in biomass and canopy architecture of both the weed and the crop

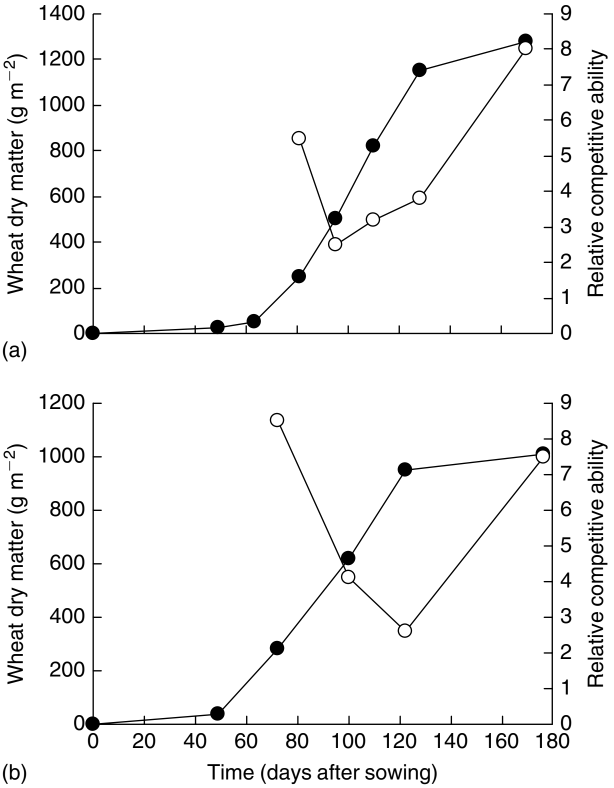


FIGURE 3

*Changes in (●) wheat dry matter production and (○) relative competitive ability (Cousens, 1991) of wild radish (*Raphanus raphanistrum*) against wheat in (a) 2003 and (b) 2004 showing the increase in competitiveness of wild radish in the second half of the growing season. The relative competitive ability is the relative changes in the biomass of two competing species as the number of plants of the respective species changes. A value of 1 means both plants have an equal effect on each another and a value greater than 1 means wild radish has a competitive advantage over wheat. Note that the initial decline in the relative competitive ability of wild radish (an indeterminate species) coincided with the increase in the rate of dry matter production in wheat shoot and it resurged when the rate of increase in wheat shoot dry matter slowed down as it approached maturity. (Source: Eslami, 2006.)*

as well as to changes in the availability of soil water and nutrients. Therefore, the competitive relationship between the crop and the weed may change over time and would reflect changes in the resource most limiting to growth. In a field study in South Australia, Eslami (2006) found that the competitiveness of wild radish against spring wheat (measured as the RCA) changed markedly during the growing season. In successive years, wild radish was more competitive than wheat during the early vegetative phase but declined sharply as wheat reached its period of rapid vegetative growth (80–120 days after sowing). The competitiveness of wild radish increased late in the season, during grain filling when the growth rate of wheat slowed and wild radish canopy height exceeded that of wheat (Figure 3). The changes in the competitiveness of the weed in relation to the important stages of yield determination in the crop will have a marked effect on the yield reduction by crop–weed competition.

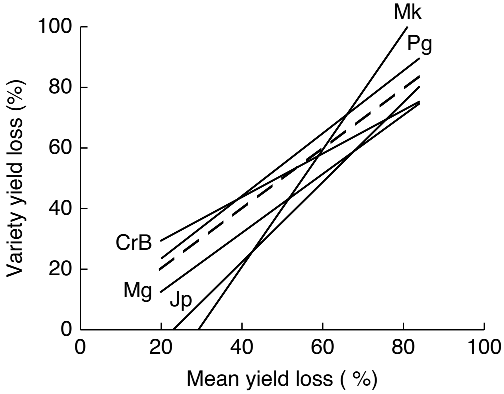


FIGURE 4

Relationship between relative yield loss of an individual variety and mean relative yield loss, averaged over all varieties, for selected field pea varieties grown in four environments differing in the level of competition. The different competitive environments were field peas grown with Lolium rigidum *or wheat over two successive years. The varieties are Jupiter (Jp), Morgan (Mg), Mukta (Mk), Cressy Blue (CrB) and Progreta (Pg). The average response of the 17 genotypes that were grown in both years is shown by the dashed line. (Source: McDonald (2003). Reproduced with permission of Blackwell Publishing.)*

6.5. Weed burden

The competitive ability of a crop variety can also be affected by the level of competition pressure from weeds under which it is growing and the traits that are important to competitive ability may also depend on the level of competition. Figure 4 shows that different varieties of field pea (*Pisum sativum*) show different responses to the intensity of competition. The short semi-leafless variety Mukta, for example, had very low yields when weed numbers were high, but showed little loss in yield when weed populations were low. In contrast, the tall, vigorous variety Morgan showed a consistently low loss in yield across all levels of competitive pressures, while the semi-leafless line Progreta shows a consistently low competitive ability.

7. VARIATION IN COMPETITIVE ABILITY AMONG CROP SPECIES

There is considerable variation in the competitive ability of different crop species. The differences in interspecific competitiveness reflect the inherent vigour of the seedlings as well as the management practices under which the crop is grown. For example, barley (*Hordeum vulgare*) is generally considered to be a superior competitor with weeds than wheat. Short-stature crops such as lentils and chickpeas are poor competitors with weeds. However, the poor competitive ability of these crops is also influenced by the production system in which they are grown. Pulses are generally grown at a lower plant density than cereals (20–60 plants m^{-2} cf. 100–300 plants m^{-2}), which will reduce their competitive ability. In some regions, such as south-eastern Australia, sowing times for pulses are delayed from autumn to the cooler and wetter winter season to avoid foliar diseases, which reduces the early growth rate of the crops and their ability to compete against weeds. From an agronomic viewpoint, it is important that such poorly competitive crops are grown in fields where weeds have been well managed in previous phases of the rotation.

Pavlychenko and Harrington (1934) assessed differences in competitive ability between crop species in Canada and ranked barley and cereal rye (*Secale cereale*) as more competitive than wheat and flax (*Linum* *usitatissimum*). Similarly Bell and Nalewaja (1968) showed that barley was much more competitive against wild oat (*Avena* sp.) than wheat. Nalewaja (1978) in the USA showed that cereal rye was more competitive than barley or wheat. In the UK, barley was more competitive than oilseed rape (*Brassica napus*) or field peas (Lutman et al., 1994) and in Denmark, Melander (1994) ranked peas and oilseed rape as less competitive than rye, wheat or barley. In a later study in the UK, Seavers and Wright (1999) found oats (*Avena sativa*) to be most suppressive against *Galium aparine*, followed by barley and wheat.

Based on research at a single site in southern New South Wales, Australia, Lemerle et al. (1995) concluded that the order of decreasing competitive ability against a stand of annual ryegrass at 300 plants m^{-2} was oats, cereal rye, triticale (× *Triticosecale*), oilseed rape, barley, wheat, field pea and lupin. In this study, differences in the competitive ability between barley and wheat were very small and this could be related to the highly acidic soil type of the experimental site that adversely affected barley growth. In contrast, Walker et al. (1998) in southern Queensland, Australia, showed a large competitive advantage of barley over wheat when grown in the presence of *Avena ludoviciana* and *Phalaris paradoxa*. These contrasting results for the relative competitiveness of wheat and barley illustrate the importance of general adaptation to the competitive ability of crops.

Apart from factors such as plant density, the differences in competitive ability between cereals and pulse crops noted above may be related to the physiology, morphology and phenology of these crops. For example, Evans (1993) showed there was considerable variation in the relationship between leaf area index (LAI) and crop growth rate (CGR) among different species. Compared to wheat, the CGRs of soybean (*Glycine max*) and field bean (*Phaseolus vulgaris*) were less and the maximum CGRs were reached at a lower LAI. While the planophile leaf orientation of the legumes most likely enhanced light interception at low LAIs, the energy cost of symbiotic nitrogen fixation limited their CGRs. Consequently, growth of wheat was consistently more rapid than the pulse crops at a given LAI, which would enhance its competitive ability relative to that of the pulse crops.

In summary, it appears that of the broadacre crops, cereals are more competitive than oilseed rape and canola, whereas pulses are poorly competitive. Among the cereals, cereal rye, oats and barley tend to be more competitive than wheat. However, it is difficult to make direct comparisons of competitive ability of diverse crop species because these can be due in part to differences in management practices, such as plant densities and sowing times. In any case, direct comparisons of the competitive ability of crop and pasture species may not be relevant to farmers: the competitive ability of crops should be assessed within the context of the cropping system in which they are grown, which takes into account differences in agronomy that affect competitiveness, and the environmental conditions under which the agricultural system operates, which will influence the levels of productivity of the crop and the weed species.

8. TRAITS ASSOCIATED WITH COMPETITIVE ABILITY

Donald (Donald, 1963, 1968, 1981; Hamblin and Donald, 1974; Donald and Hamblin, 1976), Sedgley (1991) and Lemerle et al. (2001a) have reviewed the large amount of research on the factors associated with competitive ability in crops. Much of the early work dealt with plants in mixed communities, such as mixed pastures or segregating populations in plant breeding programmes (Donald, 1968, 1981; Donald and Hamblin, 1976). Recently, the focus has shifted to using competitive crops as a means of reducing weed growth (Lemerle et al., 2001a). However, despite the diverse array of agricultural production systems that have been used and the substantial improvements in yield potential of crops over this time, a relatively small number of traits are consistently identified as contributing to competitive ability.

Donald (1968) argued that the ability to use an immediate supply of a resource rapidly and to increase the area over which it competes against its neighbours are key factors that contribute to the competitiveness of a plant within a community. By this means, the competitive advantage of a plant can be established early in the growth cycle. This idea was illustrated in the work of Soetono and Donald (1980) which demonstrated that seedlings of barley which emerged first in a crop maintained a competitive advantage over their neighbours throughout the growing season and had a higher grain yield. In many cropping systems, crops may be tolerant to weed competition for only a short time early in the growing season (Aldrich, 1984b) and the effect of competition is established relatively early in the season. Wheat, for example, was found to be tolerant to the presence of *L. rigidum* up to the two-leaf stage but competition subsequently reduced growth of wheat seedlings up to six weeks after emergence (Smith and Levick, 1974). Traits such as rapid seedling establishment and biomass accumulation can contribute to the ability to suppress weed growth by wheat (Coleman et al., 2001) and rice (Zhao et al., 2006b, c, 2007). The ability to capture and exploit resources early may be particularly important in systems based on annual plants where there is a well-defined growing season and there is a limited time over which resources can be exploited.

8.1. Shoot traits

Donald and Hamblin (1976) and Lemerle et al. (2001a) identified a number of traits they considered contributed to competitiveness in plants which would lead to high grain yields in a range of ecosystems (Table 3). They suggested competitive cereals were taller than their neighbours, with horizontal leaves and an extensive leaf display that shaded neighbouring plants and developed a vigorous root system. Studies across a range of species and environments confirm the importance of these traits in cereal and broadleaf crops (Table 4). A variety with these characteristics is effective in capturing light, water and nutrients from neighbouring plants.

Table 3 Characteristics of the Cereal Ideotype for High Grain Production in Different Ecosystems

	Ecosystem		
Traits	**Isolated Plants**	**Crop–Weed Mixture**	**Dense Crop Monoculture**
Competitive ability	Of no significance	Strong competitive ability essential	Low intraspecific competitive ability
Growth habit	Lax or prostrate habit	Taller than neighbours, especially during early growth	Erect for minimum interplant competition
Leaf shape	Many long, wide, thin horizontal	Many long, wide, thin horizontal	Small, erect leaves
Canopy architecture	Extensive leaf display for maximum light interception	Extensive leaf display for maximum light interception, especially during early growth	Minimum leaf display sufficient only to form an adequate ear; minimum interference with foliage of like neighbours
Tillering	Free tillering High survival	Free tillering	Sparse or nil tillering
Root system	Rapid and sustained root growth	Early rapid growth of roots, greater than that of the neighbours, particularly in soil layers likely to be important in competition for water and nutrients	Adequate to ensure sufficient exploitation of the soil environment by the whole community of root by the end of the growing season

Source: Donald and Hamblin (1976); Lemerle et al. (2001b).

Table 4 Traits associated with Competitive Ability among a Range of Crops for (a) Interspecific Competition (Crop–Weed Interactions) and (b) Intraspecific Competition among Spring Wheat Genotypes

Crop	Traits associated with Competitiveness	Weed Species	More Competitive Trait	Reference
	(a) Interspecific competition			
Aerobic rice	Early height, tiller number, vigour, biomass	Natural population	Tall High tiller numbers High biomass	Zhao et al. (2006a)
	Canopy closure	Natural population	Early canopy closure	Zhao et al. (2007)
Barley	Early biomass	Natural population	Greater biomass	Bertholdsson (2005)
	Height and head type	Oats	Tall	Watson et al. (2006)
	Height and head type	Wild oat	Tall Hulled	O'Donovan et al. (2000)
Bread wheat Durum wheat	Early biomass, height, tillering	Annual ryegrass	Tall High tiller numbers High biomass	Lemerle et al. (1996)
Chickpea	Height, branch angle	Natural population	Tall Erect growth habit	Paolini et al. (2006)
Clover	Canopy height	Natural population	Tall	den Hollander (2007)
Cowpea	Growth habit, LA	Purslane; sunflower	Erect growth habit High LAI	Wang et al. (2007)
Field pea	Early growth rate, leaf area, root growth	Maize	High leaf area High root growth	Semere and Froud-Williams (2001)
	Height	Annual ryegrass; wheat	Tall	McDonald (2003)
Maize	Height, biomass, LAI, RGR	Natural population	Tall High biomass High LAI High RGR	Mohammadi (2007)
Oilseed rape	Biomass, earliness, light interception by floral layer	Italian ryegrass	High biomass Early maturity High light interception	Sim et al. (2007)
Rice	Root growth	Natural population	High root growth	Fofana and Rauber (2000)
	Crop biomass at tillering	Natural population	High biomass	Ni et al. (2000)
	Crop height and LAI	Natural population	Tall High LAI	Garrity et al. (1992)

	SLA, LAI, tillering capacity	Natural population	High SLA High LAI High tillering capacity	Dingkuhn et al. (1999)
	LAI, tillering	*Brachiaria brizantha* *B. decumbens*	High LAI High tillering	Fischer et al. (2001)
Rice	LAI, root dry matter		High LAI High root dry matter	Gibson and Fischer (2004)
Soybean	Height	White mustard	Tall	Jannink et al. (2000)
	Maturity	Natural populations	Late	Nordby et al. (2007)
	Canopy area, height	Natural population	No relationships	Bussan et al. (1997)
Spring wheat	Early biomass	Natural population	High biomass	Bertholdsson (2005)
	LAI, tiller number	Annual ryegrass; wheat	High LAI High tiller number	Coleman et al. (2001)
	Height	Oats	Tall	Vandeleur and Gill (2004)
	Leaf length and width, light interception, flag leaf length	Oats		
	Height,	Natural population	Tall	Murphy et al. (2008)
	Height	*Avena sativa* *A. strigosa*	Tall	Cousens et al. (2003)
	Height	Annual ryegrass	Tall	Reeves and Brooke (1977)
	Height	*Aegilops cylindrica*	Tall	Seefeldt et al. (1999)
	Height, leaf length	Annual ryegrass	Cross-dependent	Mokhtari et al. (2002)
Sweet corn		*Panicum milliaceum*	Tall	Williams et al. (2008)
Winter wheat	Height	Jointed goat grass	Tall	Ogg and Seefeldt (1999)
	Height	Italian ryegrass	Tall	Appleby et al. (1976)
	Height	Downy brome	Tall	Blackshaw (1994)
	Tiller no., canopy diameter, plant height	Downy brome	Low tiller number short	Challaiah et al. (1986)
	Height Light interception	Natural population summer annuals	Tall High light interception late in the season	Wicks et al. (1986)
	(b) Intraspecific competition			
Spring wheat	Height		Tall	Khalifa and Qualset (1975)
	Height		Tall	Fischer (1975)

In contrast, in monocultures or weed-free conditions, a poorly competitive ideotype leads to a more equal share of the available resources among individuals in the community. Individual fitness is sacrificed to improve the total productivity of the community.

8.2. Root traits

Few studies examined the importance of root traits to competitive ability of crop varieties. The root:shoot ratio of wild relatives of wheat is higher than that of cultivated wheat (Evans, 1993) and it has tended to fall with the development of modern varieties (Siddique et al., 1990; Evans, 1993; Waines and Ehdaie, 2007). This trend is consistent with the general reduction in competitiveness in modern wheat varieties (Murphy et al., 2008) but the extent to which it has contributed to the loss of competitiveness has not been critically examined. Reynolds et al. (1994) with wheat and Sadras et al. (2000) with sunflower found older varieties were more responsive to reduction in intraspecific competition. While a reduction in height and changes in leaf size and canopy architecture have been suggested as reasons for the reduction in competitiveness among modern semi-dwarf wheat varieties, there is no consistent relationship between reductions in height and changes in root length and/or root biomass (Evans, 1993; Richards et al., 2007).

Root traits are important for the efficient acquisition of soil resources and thus they have a potential role in enhancing competitiveness under specific conditions. In common bean (*P. vulgaris*), shallow roots are more effective than deep roots in foraging for and taking up phosphorus (Rubio et al., 2003). This difference in root architecture may thus affect competitive ability when phosphorus is a major limitation. Chapter 13 discusses selection for weak root gravitropism that enables roots to colonise surface soil and improve capture of phosphorus.

Root architecture may also be important for water uptake and competitive ability in rainfed systems. However, the most appropriate root morphology may depend on the pattern of rainfall during the growing season. When plants grow largely on soil moisture stored within the subsoil, a large and deep root system with a high root:shoot ratio may be an advantage, whereas when frequent rainfall during the growing season is the main source of moisture for the crop, a smaller, shallower root system with a low root:shoot ratio may be more beneficial (Schwinning and Ehleringer, 2001). Varieties of wheat adapted to environments with deep stored soil moisture tended to have a narrow seminal root angle and deeper roots, whereas varieties adapted to in-season rainfall tended to have a wider seminal root angle and a shallower root system (Manschadi et al., 2008). The G × E interaction involving root traits affecting water uptake is analysed in Chapter 10 (Section 4) for maize in USA environments, whereas Chapter 13 (Section 4) discusses the effects of root vigour on capture of both water and nitrogen, and on the interaction between soil tillage and diseases.

Most of the work on the importance of different root traits has been conducted under weed-free conditions, with many fewer studies to examine the importance of root traits in crop–weed interactions: however, the optimum patterns of root development may differ in weed-free and weedy environments. In weedy conditions, the best pattern of root growth favoured resource capture, with a greater proportion of the plant's growth going into root growth, while in weed-free conditions the optimum root traits were linked to spatial efficiency to maximise nitrogen use efficiency (Craine, 2006; Dunbabin, 2007). Using simulation modelling, Dunbabin (2007) found that traits that increased the capture of nitrogen, phosphorus and water within the first 12 weeks of growth were the most effective at improving the competitive ability of crops. This analysis supports Donald's (1963) earlier arguments about the importance of rapid use of resources to competitive ability.

While a priori, a vigorous root system would seem to be valuable to improve the competitive ability of crops; there are few experimental data to verify this, and some of the data that are published are not consistent. In rice, for example, greater root growth contributed to improved competitive ability (Fofana and Rauber, 2000; Gibson and Fischer, 2004). However, Caton et al. (2003) found that differences in root growth made little contribution to the ability of rice genotypes to compete against barnyard grass (*Echinochloa crus-galli*), a species with an aggressive root system. In this study, the least competitive variety had the highest root:shoot ratio (Figure 5). Shoot growth and especially leaf area and height explained much of the variation in the ability of a variety to grow under competition, suggesting competition for soil resources was less important than above-ground competition in determining the competitive advantage of one species over the other.

Given the relative paucity of information on the value of root growth to competitive ability in crops, it is important that further work be conducted. Modelling root growth (e.g. Craine, 2006; Dunbabin, 2007) offers a means to examine the importance of different traits which can then be tested empirically.

8.3. Interactions between root and shoot growth

One of the problems of evaluating the relative importance of root and shoot traits is that root and shoot growth are not independent traits. There is generally a strong relationship between root and shoot growth (Figure 5) with considerable interaction between the two. Improvements in early shoot growth can be associated with improved root growth and an increased ability to utilise soil nitrogen. For example, in a comparison of lines differing in early vigour, Liao et al. (2006) found that the breeding line Vigour 18, which was selected specifically for high early vigour based on shoot traits, had a greater root system and took up more nitrogen than a conventional commercial variety (see further details of these studies in Chapter 13).

The interaction between root and shoot growth leads to considerable plasticity in growth in response to variations in environmental conditions. Competition for one resource may affect competition for other resources. The interaction between root and shoot growth was described in a series of experiments by Donald (1958). By using a split pot system, he was able to separate the effects of competition for light and for nutrients and demonstrated that competition for a single factor consists of two interacting components. Shading reduces the growth of the plant that in turn reduced root growth and a diminished capacity to exploit soil water and nutrients. Conversely, a reduced supply of nitrogen caused by competition between root systems will reduce leaf growth and lead to lower light interception.

Using a similar approach, Semere and Froud-Williams (2001) found that root competition reduced the height and leaf area of maize and peas when grown together. When two pea varieties that differed in their competitive ability were examined, the differences in root competitive ability were the same as the difference

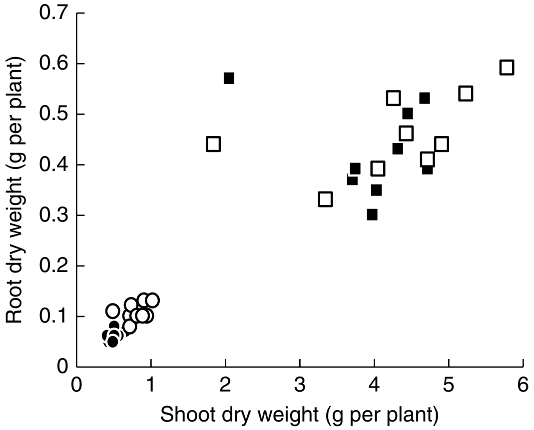


FIGURE 5

*Relationship between shoot and root dry weight among nine cultivars of rice grown with neighbouring plants of barnyard grass (*Echinochloa crus-galli*) illustrating the relationship between shoot and root dry matter production. The plants were harvested at 21 days (circles) or 48 days (squares) after sowing from two separate experiments (Experiment 1 [●, ■], Experiment 2 [○, □]). The two outlying points, which show a high root:shoot ratio, are values for the least competitive cultivar. (Source: Caton et al., 2003.)*

in the shoot competitive ability. They found no interaction between the effects of root and shoot competition between peas and maize and concluded that the effects of root and shoot competition were additive.

Except at very low plant densities, root and shoot competition occurs in concert and it is difficult to quantify the relative importance of above- and below-ground competition. Examples of additive and interactive effects of root and shoot growth have been reported and the nature of the interaction may be determined by the specific species that are competing against each other. The significance to the competitiveness of a plant of the ability to distinguish own roots from that of its neighbours (self and non-self recognition) is not understood, but it may play a role in allocating resources into root growth. Chapter 9 (Section 5) briefly looks at self/non-self recognition of root systems from the perspectives of kin selection and community-level productivity.

9. THE TRADE-OFF BETWEEN YIELD AND COMPETITIVE ABILITY

A number of studies of intraspecific and interspecific competition have demonstrated that genotypes that do well under competition may not necessarily yield well in pure stands. These results suggest there may be a cost associated with competitive ability that can limit yield when the source of competition is removed. Traits that contribute to competitive ability (Tables 3 and 4) may limit the yield potential of a crop. However, while this effect is often reported, the fitness costs associated with improving crop competitive ability are not well understood (Lemerle et al., 2001a). In this section, the relationship between yield and competitive ability will be examined in intraspecific and interspecific competition. The trade-off between competitive ability of individual plants and yield per land area is discussed in Box 2 of Chapter 9.

9.1. Selection of genotypes

Many experiments which have demonstrated a negative relationship between competitive ability and yield have used a historical set of varieties which show a wide range in yield potential or have used crosses between low and high yielding varieties that have different competitive abilities. The value of traits like height, leaf size and disposition is confounded by the significant differences in yield potential or by differences in characteristics such as maturity, which are also important to yield. Simple phenotypic correlations between yield and different traits among genotypes that have large differences in yield potential may bias the assessment of the effects of some of these traits and may have contributed to the lack of clarity in our understanding of the fitness costs associated with competitive ability. Ideally, the effects of specific traits like leaf size or height should be assessed in genotypes that are similar in other aspects of growth. Using near isogenic lines differing in the traits of interest would be a powerful way of examining these effects.

9.2. Intraspecific competition

An inverse relationship between the success of the individual and the success of the community has often been reported in comparisons of growth and yield in intergenotypic mixtures and pure stands (Donald, 1981). Under natural selection driven by competition, plant types that have high competitive ability will be more successful in mixtures and will tend to become more dominant with succeeding generations. This effect is illustrated in Figure 6, which shows that the proportion of short plants (≤90 cm) in a segregating population fell from 22 to 9% within three generations of natural selection. These proportions were much lower than their expected frequency in the population, which suggests the short genotypes were less competitive than the tall genotypes in a hybrid bulk population. However, the short genotype was the more productive in pure stands. Similar results have been reported in barley (Hamblin and Donald, 1974) and rice (Jennings and Aquino, 1968; Kawano et al., 1974) when genotypes differing in height and leafiness have been grown as mixtures and in pure stands.

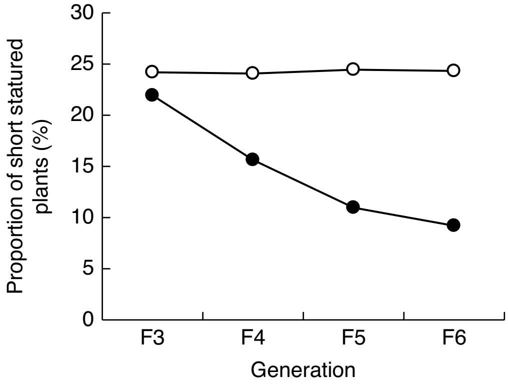


FIGURE 6

Changes in the proportion of short stature wheat plants (<90 cm) under natural selection (●) in populations derived from a cross between a short and tall variety, compared with the expected proportion within the population (○). Plants from each generation were grown at the same location and the height measured on a sample of plants from each plot. (Source: Khalifa and Qualset, 1975.)

Recognising that traits that enhance competitive ability may limit a variety's yield potential, Donald developed the concept of the communal plant type (Donald, 1968) which has the following features (Donald, 1981):

(i) the characteristics enhance the productivity of the crop rather than the individual plant;

(ii) the plant has a weak competitive ability and its growth is likely to be significantly suppressed when it is grown in mixtures with other genotypes;

(iii) yield per plant may be low, but when grown at a sufficiently high density to fully exploit the environment, they are capable of producing high crop yields.

Based on these principles, Donald developed an ideotype for small grained cereals that would allow varieties to produce high yields in pure stands and which was later extended to annual grain crops generally (Donald, 1968; Donald and Hamblin, 1976, 1983). The main traits were early maturity, short stature, small erect leaves, reduced branches or tillers and a high harvest index. The ideotype would need to be sown at high densities or in narrow rows to achieve its potential yield. Implicit in this model is that there would be no or minimal weed competition. Many modern high yielding varieties of wheat, rice and barley have a number of the characteristics of this ideotype, which infers that Donald's arguments were fundamentally sound and that the competitive ability of modern genotypes has been reduced. This is supported by a number of studies involving historical wheat (Reynolds et al., 1994; Lemerle et al., 1996; Vandeleur and Gill, 2004; Murphy et al., 2008) and sunflower varieties (Sadras et al., 2000) where the higher yields of modern varieties have been accompanied by reduced competitive ability.

9.3. Interspecific competition

Not surprisingly, there is much overlap in the traits that contribute to competitive ability under intraspecific and interspecific competition (Tables 3 and 4). Tall leafy crops with large and extensive root systems may be effective competitors against weeds, but their strong competitive ability may limit yield potential if this trait is expressed in monoculture. The ability to distinguish competing roots from the same or different genotypes may modify this response but there have been no studies that have examined this aspect of competition specifically. The comparisons of old and modern wheat varieties cited above show that there has been a reduction in the competitive ability of modern cultivars as selection has primarily been for high yield under weed-free conditions. The trade-off between productivity and competitiveness may not be a major problem where weed control is difficult, in which case the benefits of greater competitiveness can outweigh the potential limitations to yield. Much of the earlier work has suggested there may be a nexus between high competitiveness and low yield potential, but this is not necessarily the case (Fischer et al., 2001). For example, when genotypes of similar height are compared, competitive yet high yielding varieties can be identified (Gibson and Fischer, 2004), suggesting that it may be possible to improve competitive ability without penalising yield potential.

9.4. Potential causes of trade-off between competitive ability and yield potential

The competitiveness of a variety relies on its ability to obtain or utilise a greater proportion of the growth resources than its neighbours. There are a number of possible consequences of a plant's competitive characteristics. First, there may be an investment in additional shoot and root growth that would not occur under a non-competitive situation and this may limit yield. Second, the level of crop vigour, which is important to competitive ability, may alter the partitioning of water use during the growing season and affect WUE in rainfed systems. The effect of this will depend on the degree to which the crop relies on growing season rainfall and the timing and amount of the rainfall events. Also, as noted earlier, root and shoot growth show strong allometric relationships and more vigorous seedlings may improve root growth, which may enhance water uptake. However, there has been little critical evaluation of the impact of genetic improvement in early vigour on yield. In one of the few studies, Botwright et al. (2002) found a strong environmental effect on the value of early vigour to yield, with the greatest benefit in years and sites with high rainfall and no advantage under low rainfall. Finally, in some cases, time to flower has been found to be associated with greater weed suppression (Table 4). Maturity can have a marked effect on yield and alterations in timing of crop development to improve competitiveness can result in altered yield potential.

9.4.1. Resource allocation and dry matter partitioning

Much of the discussion on the fitness costs associated with increased competitive ability has concentrated on the effects of dry matter partitioning within the plant. As discussed earlier, changes in dry matter partitioning induced by the presence of neighbouring plants can occur before competition occurs. Changes in the red:far red ratio within the plant canopy which are perceived by photoreceptors can cause changes in morphology and dry matter partitioning, such as stem elongation, specific leaf area and root:shoot ratio (Ballaré and Casal, 2000; Murphy and Dudley, 2007). The role of these responses to environmental signals in crop–weed interactions is poorly understood, but further work in this area may allow these responses to be manipulated either by crop management (agronomy) or by plant breeding to improve competitiveness.

Much more work has examined the effects of resource availability on dry matter partitioning. As the availability of a resource declines, plants respond by preferentially partitioning growth to maximise the acquisition of the most limiting resource (Chapin, 1991). For example, shading can cause plants to allocate more resources to stem and leaf growth and less to roots, while nutrient and water stress can cause plants to increase their root:shoot ratio and increase their capacity to take up the limiting nutrient. In stressful environments, the allocation of resources to below-ground growth may be high which may significantly reduce above-ground growth (Hamblin et al., 1990). In the presence of competitors, the availability of growth resources will decline but the more competitive plant will be the one that is better able to capture and exploit a diminishing resource. This may lead to an alteration in the pattern of growth to use the most limiting resource more effectively than competitors.

In competition for nutrients and water, for example, there may be a large investment in root growth (Hamblin et al., 1990). However, resource availability is highly variable. The best strategy would be an ability to alter the pattern of growth in response to competitive pressures but the unpredictability of competition would favour evolution of stable adaptive traits leading to preferential allocation of growth to maximise root length (Craine, 2006). That is, the plant invests its resources to maximise its ability to exploit a limiting resource. While this comes at some cost, it enhances its productivity and its ability to compete against neighbouring plants. In an extreme example of this principle, it has been argued that some plant species that have a very narrow edaphic range have achieved their success by evolving traits, such as large root systems and a high root:shoot ratio, that severely limit their competitiveness in environments outside their adapted range and which restrict their distribution in the landscape (Poort and Lambers, 2003). These examples illustrate how changes in dry matter partitioning can enhance competitiveness under specific conditions, but may limit fitness in other habitats. This principle is applicable to competition in cropping systems more generally.

Modelling root growth suggests that there are differences in traits in weedy and non-weedy crops that may lead to trade-offs between yield and competitiveness. Craine (2006) used a cost–benefit approach to examine the effect of competition for nitrogen on resource allocation to roots. Without competition, a plant can invest relatively little of its carbon and nitrogen resources in root growth and can meet its nitrogen demand with a relatively low root length density. However, under competition for nitrogen, root growth increases and the plant allocates more carbon and nitrogen to sustain root growth than is optimal for the plant in the absence of competition. The overinvestment in new root growth deprived the proportion of soil nitrogen that may have been otherwise acquired by competitors, providing the plant with a competitive advantage. The analysis was consistent with Dunbabin's (2007) analysis of root growth in weedy crops which showed that root traits that increased the capture of resources were important, and with field studies (Hamblin et al., 1990).

Many of the shoot traits that contribute to greater competitiveness (Table 3) are also associated with low potential yields. In wheat, for example, reduced height, shorter coleoptiles, reduced leafiness and fewer tillers which have improved the yield potential of cereals (Evans, 1981, 1993) reduce the ability of the crop to compete against weeds (Table 3). Height in particular is frequently found to be important to competitiveness in a range of cereal crops (Table 4): tall varieties are generally more competitive than short varieties, largely because they are able to compete more effectively for light than short varieties (Fischer, 1975), although there may also be an effect from a more vigorous root system (Siddique et al., 1990; Waines and Ehdaie, 2007). In cereals, it is well established that the growing stem is an important sink for assimilate during stem elongation and competes strongly with the developing spike (Evans, 1993). Reducing the supply of assimilate to the spike can limit the production of fertile florets and the potential number of grains m^{-2} able to be set by the crop (Fischer, 1983; Slafer et al., 1990; Miralles and Slafer, 1995, 1997). Consequently, tall varieties tend to produce fewer grains m^{-2}, which limits their potential yield (Miralles and Slafer, 1997).

The trade-off between competitive ability, caused by genetic variation in height, and yield is most evident in experiments that have compared tall and semi-dwarf varieties but these comparisons may no longer be relevant for modern plant breeding programmes. In wheat, for example, the introgression of semi-dwarf genes into modern varieties is widespread and most wheat breeding programmes now have a relatively narrow range in height within their populations. Recent work has suggested that high yield is not incompatible with high competitive ability as significant variation in competitive ability can be detected among genotypes when the differences in height are reduced (Lanning et al., 1997; Ni et al., 2000).

9.4.2. Early vigour

Early vigour, which refers to early leaf area development and growth rate of the crop, has often been associated with improved competitive ability (Tables 3 and 4). Rapid canopy closure allows crops to quickly shade the ground and competing plants. Vigorous early growth may also promote greater root growth and improve WUE (Siddique et al., 1990; Richards et al., 2007; Richards, 2008), which may contribute to higher yields in water and nutrient-limited environments (Section 4 in Chapter 13).

It has been suggested that a penalty for rapid early growth may be a reduction in available soil moisture at anthesis, leading to reduced grain set and small grains (Richards, 1991; Soltani and Galeshi, 2002; Asseng et al., 2003), especially where the crop relies on stored soil moisture rather than in-season rainfall. For example, in the northern cereal belt of Australia, a region where wheat production relies on the amount of fallow moisture at sowing, increasing crop plant density can reduce grain yield if there is insufficient stored moisture at sowing (Fawcett, 1964). This generally does not occur in southern Australia where crops rely on growing season rainfall (Lemerle et al., 2004), although it may happen in years where there is below average rainfall or on heavy soils. Asseng et al. (2003) modelled the effect of increased seedling leaf area and found that greater early vigour could reduce yield in the northern cereal belt and on heavy soils in the southern region.

Data from two rainfed trials in South Australia (Sloane, 1999) illustrate the adverse effect of high early vigour on yield (Figure 7). At both sites, seasonal rainfall, and in particular rainfall during stem elongation and grain filling, was 40–46% below the long-term averages. Early vigour was manipulated by varying the inputs (rate of nitrogen and plant density) and by growing varieties differing in early vigour. Overall there was a negative correlation between early vigour and grain yield, which was related to the number of grains m^{-2}. However, the negative relationship was stronger when crop vigour was manipulated by increasing input supply than by the level of genetic variation in vigour among the lines. By a combination of increased sowing rate and a higher rate of nitrogen, early dry matter production was increased by 59–75%, but grain yield was reduced by 15%. There was a reduction in kernel numbers of 7–12% and in kernel weight of 3–6%. It is likely that in these trials, the reduction in yield was caused by high water use early which led to a reduction in soil water reserves, intensifying the severity of water deficit during the critical pre-anthesis period (Sloane et al., 2004). The data suggest that in a year of low rainfall, agronomic practices are more likely to cause a large reduction in yield in comparison to yield differences associated with variation in early vigour among genotypes.

The plant density used by Sloane (1999) in the high vigour treatment in these experiments (400 seed m^{-2}) was considerably greater than that recommended for cereals in the region (150–200 seed m^{-2}), and more modest increases in sowing rates may enable weeds to be suppressed without compromising grain yield. In an extensive series of trials examining the effects of plant density on competitive ability, Lemerle et al. (2004) only observed a yield penalty from increased early vigour if the sowing rate was considerably greater than 200 plants m^{-2} and this only occurred in weed-free conditions. The yield penalty was relatively small, being less than 10%. In the presence of weeds (*L. rigidum*), wheat grain yield generally increased up to the highest plant density.

There are few field studies to assess the effects of genetic improvements in early vigour on crop yield. In wheat, Condon et al. (2002) and Asseng et al. (2003) modelled the effects of early vigour and concluded that the greatest benefit of early vigour would be in the Mediterranean environments of southern and western Australia. However, experimental data from this region suggest there are strong season and site effects on the benefits of improved early growth. Botwright et al. (2002) found that high vigour lines produced an average 10% greater leaf area 50 days after sowing, but this translated into higher yield only in the wetter of the 2 years. Sloane (1999) examined early vigour by measuring light interception at 66 days after sowing (Zadoks growth stage 30–33) among 348 genotypes of wheat and found a significant variation in early vigour and yield but the two were not significantly correlated ($r = 0.11$).

In summary, genetic improvements in early vigour may not result in a significant yield penalty and provide a low-risk strategy to improve competitive ability. While the increases in early growth by agronomic management can be large, high inputs can cause a yield penalty to the crop possibly because of excessive pre-anthesis water use.

9.4.3. Flowering time and crop duration

The ability to suppress weed growth is sometimes related to the duration of crop growth (Table 4). Both early and later maturity can contribute to competitive ability. Coleman et al. (2001) found that ryegrass was suppressed more in wheat lines that were later flowering. Similarly in rice (Dingkuhn et al., 1999) and soybean (Monks and Oliver, 1988; Nordby et al., 2007), late maturing genotypes tended to be more suppressive of weeds. However, in oilseed rape, greater competitive ability was associated with early stem extension (Sim et al., 2007). The importance of crop duration to competitive ability appears to vary with the environment and the crop and weed species. Nevertheless, having cultivars with appropriate rates of development to

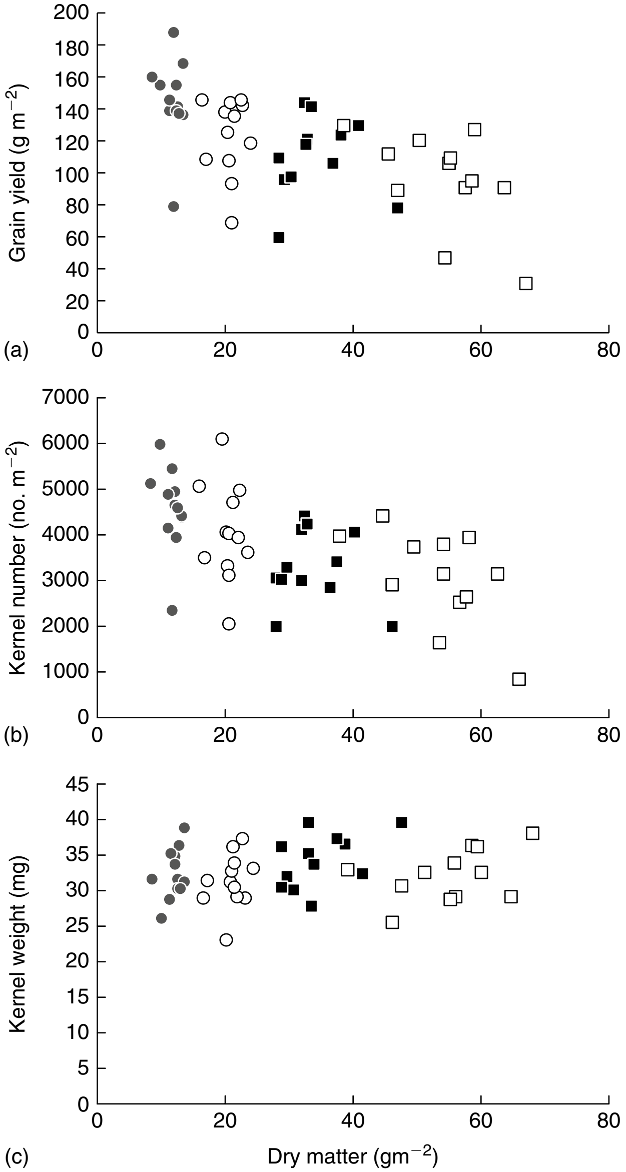


FIGURE 7

Relationship between dry matter production at tillering (Zadoks growth stage 22–24) and (a) grain yield, (b) kernels m^{-2} and (c) kernel weight for 12 varieties of wheat grown at two sites (Roseworthy [●, ○] and Kapunda [■, □]) using low and high vigour treatments. The low vigour treatment (●, ■) was a plant population of 200 seeds m^{-2} and 20 kg N ha^{-1} and the high vigour treatment (○, □) was a sowing rate of 400 seeds m^{-2} and 80 kg N ha^{-1}. (Source: Sloane, 1999.)

minimise exposure to environmental stress is an important principle of crop adaptation and will contribute to a variety's competitive ability. Selecting competitive genotypes that flower or mature too early or late for the environment may limit the yield potential of the cultivar in the absence of weeds.

9.5. A modified competitive ideotype

In wheat, grain yield is often strongly correlated with kernel number (Fischer, 1975, 1983; Sinclair and Jamieson, 2008). While there may be some debate about the underlying cause of this relationship (Sinclair and Jamieson, 2006, 2008; Fischer, 2008), there is a large body of experimental data that shows the partitioning of dry matter to the developing spike in the period leading up to ear emergence has a large influence on kernel number and hence yield potential (Section 3.2.2 in Chapter 15; Section 5 in Chapter 12). Much of the yield increases from genetic improvement or agronomy can be traced back to an improved allocation of resources to the ear during this critical phase of growth. While the focus on weed management has been on early removal of weeds to minimise competition, this may reflect the need to minimise competition for resources later in the growing season, at a time when allocation of carbon and nitrogen to the developing ear is important.

The original non-competitive ideotype suggested by Hamblin and Donald (1974) was based on minimising interplant competition under weed-free conditions. It assumed a relatively constant (and low) level of competition during the life of the crop, whereas in crop–weed competition, it is likely that competition will change as the crop and weeds compete against one another (Figure 3). Lemerle et al. (2001a) suggested a modified ideotype that would allow weed suppression early and to reduce intraspecific competition at later stages of development. By possessing traits such as rapid emergence, large and floppy initial leaves, tall seedlings and high early vigour, the crop could compete against weeds to reduce the competitive pressures later, which would allow less competitive traits such as small erect leaves and reduced mature height to be expressed later without affecting yielding ability and weed suppression. Among cereals, such traits are expressed to some extent by barley, which is known for its superior competitive ability than wheat. If the costs of investment in seedling competitive ability are not too great, yield potential under weed-free conditions may not be sacrificed.

10. BREEDING FOR INTERSPECIFIC COMPETITIVE ABILITY

Despite the large volume of work that has demonstrated considerable variation in competitive ability within crop species, there has been little effort to breed specifically for competitive ability. Gibson and Fischer (2004) attribute this to (i) the success of herbicides in controlling weeds and (ii) the trade-off between yield and competitive ability. While there is now evidence from different crops that competitive ability can be compatible with high yield potential, there are still a number of issues associated with breeding for improved interspecific competitiveness. Three of these will be highlighted: the heritability of competitive traits, the G × E interaction and the importance of general adaptation to competitive ability.

10.1. Heritability of competitive traits

To make progress in developing weed-competitive crop cultivars, traits associated with weed competitive ability need to have reasonable heritability. As seen in Table 4, plant height appears to be a common trait associated with competitive ability across crop species. The introduction of gibberellic acid (GA) insensitive dwarfing genes in wheat *Rht-B1b* (*Rht1*) and *Rht-D1b* (*Rht2*) has reduced not only plant height but also early leaf area development (Rebetzke and Richards, 1999). As these dwarfing genes tend to be dominant and have a major effect on crop height, it is not surprising that heritability for wheat height tends to be high (Rebetzke and Richards, 1999; Coleman et al., 2001). Similarly crop height had high heritability under weedy and weed-free conditions in rice (Zhao et al., 2006b) and soybean (Jannink et al., 2000) (Table 5).

Table 5 Heritability of Crop Traits involved in Weed Competition

Crop	Type	Trait	Heritability Weed-Free	Weedy	Reference
Rice	Broad sense	Early crop vigour	0.65	0.85	Zhao et al. (2006b)
		Final plant height	0.91	0.92	
		Weed biomass		0.64	
		Weed rating		0.75	
Wheat	Narrow sense	Breadth leaf 2	0.44		Coleman et al. (2001)
		Tiller number	0.34		
		LAI	0.18		
		Dry matter start of tillering	0.46		
		Height at anthesis	0.90		
		Grain yield	0.21		
Wheat	Narrow sense	Breadth leaf 2	0.76		Rebetzke and Richards (1999)
		Breadth leaf 3	0.84		
		Length leaf 2	0.67		
		Leaf area	0.30		
		Plant biomass	0.35		
		Specific leaf area	0.33		
Wheat	Narrow sense	Plant height	0.68–0.73		Rebetzke and Richards (1999)
		Coleoptile length	0.85–0.89		
Wheat	Broad sense	Breadth leaf 4	0.19–0.25	−0.11 to 0.51	Mokhtari et al. (2002)
		Height 69 DAS	0.40–0.59	0.35–0.51	
		Grain yield	0.17–0.31	0.31–0.55	
		Yield loss (%)		0.25–0.57	
Soybean	Narrow sense	Early height		0.64	Jannink et al. (2000)
		Early light interception		0.19	
		Specific leaf area		0.29	
		Weed biomass		0.15	

Unfortunately, under good growing conditions (e.g. high fertility and available water), plant height can reduce the harvest index and grain yield of wheat (Coleman et al., 2001) and selection for tallness is not favoured by plant breeders as an approach for developing weed-competitive crop cultivars. Also tall crops are more prone to lodging under high yielding conditions, which will further limit yield potential. In soybean, moderate broad-sense heritability of early height ($H = 0.64$) and its genetic correlation with weed suppression ($r_g = 0.81$) made it an ideal selection criterion for the development of weed-competitive cultivars (Jannink et al., 2000). However, in some of the crosses used in this study, there were strong negative relationships between early height and grain yield. The results indicate that even in broadleaf crops, increased plant height for weed suppression may have a significant trade-off in yielding ability.

Zhao et al. (2006a) undertook a detailed study of weed competitive ability of 40 rice cultivars and found that early crop vigour and grain yield measured under weed-free conditions explained a combined 87%

of cultivar variation in weedy yield and 40% variation in weed biomass. Even more importantly, weed-free yield and early crop vigour were moderately heritable ($H = 0.38–0.68$) and were highly genetically correlated with weedy yield ($r_g = 1.00$ and 0.88, respectively) and weed biomass ($r_g = -0.89$ and -0.67, respectively). Based on this study, indirect selection on these two traits was predicted to be efficient for improving yield under weed competition and weed-suppressive ability of aerobic rice.

Early crop vigour assessed as a visual rating of early biomass will integrate various traits such as leaf length, leaf breadth, specific leaf area and tiller production. It could be argued that for the purpose of phenotype selection, direct morphometric crop traits could be more useful. Coleman et al. (2001) used a doubled haploid population of spring wheat to study the contribution of plant traits to competitive ability with weeds. Width of leaf 2, canopy height, LAI of wheat, tiller number and days to anthesis contributed to competitive ability but there was a significant impact of the environment on the relative contribution of crops traits to competitive ability. The narrow-sense heritability of these traits ranged from $h_N^2 = 0.31$ for LAI, $h_N^2 = 0.34$ for tiller number per plant, $h_N^2 = 0.44$ for leaf 2 width and $h_N^2 = 0.99$ for anthesis time (Table 5). Heritability of early vigour traits that contributed to competitive ability has also been investigated by other researchers under weed-free conditions. In a comparison of Australian and overseas wheat cultivars, Rebetzke and Richards (1999) found Australian cultivars to be least vigorous, with a number of overseas lines producing 75% more leaf area than representative Australian wheats. In this study, significant G × E interaction slightly reduced the broad-sense heritability of early vigour assessed as leaf area ($H = 0.87$) compared with leaf breadth ($H = 0.96$) and length ($H = 0.97$). In a further study of breeding lines, they found that narrow-sense heritabilities for seedling leaf width and breadth were high but low for seedling leaf area, specific leaf area and biomass (Table 5). However, there was a reasonably high genetic correlation between leaf breadth and leaf area suggesting that good genetic gain in leaf area could be achieved by selection for leaf width. A diallel cross among *indica* rice lines demonstrated embryo size, an important determinant of early vigour in cereals (Lopez Castaneda et al., 1996), to be highly heritable and under additive genetic control (Pandey et al., 1994).

The survey of heritabilities indicates that while yield and weed suppression show relatively low heritabilities due to high G × E interactions, many of the seedling traits associated with early vigour show reasonably high heritability. This suggests that progress in competitiveness may be achieved by indirect selection under weed-free conditions.

10.2. Genotype × environment interactions

The G × E interaction reflects the stability of a trait across a range of growing conditions. Greater genetic gains can be made if there is a relatively low G × E interaction as the desirable traits can be expressed in a broad range of environments and consistent levels of genotypic variation can be detected.

Competitiveness often shows large G × E interactions (Lemerle et al., 2001b; McDonald, 2003). This is not surprising since there will be environmental effects not only on the growth and yield of the crop but also on the weed species. In a study of 12 commercial genotypes of wheat in 12 experiments conducted over two years, Lemerle et al. (2001b) found that G × E interaction accounted for 81% of the variation in grain yield, while the Genotype × Weed and Genotype × Environment × Weed interaction described only 0.3 and 4% of the variation in grain yield, respectively. However, the range in competitiveness among the varieties selected for this study was relatively small, which would have contributed to the large environmental effect.

In a number of cases, the G × E effect has been found to be low. Jannink et al. (2000) with soybean and Murphy et al. (2008) with wheat found consistent rankings among the genotypes for competitive ability and relatively little effect of environment on the expression of weed competitive traits. The different results to those reported by Lemerle et al. (2001b) and McDonald (2003) probably reflect the inherent variability in the environment in which the different experiments were conducted and also the level of genetic variation in competitive ability among the varieties used. The work of Lemerle et al. (2001b) was conducted over a wide range of rainfall and soil types in two seasons and there was a 10-fold variation in grain yield among the experiments, while there was a 3–4-fold difference in yield in the two years in which McDonald (2003) conducted his experiments. Consequently, environmental variation and the G × E interaction dominated the variation in yield. However, the experiments of Jannink et al. (2000) and Murphy et al. (2008) were conducted in successive seasons at the same location and environmental variation was considerably less.

Even traits associated with greater competitive ability can show high G × E interactions. Early vigour, for example, is consistently identified as a desirable trait to improve competitive ability. As discussed previously, modelling has suggested that the value of early vigour is greatest in Mediterranean type climates, and especially on sandy soils where leaching of water and nitrogen can be high (Condon et al., 2002; Asseng et al., 2003) but the value of the trait is strongly affected by environmental conditions (Botwright et al., 2002).

10.3. The importance of adaptation to competitive ability

In most cases, high yield is the major objective of plant breeding. This involves developing cultivars that are well adapted to the target environment, that is, they have appropriate maturity and are resistant and/or tolerant to the range of biotic and abiotic stresses commonly encountered. A number of studies on genetic differences in competitive ability show significant correlations between grain yield under weedy and weed-free conditions (Lemerle et al., 2001b, 2006). This demonstrates that high yield and adaptation are important for competitive ability, which has important consequences for breeding for competitive ability. Competitive traits need to be introduced into adapted varieties, as greater competitive ability by itself is not a guarantee of high grain yield.

In the work of Lemerle et al. (2001b) referred to previously, experiments were conducted over a wide range of sites and environmental variation and the G × E interaction explained the large majority of the observed variation in yield. The strong correlation between yield in weedy and weed-free conditions found in this study indicated there was little genetic variation in competitiveness among the cultivars tested and therefore the large G × E interaction reflected their general adaptation.

11. KNOWLEDGE GAPS AND FUTURE RESEARCH DIRECTIONS

Despite the large amount of work on plant competition, there are still a number of gaps in our knowledge. For example, while many traits have been suggested as contributing to improved competitive ability, the value of many of these traits and their potential to adversely affect yield potential are not well documented within breeding populations. The value of specific root traits also needs to be assessed under realistic conditions. There are three areas where significant improvements in our understanding of the ecology of competitive relationships and plant genetic improvement are possible: the development of molecular markers, the use of DNA to track root growth and the development of models which utilise physiological and genetic information to assess the effects of specific traits.

11.1. Molecular mapping of competitive traits

Improving the competitive ability of crops will assist with the sustainable management of weeds. However, competitive ability is a complex trait and there are no current examples of varieties that have been bred specifically for their competitive ability. Genetic improvement will depend on either screening germplasm in the presence and absence of weeds or selection for traits that are linked to competitive ability, such as light interception, leaf size and early vigour. Many of these traits are not simply inherited but show a quantitative expression. In addition, they may show a large environmental variation. Consequently, phenotypic selection for competitive ability is difficult. To assist selection, molecular markers that are linked to genomic regions that control the traits of interest (quantitative trait loci, or QTL) can be used to improve the efficiency of selection. QTL for traits associated with competitiveness have been identified in wheat (Sloane, 1999; Coleman et al., 2001; Rebetzke et al., 2001), rice (Zhang et al., 2005), sorghum (*Sorghum bicolor*) and rice for resistance to the parasitic weed *Striga* (Stevens, 2008). However, to date, these QTL have not been used to improve weed competitiveness in commercial breeding.

Apart from their use in marker-aided selection, QTLs can be used to develop structured populations to test the value of specific traits associated with improved competitiveness. For example, QTL for leaf size or root growth can be used to identify lines with high and low expression of these traits and the lines compared under different levels of competition. In this way, genetic information can be used to assess the ecological value of these traits.

11.2. Measuring roots growth using DNA-based technologies

Measuring root growth and distribution in the field is difficult and often imprecise, yet understanding the importance of the patterns of root growth to water and nutrient uptake is fundamental to improving our understanding of competition. Until recently, measuring root growth and distribution depended on physical sampling and extraction of roots and often the fine roots could not be measured. However, DNA-based methods have been developed to allow root growth of individual species to be measured (Linder et al., 2000; McNickle et al., 2008). Using species-specific primers, the roots from 10 species growing together in soil were identified (McNickle et al., 2008). Only small amounts of DNA were needed to identify the roots. The use of DNA-based methods to examine the dynamics of root growth between competing species in a more precise way than previously and linking this to other measurements of soil resource use has the potential to improve our understanding of root ecology and its contribution to plant competition.

11.3. Modelling

Simulation models are now widely used in many areas of plant ecology, in both agricultural and natural systems. A weakness of simulation models is their limited ability to predict differences in genotype responses and G × E interactions, yet this is a cornerstone of plant breeding programmes. Genotypes are often characterised by using empirically derived coefficients and so one of the challenges of modelling is to develop stable coefficients that enable plant responses to be predicted across environments (Hunt et al., 2003). To this end, using information about the plant genome to link genetic information to plant phenotype can be a powerful tool to explore interplant competition and the importance of specific genetic characteristics on competitive ability. The statement by Hammer et al. (2006) that ‘genes have become tangible rather than virtual entities’ reflects recent advances in genomics and highlights the opportunities to exploit this information in plant improvement and crop management. Genetic analysis of competitiveness to identify QTL and genes will provide information that can be used in crop simulation models. Gene-based modelling provides an opportunity to test the value of specific traits associated with competitiveness across a diverse set of environmental conditions (White and Hoogenboom, 2003; Hoogenboom et al., 2004; White, 2006). Chapter 10 summarises the state-of-the-art in this new generation of models bridging genetics and whole-crop processes.

12. CONCLUSIONS

Weeds cause significant losses in yield and reduce the quality of grain crops. Whenever two plants grow near to one another, they will interact by altering the environment in which they grow, which will influence their acquisition of these resources and their growth. Plants can sense the presence of neighbours through changes in the ratio of red:far red light even before the onset of competition for physical resources. There is some evidence that roots can respond to the presence of neighbouring roots and can distinguish roots from the same plant from roots of neighbouring plants, which has been described as ‘self’ versus ‘non-self’ recognition. However, what impact such recognition systems have on the behaviour of different species and the outcome of competition has not been investigated.

There is some evidence that weeds not only acquire growth factors more effectively but also possess superior resource use efficiency than crops. These attributes enable weeds to be highly resilient in cropping systems and can cause large yield losses even when present at low densities. However, spatial aggregation of weeds in the field causes some reduction in weed impact as compared to uniform weed distribution.

More competitive crop cultivars may provide an opportunity to use herbicides less frequently or enable their use at lower rates to achieve an acceptable weed control. The corollary of this is that if herbicide efficacy is reduced for some reason, a high level of competitiveness will still limit yield losses from weed competition and reduce weed seed production.

Plant height tends to be the most common shoot trait implicated in competitive ability of different crops. However, tall plants invariably possess low harvest index and this trait is not of interest to plant breeders because of this serious trade-off. There has been emerging evidence of the importance of early crop vigour for competitive ability. Arguably early vigour could be a useful substitute for plant height for developing weed-competitive crop cultivars. Recent work in several crops has suggested that high yield is compatible with high competitive ability as significant variation in competitive ability can be found in genotypes of similar height.

Understandably, there has been much more work on shoot traits associated with competitive ability as compared to root traits. Not only are the roots difficult to study in the field, it is also near impossible to separate intermingled root systems of different species. Modelling studies suggest that optimal investment of resources in root growth is different in weedy and weed-free situations. Without competition from neighbours, a plant can invest relatively little of its carbon and nitrogen in root growth as it can meet its nitrogen and water demand with a relatively low root length density. Under high fertility and irrigated situations, overinvestment in root could have a yield penalty. However, vigorous early shoot growth may also promote greater root growth and improve water and nutrient acquisition and contribute to higher yields in both weedy and weed-free conditions in water and nutrient-limited environments.

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CHAPTER 19

Dynamic and Functional Monitoring Technologies for Applications in Crop Management

Daniel Rodriguez, Andrew J. Robson and Robert Belford

1. BACKGROUND

The profitable management of the spatial variation of crop performance across paddocks and farms will rely increasingly on the availability of rapid, accurate and affordable techniques to spatially monitor the condition of crops and predict the likelihood of economic responses to tactical interventions and strategic business plans. Here, we argue that applying (i) eco-physiological principles that govern the growth and function of crops and (ii) a systems approach to integrate sensing and predictive technologies, will offer considerable opportunities to improve tactical and strategic decision-making in farming systems. In this chapter, we make a case for the development of more functional and dynamic monitoring technologies with applications in crop management at the site, paddock and whole-farm scales.

This chapter presents three case studies in eastern Australia. First, we look at water- and nitrogen-stressed crops from the viewpoint of sensing techniques to quantify crop physiological stress in a way that allows for accurate and timely tactical intervention, for example for nitrogen fertiliser. Second, we explore the application of physiological, modelling and remote sensing approaches to determine optimum time for the harvest of peanut crops. Third, we describe a functional whole-farm modelling approach that integrates the strategic planning of cropping systems with tactical management through knowledge of seasonal information and spatial variability. The chapter concludes with a summary and discussion of future directions in the integration of physiology and more functional approaches to manage spatial and temporal variability in crop performance.

2. FUNCTIONAL SENSING APPROACHES: QUANTIFYING THE PHYSIOLOGICAL STATUS OF CROPS UNDER WATER AND NITROGEN STRESSES

One of the biggest hurdles for the adoption of precision agriculture in broad-acre cropping systems has been the slow development of rapid, accurate and affordable techniques to quantify likely economic responses to changes in crop management. A prime example of this is in-crop site-specific management of nitrogen.

Multispectral and hyperspectral sensors have been widely used to assess the spatial variation in the nitrogen status of crops (Price and Bausch, 1995; Inoue and Moran, 1997; Filella and Peñuelas, 1994; Blackmer et al., 1996; Stone et al., 1997). In principle, these techniques are based on the absorption of light in the visible portion of the spectrum (0.4–0.7 μm) and reflection of near infrared light (NIR, 0.7–0.9 μm) by plant tissues. However, practical and commercial applications of this technique have been limited (e.g. Link et al., 2005), as it has been difficult to determine if the relationship between spectral responses and the crop condition that alters canopy size, for example nitrogen or water stress, is truly a unique functional spectral signature of the stress or simply an artefact of changes in canopy density. This is particularly the case for rainfed crops when more than one stress signal can be present at any time (Barnes et al., 2000; Tilling et al., 2007).

2.1. Water stress

Water deficit is a trademark of most rainfed crop growing environments, where the potential for crop response to in-season tactical management of nitrogen heavily relies on mostly unpredictable in-crop rainfall. In southern Australia, rainfall is winter dominant, with a sharp drop in rainfall and rise in temperature after the time of flowering when cereal crops are filling grains. In addition, spatial patterns in canopy density might not directly reflect changes in N supply and the potential for response to in-season addition of N, making the use of spectral indices from canopies alone unsuitable for variable rate applications of N fertiliser. The combination of spectral and thermal properties of the canopy has been used to produce maps of water stress, N status and canopy density, when variations in all of these factors are simultaneously present in the field (Rodriguez et al., 2005a; Fitzgerald et al., 2006; Tilling et al., 2007).

Under rainfed conditions, matching nitrogen supply and water availability are key to the success of wheat crops (Section 3.2 in Chapter 6 and Section 2.2 in Chapter 8). Shortage of nitrogen can impair yield and reduce water use efficiency, whereas excess nitrogen, particularly early in the season, can reduce grain yield through the production of excessive biomass and the haying-off of the crop under terminal drought (Van Herwaarden et al., 1998a, b). Therefore, the development of spatial indices able to identify areas in the field of potentially positive response to management intervention such as top dressing of nitrogen fertiliser becomes paramount. In this section, we describe the development of an index of the physiological status of the crop based on the air-to-canopy temperature differential, that could assist in identifying field areas with high and low potential for response to management.

2.1.1. Canopy temperature and related water stress indices

The use of canopy temperature to quantify water stress in plants is based on the assumption that, as water becomes limiting, transpiration is reduced and plant temperature increases (Jackson et al., 1988). Canopy temperature is related to the water status of the crop, net radiation, vapour pressure deficit (VPD) and wind speed. Spatial variability in the water status of field crops can be caused by spatial patterns of soil type, subsoil constraints such as salinity, acidity and sodicity, soil strength (Sadras et al., 2004b; Rodriguez et al., 2006b) or pests and diseases (Heap and McKay, 2005). These conditions can lead to changes in canopy transpiration as a result of active regulation of stomatal aperture (Pinter et al., 1979; Nilsson, 1995). These spatial changes in canopy temperature can be remotely recorded in real time by thermographic imaging. Figure 1 shows a proximal image of a crop canopy; the technology can also be applied at larger scales of canopy, field and farm, and thus has clear advantages over point-based infrared (IR) thermometry to reveal spatial patterns in temperature (Chaerle and Van Der Straten, 2000). Inoue and Moran (1997) showed that thermal imaging of a crop canopy could reveal the spatial differences in canopy surface temperatures and suggested that differences in the physiological status of the plants could be easily detected using this technology. From the combination of micrometeorological data and digital thermal images, spatial patterns for canopy conductance, canopy transpiration and irrigation requirements could be derived (Inoue and Moran, 1997).

One of the main drawbacks of the technology is that thermal images are complex combinations of crop and soil thermal emissions. Particularly before full ground cover is achieved, important differences between the actual crop temperature and the sensed canopy temperature exist (Wanjura et al., 2004). Methods to retrieve useful information from thermal images of potted plants (Leinonen and Jones, 2004) and from full crop canopies (Mihailovic and Eitzinger, 2007) have been developed. The former requires the overlaying of thermal and visible images, and a classification procedure using sophisticated imaging software. Mihailovic and Eitzinger (2007) instead dynamically (i.e. at hourly intervals) calculate the soil and crop thermal balance from the partitioning of the energy over the crop canopy and its bare fraction. However, this is still a point-based model that would be difficult to upscale to paddock level. Rodriguez et al. (2005a) devised a simple alternative to retrieve the temperature of the crop from digital thermal images and ground cover measurement from wheat canopies varying in ground cover. This was based on (i) the relationship between absorbed

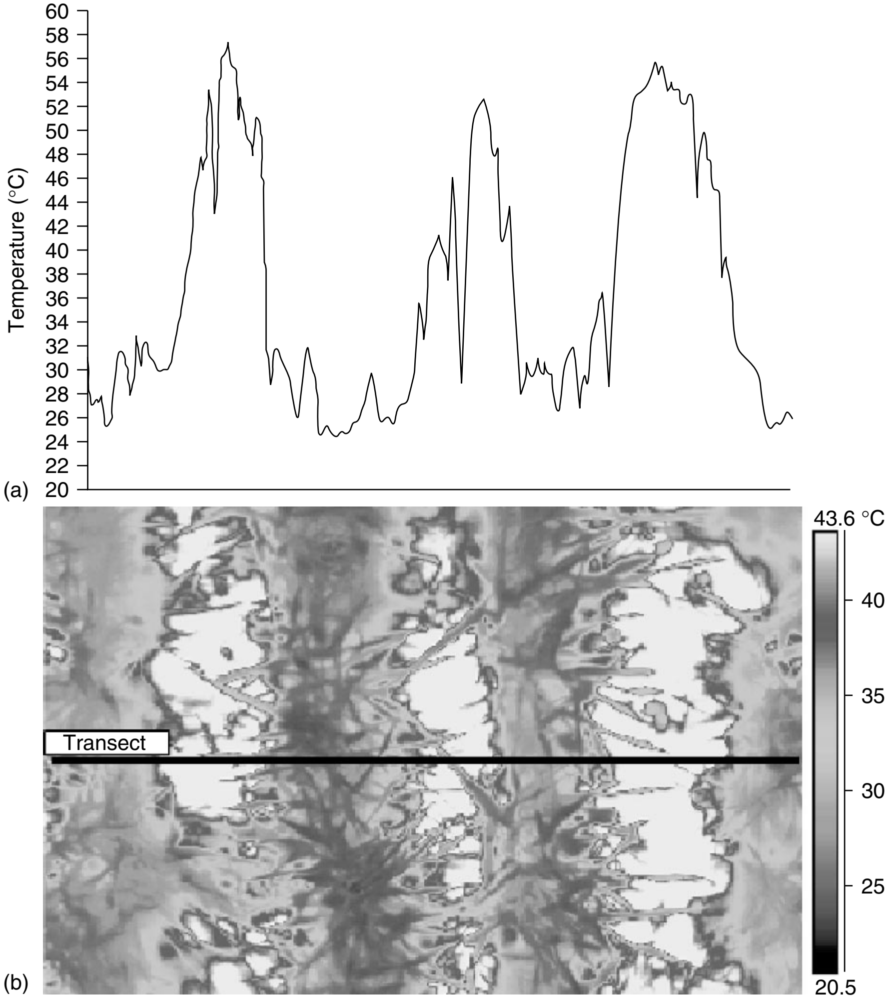


FIGURE 1

(a) Profile of crop and soil temperatures derived from (b) a digital thermal image of a wheat canopy taken at 3 m above ground level at Zadoks stage 31 (first node). (Source: Rodriguez et al., 2005.) See colour version of this figure in Plate 3.

photosynthetic active radiation (PAR) and spectral reflectance (Gallo et al., 1985; Inoue and Iwasaki, 1990), and (ii) the stability of the relation between fractional intercepted PAR and spectral reflectance indices in relation to solar zenith angle or time of the day (Pinter, 1993).

However, canopy temperature alone, particularly if it is not determined in real time from a thermal image of the whole area under study, cannot be used as an absolute estimator of the physiological status of the crop. This is because canopy temperature depends on its energy budget resulting from incoming solar radiation, outgoing long wave radiation, and latent and sensitive heat fluxes, which are affected by rapidly changing micrometeorological conditions (Dunin et al., 1991). Therefore, spatial temperature information becomes meaningful when adjusted by micrometeorological conditions close to the time of image acquisition, for example VPD, or incorporated into a stress index (Inoue, 1991).

Based on the work of Idso et al. (1981) and Idso (1982), Rodriguez et al. (2005a) defined a canopy stress index (CSI) as the difference between canopy (T_c) and air temperature (T_a) normalised by VPD:

$$\mathrm{CSI} = \frac{T_c - T_a}{\mathrm{VPD}} \quad (^\circ\mathrm{C\,kPa}^{-1}) \tag{1}$$

The CSI is expected to be positive and high if the capacity of the canopy to dissipate heat is reduced as when stomata close. A range of environmental factors could cause stomatal closure, including drought (Jones et al., 1995) and pests and diseases affecting vascular tissue, roots or foliage (Boccara et al., 2001; Chaerle et al., 1999; Bowden et al., 1990; Sadras and Wilson, 1997). Stomatal closure can also be induced by shortage of nutrients (Radin et al., 1985; Broadley et al., 2001), and by hormonal signals (Bringham, 2001). Consequently, CSI is an index of the general physiological status of a canopy. Chapter 15 (Section 6.2) outlines surrogate measures for stomatal aperture traits with application in plant breeding, including thermal-based techniques.

Environmental variation in wheat yield is primarily related to number of kernels per unit area which is in turn a direct function of the rate of crop growth between late stem elongation and early post-flowering

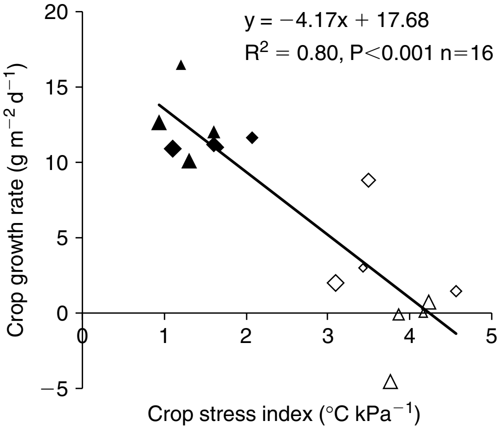


FIGURE 2

Wheat growth rate around anthesis as a function of the crop stress index calculated at anthesis, for irrigated (filled symbols) and rainfed (open symbols) plots, high (diamonds) and low (triangles) plant densities, and four levels of nitrogen (0, 16, 39 and 163 kgN ha^{-1}), represented by the increasing size of the symbols. Each point is the average of three replications. (Source: Rodriguez et al., 2005.)

(Section 5 in Chapter 12; Section 3.2.2 in Chapter 15; Fischer, 1980; Savin and Slafer, 1991; Robertson and Giunta, 1994; Abbate et al., 1997). Relationships between canopy temperature depression and grain yield have also been reported for wheat (Amani et al., 1996; Rodriguez et al., 2005a). At the crop level, Rodriguez et al. (2005a) showed that the CSI was related to the growth rate of a wheat crop around anthesis (Figure 2) under contrasting rates of irrigation, canopy density and nitrogen supply (Figure 3). This confirms how functional applications of remotely sensed information can be used to develop meaningful indices of the physiological status of a crop and even expected changes in growth and grain yield.

Functional indices derived from remotely sensed data, such as CSI, can also provide a simple and elegant link with crop models to spatially simulate key physiological traits of wheat canopies, that is 'spatialise' crop models. This would allow the application of a crop model over areas larger than that for which it had been originally developed (Faivre et al., 2004). This might require more refined models (Rodriguez et al., 2001; Mihailovic and Eitzinger, 2007) able to relate existing remotely sensed information to unavailable data, that is spatial variation in soil properties, landscape properties and crop condition, needed for model calculations and outputs at larger scales than the point.

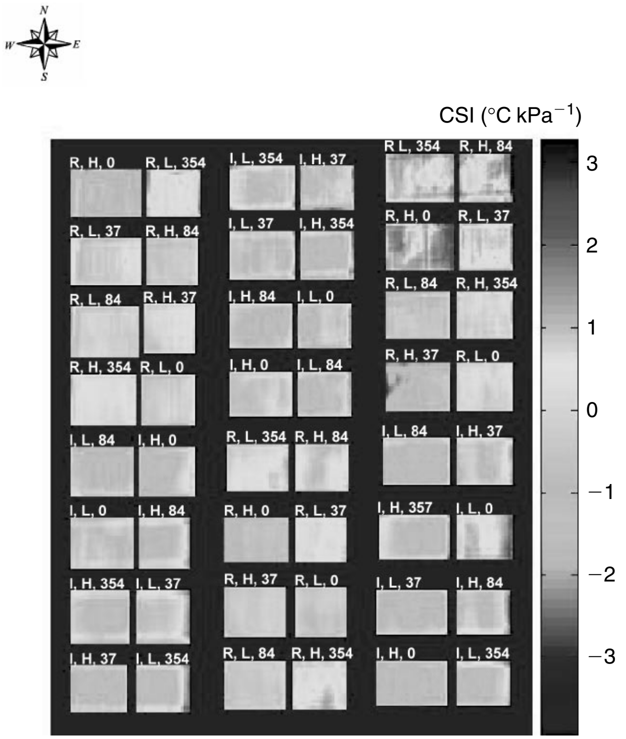


FIGURE 3

Canopy stress index (CSI, C° kPa^{-1}) from an aerial digital thermal image taken on 10 October 2004 at noon over a trial at Horsham (36.65°S, 142.10°W), Victoria, Australia. Labels indicate: R and I – rainfed and irrigated plots, H and L – high and low plant densities, and 0, 16, 39 and 163 are kgN ha^{-1} at sowing. (Source: Rodriguez et al., 2005.) See colour version of this figure in Plate 4.

2.2. Nitrogen stress

Rapid, reliable and relatively inexpensive estimates of crop N status can be made from the analysis of stem juices (Follett et al., 1992) or from estimates of leaf chlorophyll content (Wood et al., 1993). However, these are point estimates that are of limited use when large and highly variable paddocks need to be managed. Remotely sensed spectral indices derived from the reflectance of whole canopies in the green and NIR have been successfully applied to reduce in-crop N inputs without reducing grain yield in irrigated maize (Bausch and Diker, 2001). In addition, many indices based on ratios of reflectance in the visible and NIR parts of the spectrum have been developed, all aimed at assessing crop chlorophyll, plant health or crop nitrogen content.

In nitrogen-deficient crops, chlorophyll reduction increases light reflectance in the visible part of the spectrum (Yoder and Pettigrew-Crosby, 1995). Relative spectral indices of the N nutrition of wheat crops have been developed from comparisons with readings from well-fertilised strips (Raun et al., 2001) or calibration stamps (Raun et al., 2005). This avoids the need for calibrating the relationship between nitrogen content and crop reflectance, at different growth stages or for cultivars/species, and the need to convert data to surface reflectance factors (Pinter et al., 2003). However, as we mentioned above, the main source of variation in field crops is the simultaneous presence of water and N stress. Moran et al. (1989) found that water-stressed canopies of alfalfa had a lower spectral reflectance in both the NIR (0.7–0.9 μm) and red (0.63–0.69 μm) wavebands due to changes in canopy architecture. They also found that the Perpendicular Vegetation Index (PVI; Richardson and Wiegand, 1977) decreased with stress-induced changes in the architecture of the crop, while the NIR/red ratio remained relatively constant. Bowman (1989) showed that the reflectance from cotton canopies in the NIR and short-wave IR regions (0.81, 1.67 and 2.21 μm) increased as the relative water content of the leaves decreased. Thus, the spectral signatures from nutrient deficiencies change when water deficiency is present and this change reduces, if not removes, symptom-specific spectral characteristics. In addition, the spectral signature of water-stressed crops can be further confounded by the increasing proportions of bare soil and the reduced signals from smaller canopies.

2.2.1. Nitrogen stress indices

Rodriguez et al. (2006a) overcame this problem with a simple canopy reflectance index that was greatly independent of water supply and the degree of ground cover. They used: (i) simple planar domain geometry (Figure 4) to account for mixed signals from the canopy and visible soil when ground cover is low, and (ii) a nitrogen stress index (NS_{index}) as a more functional prediction target than the N concentration in shoots. The NS_{index} was derived from relationships of N concentration in shoots and total above ground biomass (Figure 5). This approach is similar to that of nitrogen dilution curves described in Chapter 8 (Section 2.3). In Figure 5, our NS_{index} was derived as the relative distance between the actual N concentration and two envelope functions describing the maximum and minimum concentrations as a function of total dry matter. This approach allows comparison of N status of crops growing under a wide range of phenological stages, environmental conditions, sites and seasons, and is based on the assumption that crop N accumulation is related to crop growth rate and biomass accumulation (Lemaire and Meynard, 1997; Section 2 in Chapter 8).

The NS_{index} relies on the inter-regulation of multiple crop physiological processes, including N uptake, crop carbon assimilation (and thus growth rate), and carbon and nitrogen allocation between organs, all of which are influenced by the water status of the crop. For example, water-stressed plants usually have lower biomass but similar shoot N concentration when compared with well-irrigated treatments (Figure 5). This obviously modifies the amount of nitrogen detected in the crop when it is calculated or sensed per unit area, for example as when using the canopy chlorophyll content index (CCCi) (E-Shikha et al., 2008). Therefore, combining both simple canopy architecture parameters and a more functional predictive target (i.e. NS_{index}) helped to explain up to 70% of the observed spatial variability in crop nitrogen nutrition as early as Zadoks 33, that is third node (Figure 6).

This approach has potential for direct application to farm properties by developing integrated thermal and spectral image acquisition systems at the scale required for tactical decision-making – this will vary from region to region, and with the cropping system in place, the degree of spatial variability present and the economic benefits to be gained from flexible tactical management, for example of nitrogen fertiliser (Robertson et al., 2007). At the farm level (in-field) operation, there are now several commercial machines that use the principle of red/IR reflectance to determine the chlorophyll content (and use this information to infer crop nitrogen status); some of these can be linked to variable rate fertiliser applicators (Link et al., 2005).

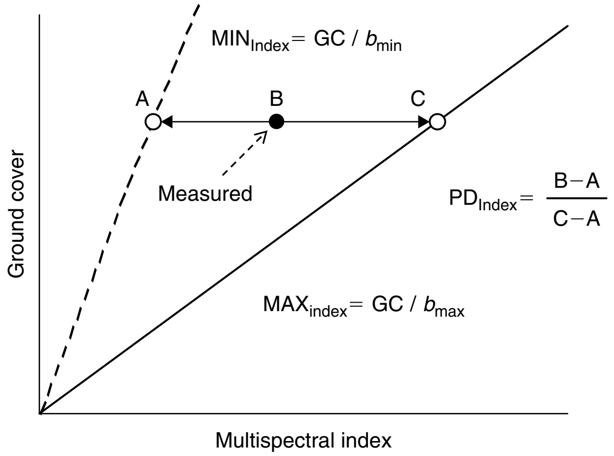


FIGURE 4

Shape of a planar domain index (PD_{Index}) for soil/canopy mixed spectral information as in Clarke et al. (2001). (Source: Rodriguez et al., 2006a.)

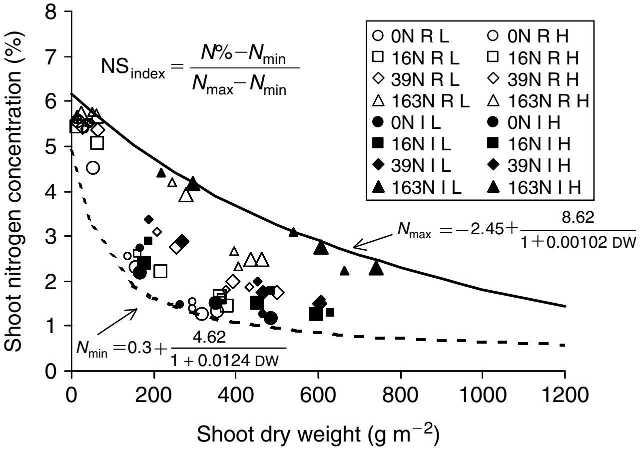


FIGURE 5

Derivation of the nitrogen stress index (NS_{index}) from the relationship between shoot nitrogen concentration and shoot dry weight. Symbols in the figure identify nitrogen rates (0, 16, 39 and 163 kg N ha^{-1}), irrigation treatments (R = rainfed, I = irrigated) and sowing density (L = low, H = high). N_{max} and N_{min} are the manually fitted upper and lower bounds of the relationship between shoot N concentration and shoot dry weight. (Source: Rodriguez et al., 2006a.)

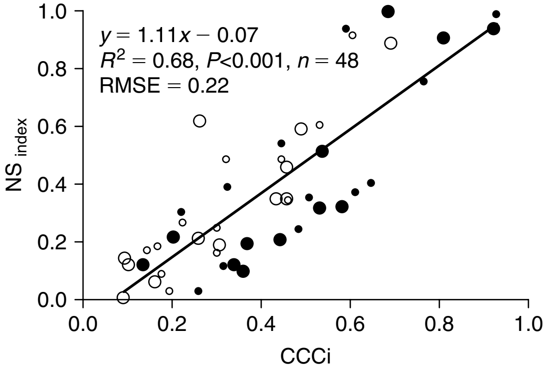


FIGURE 6

Relationships between the nitrogen nutrition index (NS_{index}) and the planar domain canopy chlorophyll content index (CCCi) in wheat. Open and closed symbols indicate rainfed and irrigated treatments, and small and large symbols show the low and high plant densities, respectively. RMSE is the root mean squared error. (Source: Rodriguez et al., 2006a.)

The next step is to develop sensor systems to calculate the more sophisticated indices (e.g. NS_{index}) 'on-the-go', that are linked to expected seasonal conditions (see http://www.longpaddock.qld.gov.au/), or probabilities of achieving an economic return (http://www.apsru.gov.au/apsru/Products/Whopper/ and www.yieldprophet.com.au).

3. FUNCTIONAL SENSING APPROACHES: HARVEST MANAGEMENT IN PEANUT

We have discussed the application of physiology and sensing to the nitrogen management of cereals, where profit is a primary function of grain yield. By contrast, high-value crops present different management challenges, with crop quality being paramount to optimise returns. Peanuts grown in the summer rainfall environments of northern Australia provide a good example: they have indeterminate flowering, subterranean podding and high spatial variability of yield and time of maturity. These factors combine to make maturity assessment of the peanut crop a very difficult task; an estimated $6.3 million is lost annually as a result of suboptimal harvest timing in Australia (White et al., 1997).

Harvesting the crop too early can result in reduced kernel size, whereas crops harvested too late may suffer from extensive pod losses due to weakened peg strength during cutting and threshing. In dry-finish seasons and when soil temperatures during pod filling are high, aflatoxin contamination (a deadly food toxin caused by the soilborne fungi *Aspergillus flavus* or *A. parasiticus*) can cause significant economic losses (Dorner et al., 1989). When the risk of aflatoxin contamination is high, early harvesting of peanuts is recommended, so it is important to identify those areas that are reaching maturity. Current techniques to assess maturity include the 'hull scrape' (Williams and Drexler, 1981) and 'shell-out' techniques (Shorter and Simpson, 1987). These are predominantly physiological-based measurements of the harvested peanut kernel and shell, without any direct assessment of the plant canopy. Both methods are slow and, being point source, do not account for spatial variability of pod maturity.

3.1. Spatial prediction of crop maturity in peanut

In this section, we demonstrate the potential to predict spatial variation in peanut crop maturity by integrating remote sensing imagery and modelling (Trudgill et al., 2005). The rationale is that maturity of pods is related to soil temperature, and that soil temperature is, in turn, influenced by canopy cover. Remotely monitoring canopy dynamics and modelling the effect of canopy size on soil temperature would account for a large part of the spatial variation in crop maturity.

The study was conducted during the 2003/2004 growing season in a commercial peanut crop grown in the South Burnett region of Queensland. This is a subtropical region of slopes and plains with a summer dominant rainfall (annual average 750 mm). Peanuts are grown on medium (~1 m) to deep (1.8 m) Red Ferrosols (Isbell, 1998) that hold between 100 and 140 mm plant available water (PAW).

Satellite imagery (QuickBird) was used to derive a normalised difference vegetation index (NDVI) transformation:

$$\mathrm{NDVI} = \frac{\mathrm{NIR} - \mathrm{red}}{\mathrm{NIR} + \mathrm{red}} \tag{2}$$

The selected area of the selected crop was segregated into five NDVI classes using an unsupervised classification. The classes were then assigned a colour: black, blue, green, yellow or red, to represent a progression from low to high NDVI.

3.2. Ground truthing

A non-differential global positioning system (GPS) was used to locate sample areas within each of the NDVI classes. Each sample was selected from a 'large' homogenous area (at least 200 m^2) of each colour class. Three plant samples (intact peanut bushes) per zone were sampled and dried for three days at 40 °C before pods were harvested. A pod subsample was taken and shelled-out to measure the percentage of pods with darkening on the internal surface of the pericarp as an index of crop maturity. The correlation between incidence of black pods and NDVI within each colour zone enabled the accuracy of this system for maturity prediction to be determined at both 0.05 and 0.01 levels of significance. The data of pods with black shells were also used to estimate the average number of days required to reach harvestable maturity (85% black shells) assuming a 2.2% daily increase in the proportion of black shells from the date of internal shell-out assessment.

3.3. Simulation of crop development and maturity from thermal time

Temperature was recorded in each of the classified regions in April 2004. Air screened temperature was recorded 1 m above the ground, and soil temperature at 0.05 m below the soil surface and adjacent to the plant meristem. The temperature data were used to simulate crop maturity time according to the model (Leong and Ong, 1983):

$$\frac{1}{t} = \frac{T - T_\mathrm{b}}{\theta} \tag{3}$$

where $1/t$ is the development rate, T the daily mean temperature (°C), T_b the base temperature for development (°C) below which the rate is zero and θ a constant identifying the thermally modified time for each development stage. Cardinal temperatures assumed in the model, according to Bell and Wright (1998), were: base temperature of 9 °C, optimum temperature between 27 and 32 °C and maximum temperature of 41 °C.

Temperature inputs to predict maturity were used in the APSIM peanut module (Keating et al., 2003; Chauhan et al., 2004), which uses radiation, ambient temperature and rainfall on a daily time step to simulate peanut maturity, growth and yield. Briefly:

(a) calculation of a single point value of date of crop maturity based on the accumulation of growing degree-days from ambient temperature (i.e. the conventional approach);

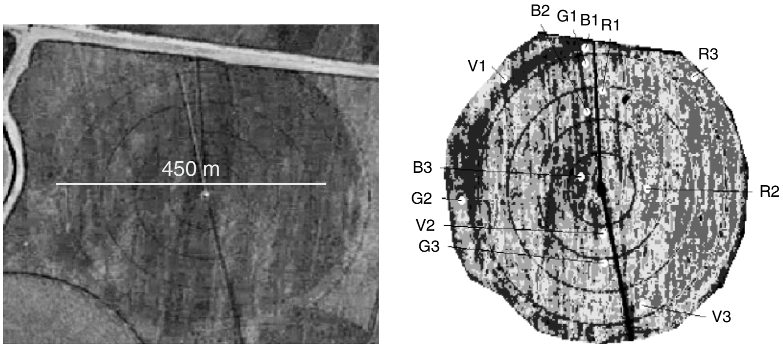
(b) calculation of a separate crop maturity date estimate for each colour class by replacing ambient temperature with actual soil temperatures;

(c) calculation of a separate crop maturity date for each colour class by replacing ambient temperatures with simulated soil temperatures for the entire pod-filling period;

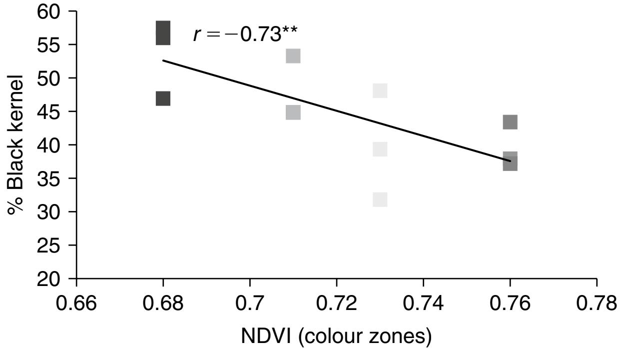
(d) extrapolation of the differences observed between soil and maximum and minimum ambient temperature during the measured period, within each colour zone to determine if the inclusion of measured (or simulated) soil temperatures, compared to ambient temperature, was better correlated with observed variations in crop maturity.

Although little variation in crop vigour could be identified with the true colour satellite image of the irrigated crop (Figure 7a), the unsupervised classification of the NDVI image identified an increased vigour region on the right half of the pivot, as identified by the red class (Figure 7b).

Pod maturity was negatively correlated ($r = -0.73$, $P = 0.005$) with NDVI at each colour zone (Figure 7c), similar to relationships observed in other peanut crops (Robson, 2007). This was related to the variation in



(a) True colour (b) Unsupervised classification



(c) Correlation between NDVI (colour zones) and % black (mature) peanut pods.

FIGURE 7

*(a) True "colour" and (b) unsupervised classification of irrigated pivot (cv. VB-97) (area = 17.6 ha); labelled points indicate growth sample locations. (c) Relationship between NDVI and percentage of mature (black) pods (**$P \leq 0.01$). (Source: Rodriguez et al., 2006.) See colour version of this figure in Plate 5.*

peanut bush size causing differing degrees of shading that ultimately influenced the amount of direct solar radiation reaching the soil surface, and therefore, the rate of crop development. Soil temperature from each colour zone showed that soils within the black and blue regions reached daily maximum temperatures up to 4 °C higher than soils in red regions (Figure 8). These results agree with observations by Chauhan et al. (2007), who reported that peanut canopy cover has a large modulating effect on topsoil temperature.

By analysing the crop maturity response using the thermal time concept in the APSIM peanut model, it was hypothesised that use of measured soil temperatures in each colour zone, rather than point source ambient temperatures, would improve the prediction of observed spatial variation in crop maturity. To test this hypothesis, we simulated maturity dates using three temperature inputs, viz., ambient temperature, measured soil temperature during the period shown in Figure 8 and measured soil temperature extrapolated for the entire pod-filling stage (Table 1).

Using ambient temperature as input, the predicted crop maturity date for the irrigated crop, irrespective of colour zone, was 158 days. Using soil temperature over the three-week period (Figure 8) resulted in a predicted maturity range of two days between the black and red zones (155–157 days from sowing) (Table 1). When observed soil temperatures were extrapolated for the entire pod-filling period, a maturity range of seven days between the black and red zones (138–145 days from sowing) was predicted (Table 1); this was consistent with the observed six-day range of pod maturity (151 days in the red region, to 145 days in the blue) measured in the field using the accepted shell-out method.

For this experiment, the use of extrapolated soil temperature for the pod-filling period gave a better prediction of maturity variation across zones than the standard use of ambient temperature. This also suggests

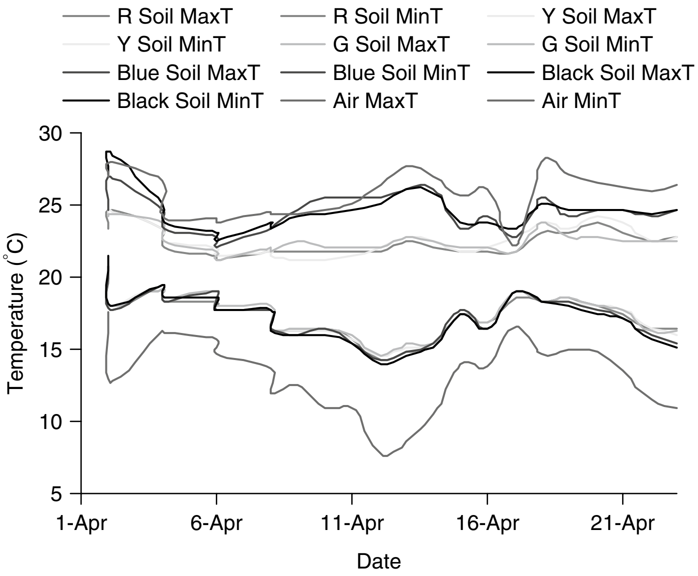


FIGURE 8

Measured soil temperature in different "colour" zones. Ambient temperature recorded during the same period is also shown. AirMaxT = maximum air temperature, AirMinT = minimum air temperature, SoilMaxT = maximum soil temperature, SoilMinT = minimum soil temperature, and the codes for colour correspond to the soil temperature in the NDVI zones identified in Figure 7. For colour codes see Plate 6.

Table 1 Comparison of Days to Observed Maturity and that predicted by the APSIM Model using Inputs of Ambient Temperature, Measured Soil Temperature and Extrapolated Soil Temperature during the Pod-Filling Period, in each Colour Zone in 2003/2004

Colour Zone	Observed Maturity[a]	Predicted Maturity from		
		Ambient Temperature	Measured Soil Temperature	Extrapolated Soil Temperature
Red	151	158	157	145
Yellow	151	158	157	144
Green	147	158	157	144
Blue	145	158	155	138
Black	Not available	158	155	138

[a] *85% pods with dark pericarp.*

that peanut bush size and the resultant variation in shading may be an important source of variation in soil temperature within a partially irrigated crop, thus allowing for indirectly measuring this variation to improve prediction of crop maturity.

Vegetation index images derived from multispectral satellite or airborne image data could be used to measure and stratify crop vigour over large areas. When combined with modelling and current approaches, such as the 'hull scrape' method at strategic locations, multispectral vegetation index images may provide growers with a more practical and accurate method for assessing and managing the spatial variability of peanut maturity. Harvest segregation based on this approach could improve quality and reduce aflatoxin risk. Further research is required to determine the cost:benefit of this technique, and its accuracy in other growing environments, including an assessment of how often disease and other factors affect the correlation between crop vigour and maturity.

4. INTEGRATING THE SPATIAL AND TEMPORAL DIMENSIONS OF ON-FARM VARIABILITY: THE ROLE OF INTEGRATIVE DYNAMIC SYSTEMS MODELS

The examples in Sections 2 and 3 provide options for farmers to change management in parts of a field to improve the quantity or quality of grain produced. Managing this spatial variability will become increasingly important as terms of trade continue to decline and input costs must be controlled. However, spatial management in a given year and field is just one of the many decisions farmers face; here we look at more dynamic and integrative approaches to help design more profitable, less risky and more sustainable farm businesses.

Particularly in rainfed agriculture, farmers operate in production environments that are always changing. With every growing season, farmers attend to numerous factors that influence their decisions; some factors are within their control, many are not. This is a daunting challenge, especially considering that in non-subsidised economies, farmers' decisions are carried out in a financial environment of diminishing economic returns, where a wrong decision could mean financial hardship, threatening the viability of the entire business. To remain viable, farmers then must manage a number of internal (e.g. financial situation, debt, availability of machinery, soils, farming system) and external (e.g. grain prices, infrastructure limitations, government intervention) variables and arrive at decisions that account for multiple trade-offs. Particularly for farming systems where a number of alternative crop and livestock enterprises could be carried out during any particular season, these decisions relate to: the mix of enterprises, matching inputs to management zones, crops and cultivars to expected seasonal conditions and soil aptitude. These farming systems are therefore highly complicated, dynamic and in most cases highly opportunistic. Opportunistic farming systems rely on management processes that enable growers to successfully vary their practices, even within the cropping season, to account for variable environmental conditions. This encompasses a number of technological solutions that in isolation have proven to be partially effective, namely precision agriculture, seasonal forecasting and cropping systems modelling, though when integrated could dramatically improve our capacity to make better decisions. In temperate to tropical environments, whole-farm decisions including cropping intensity are much more important economically than management practices aimed at the yield of individual crops, as illustrated in the analyses of farming systems of the Pampas (Sections 4 and 5 in Chapter 3) and Asia (Section 3 in Chapter 5).

4.1. The problem

Cropping in north-eastern Australia occurs mostly along an inland band that runs between Emerald (22°S) and Dubbo (33°S). Rainfall (550–750 mm) is summer dominated in the north and more evenly distributed as we move southwards towards Victoria and South Australia. In this transect, rainfall frequency increases and the size of each rainfall event decreases towards the south, affecting the fraction of evaporative losses (Sadras and Rodriguez, 2007). In eastern Australia in general and in its northern region in particular, agriculture is dramatically affected by 2–10 years climatic cycles driven by El Niño Southern Oscillation (ENSO); see Section 6.1 in Chapter 20 for ENSO-based rainfall forecasts and risk management. In north-eastern Australia, soils, that is mostly Vertosols (Isbell, 1998), usually have high capacity to store water, which together with the possibility to grow winter and summer crops partially helps to compensate for unreliable rainfall.

Wheat and sorghum are the main crops in the region, but farmers usually diversify production with livestock, chickpea, cotton, maize, peanuts and soybean. Over the years, farmers have adapted practices and farming systems to maximise the capture and retention of soil water and mineral nitrogen through fallowing (i.e. non-crop periods), and adopting reduced or zero tillage technologies (Chapter 2). Other strategies to manage climate risk include:

- use of moisture-seeking drills and press wheels to improve seed germination;
- adoption of skip-row systems to transfer water consumption from vegetative to reproductive stages and grain filling, hence reducing the impact of terminal stresses;
- introduction of cover crops or stubble retention to enhance rainfall infiltration and reduce non-productive losses of water;
- introduction of legumes in the rotation to break the cycle of weeds and diseases and improve the nitrogen balance;
- adjustment of fertiliser rates depending on seasonal forecasts (i.e. that predict the timing and amount of rainfall) to regulate crop growth and reduce risk of haying-off;
- adoption of seasonal forecasting systems and decision support tools (e.g. the APSIM models and its derivative products) to evaluate the likelihood of rainfall and achievable yields at the time of making investment decisions (Hammer et al., 2000).

In addition, many farmers have adopted highly opportunistic strategies, that is by modifying levels of investment and cropping intensity (i.e. risk attitude), primarily based on perceived (e.g. ‘gut feeling’) changes in seasonal conditions and markets, but also from changes predicted by existing seasonal climate forecasting tools (http://www.longpaddock.qld.gov.au/).

Tools and analyses to support decision-making in the highly variable environments of Australia are based on shifts in the probability distribution for rainfall or expected grain yield at the paddock level (http://www.apsru.gov.au/apsru/Products/Whopper/ and www.yieldprophet.com.au) or regional scales (Potgieter et al., 2005). In this section, we describe a functional model and rule-based framework APSFarm (Box 1) that can be used to analyse the impact of alternative tactical and strategic management options at the whole-farm level. The basic hypothesis is that the likely success of decision-making in cropping systems greatly depends on achieving some level of understanding on how seasonal variation and soil properties interact to create unique growing conditions. These unique conditions require tailored management to improve production and environmental outcomes.

4.2. Integrating temporal and spatial dimensions of variability – a case study

Based on interviews with farm managers and consultants, we set up APSFarm to simulate a 2000 ha no-till cropping farm near Emerald, Central Queensland, Australia (23.53° S, 148.16° E). Farm comprises three major soil types (i.e. management zones) of contrasting PAW capacity, that is low 120 mm on 30% of the farm, medium 150 mm on 40% of the farm and high 180 mm on the remaining 30%. Here we used APSFarm to answer whether the adoption of site-specific management of nitrogen fertilisers across the whole farm would provide economic benefits and how those benefits could be optimised by re-designing some of the key management rules and existing farm strategies.

BOX 1 APSFarm: a whole-farm level rule-based discussion support system

APSFarm (Rodriguez et al., 2007) is a multipaddock dynamic simulation environment that uses the APSIM model (Keating et al., 2003) to simulate the allocation of land, labour, time, irrigation water, livestock, machinery and finance resources at the whole-farm level. In APSFarm, available farm machinery and each farm activity determines work rates, and incurs an operating cost. Farm scale economics are monitored, and the current cash status can be used as an input to management and business decisions. The management of the farming system is modelled as a set of state and transition networks, for example finite state machines. Each paddock has a current state, for example fallow, wheat, sorghum, etc., and 'rules' that allow transition to adjacent states. These rules represent both the capacity, for example availability of machinery, land and labour, and the capability, for example cropping skills, farm business strategies and risk attitude.

These rules are usually expressed as a Boolean value (true for feasible, false otherwise), but can also be real values; higher values represent the desirability of a particular action. Each day, the model examines all paths leading away from the current state to adjacent states, and if the product of all rules associated with a path is non-zero, it becomes a candidate for action. The highest ranking path is taken, and the process repeats until nothing more can be done for that day.

In APSFarm, all farm activities are simulated based on a number of farm level and paddock level criteria. Thresholds for these criteria are obtained from interviews and discussion sessions with farmers and consultants. For example, farm level criteria can include sowing windows for each crop, definition of 'break of the season', that is millimetres of rainfall in a defined period of time, maximum fraction of farm area that could be sown to each crop, maximum work capacity ($\text{ha}\,\text{day}^{-1}$), etc. Examples of paddock level criteria include: minimum plant available water (PAW, mm) required to sow a crop, cropping history, soil type, that is plant available water capacity (PAWC), and level of ground cover, etc. Other inputs include commodity prices, production costs, available machinery, assets, farm debt, etc. Examples of outputs from APSFarm include production measures, that is individual crop yields and responses to variable management by zones; economic measures, that is crop and fallow costs, individual crop gross margin, farm annual operating return, return on investments and farm cash flow; efficiency measures, that is whole-farm water use efficiency; and environmental measures, that is deep drainage, runoff and erosion.

We compared the adoption of site-specific management of nitrogen against present farmer's practice (i.e. tactical and strategic farm management), before and after the management of the farm business was optimised using a multi-objective optimisation (Box 2) (Price et al., 2005) and the five Southern Oscillation Index (SOI) seasonal climate forecasting system (Stone et al., 1996) was adopted to predict seasonal conditions at sowing (Rodriguez et al., 2007). Present farmer's practice involves topping up soil nitrogen to achieve a target of 150 kgN ha^{-1} at sowing for wheat, 100 kgN ha^{-1} for late sorghum, 160 kgN ha^{-1} for all other sorghum sowing dates and 200 kg ha^{-1} for maize. The improved nitrogen management strategy involved changing the target N rates according to soil properties in each of the management zones (i.e. site-specific N management) and expected seasonal conditions (i.e. ENSO forecast).

Cropping enterprises included sorghum, wheat, chickpea and maize. Originally, about one-third of the cropping area was dedicated to winter crops. Depending on soil water at sowing, double cropping was considered (i.e. two consecutive crops with no or very short intervening fallow), though summer cropping was predominant. The model was run for a wet (1986–1995) and a dry (1996–2005) decade. The differential evolution (DE) algorithm was configured with a population of 150 individuals, using crossover and mutation rates of 50% (Box 2).

Table 2 shows the farmer's management rules for PAW and fraction of area sown, and the mean of each variable in the top rank of the final DE population, for the wet and dry decades. During the dry years, the optimised PAW was similar to the present farm management (Farmer), that is similar cropping intensities. However, the area sown was higher, indicating benefits from a more opportunistic cropping system, that is whenever a sowing opportunity is available, the farmer should sow a bigger proportion of available land; this accounts for existing machinery and labour constraints. Lower PAW during the wet decade indicates that a higher cropping intensity would further increase profits without significantly changing the risk profile and environmental outputs of the farm. During wetter years, the optimised maximum fraction of land allocated to each crop varied little across enterprises, and was less opportunistic than during the dry seasons.

Figure 9 shows the average annual operating return for the present and optimised farm strategy and management during dry and wet decades. Here, multi-objective optimisation techniques were used to identify strategies that maximise profits while minimising economic risk (down side risk) and soil loss. During the dry years, it would be difficult to significantly improve the profitability of this farm business, suggesting that

BOX 2 Multi-objective optimisation

In simple terms, optimisation is the attempt to maximise a system's desirable properties while simultaneously minimising its undesirable characteristics. Differential evolution (DE) algorithms draw inspiration from biological evolution. The DE approach basically involves the encoding of the design problem into an artificial genome, for example in our case the genome was characterised by the different crops that could be sown, the thresholds of plant available soil water (PAW) to decide the sowing of any crop and the maximum possible fraction of farm area dedicated to each crop. This collection of values is called the genotype. The algorithm then cycles through the following steps:

1. generates initial population, that is *n* number of randomly sampled initial farm designs;
2. turns the genotype into a phenotype, that is runs the model (APSFarm) to evaluate the attributes of those initial farm designs in terms of profit, down side risk, soil erosion, etc.;
3. selects the genotypes that perform best to create the new population for the next iteration;
4. reproduces itself, that is the selected populations are crossed and/or mutated to generate the next generation to be evaluated in the simulation (APSFarm);
5. repeats the cycle beginning with step 2, until the final number of iterations is reached or the system identifies a global optimum.

Table 2 Farmer's Management Rules, that is, Plant Available Soil Water (mm) required for Sowing Crops, and Proportion of the Total Farm Area Sown to each Crop, Before (Farmer) and After Optimisation for Wet and Dry Decades

Crop	Plant Available Water			Area Sown		
	Farmer	Wet	Dry	Farmer	Wet	Dry
Chickpea	100	88	104	0.3	0.4	0.7
Maize	110	92	107	0.2	0.4	0.6
Spring sorghum	110	88	108	0.1	0.4	0.6
Early sorghum	80	87	75	0.3	0.4	0.5
Sorghum	80	90	78	0.8	0.4	0.6
Late sorghum	60	91	89	0.3	0.5	0.5
Wheat	80	90	94	0.8	0.3	0.7

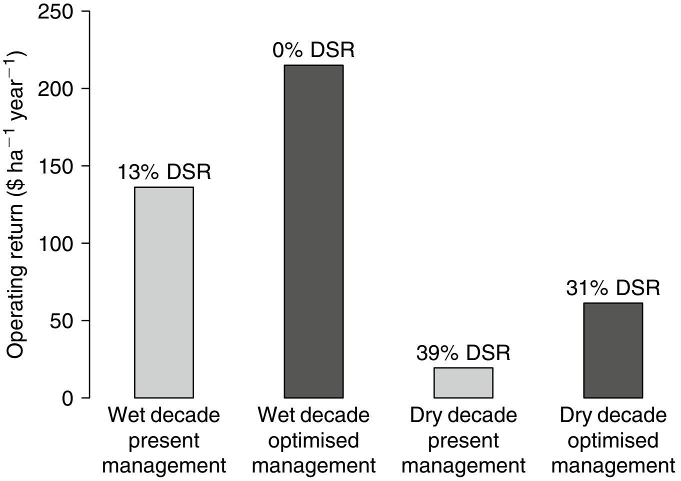


FIGURE 9

Annual operating return for the present farm strategy and management, and optimised farm strategy and management during drier and wetter than average decades. DSR is the down side risk, that is the probability of a negative economic return. (Source: Rodriguez et al., 2005).

even our best growers would be highly vulnerable to projected drying trends in a changing climate (Section 5.2 in Chapter 20). Present management could still be improved during wet years; this indicates how important it is to be able to identify good seasons early enough to make the most of those opportunities.

When good and bad seasons and therefore opportunities to change management were identified using the five SOI seasonal climate forecasting system (Stone et al., 1996), the improved farm business strategy showed a twofold increase in profits compared to the present business plan (Figure 10). The additional benefit from adopting site-specific management technologies (i.e. site-specific management of N) increased from 8% (i.e. under present business strategy) to a more significant 14% (i.e. under the improved business strategy).

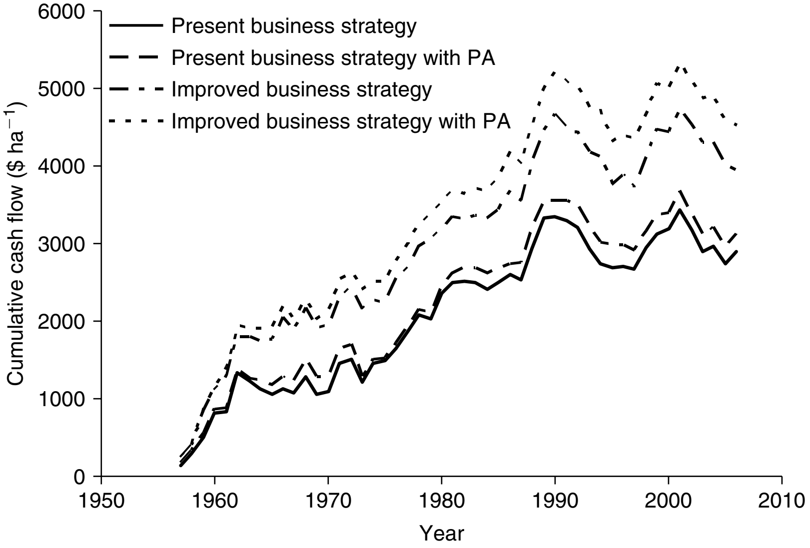


FIGURE 10

Simulated cumulative cash flow for a 2000 ha farm business in central Queensland, Australia, assuming present and optimised strategies including and excluding the adoption of site-specific management (PA) of nitrogen.

The key message from this example is that the benefit from adopting site-specific technologies might depend on how well tuned the rest of the farm business components are. In this case study, benefits from site-specific management were significant when the farm business strategy was capable of capturing the benefits and opportunities from a highly variable climate. We believe this indicates that more than ever before there is an urgent need for the generation of more functional, dynamic and integrative approaches in the analysis of the spatial and temporal dimensions of farm businesses, together with the identification and quantification of key drivers. This will help less experienced and new generations of growers to more quickly create relevant information that translates into knowledge, through the discussion of farm business scenarios and trajectories that include the potential impacts of new technologies, changes in climate and markets. This will also help the more experienced or intuitive growers adjust to the ever-changing rules of the farming game. Chapter 2 emphasises the synergy of multiple innovations applied collectively in improving agricultural output.

So far, the benefits of developing APSFarm have been threefold: (1) in the process of model design and development, APSFarm becomes the framework that ‘packages’ the knowledge and discussion while allowing farmers, consultants and researchers to identify opportunities for change and improvement; (2) modelled results provided realistic measures of trade-offs between profit–risk–environmental impact across a number of possible alternative futures; and (3) farmers benefited from the test benching and fine tuning of cropping rules by accounting for the dimensionality of their complicated production systems.

5. CONCLUSIONS AND THE WAY FORWARD

In recent years, the grains industry has developed technologies to improve site-specific management of crops; this has been based on understanding physiological principles which control the use of soil water and nutrients by plants, and how they are affected by environmental factors such as humidity, solar radiation and temperature, and timing and distribution of rainfall. In this chapter, we have described systems to manage nitrogen supply to cereals in southern Australia, and systems to determine optimum time for harvesting of peanuts in northern Australia.

This chapter also describes the development and application of more integrative systems modelling tools that can be used to explore and design more profitable, less risky and more sustainable farm businesses. This emphasises that one of the most important advances in the management of spatial variability has been the recognition of the need for more functional, dynamic and predictive systems able to translate changes in cropping practices into future likelihoods of improved economic and/or environmental returns.

Agricultural production systems are dynamic and diverse. Numerous interactions occur between soil, crop and climate, which are often difficult to identify and manage. Management decisions that relate to climate are also made at different times of the year and with different levels of significance for different farming systems. It is clear that sensing technologies have the potential to inform management decisions at a field level within a season, but when used in isolation, these technologies will rarely provide enough information for the decision-maker to confidently change management practice across a farm and seasons.

In general, decision-making in rainfed farming systems is dominated by differing degrees of risk (i.e. known probabilities of possible outcomes) and uncertainty (i.e. unknown probabilities of possible outcomes). This is why the use of crop simulation models is essential to integrate and quantify processes and factors that interact across the different dimensions of the production system, the soil, the climate, the crop and its management. Models like APSIM, CERES and CropSyst have the capability to simulate the effects of interacting resources and agronomic inputs at paddock level. APSFarm is an example of renovated efforts to deal with these factors at the whole-farm level. A modular format allows simulation of a large number of different crop types, farming systems, farm structures and major yield drivers such as soil water at sowing, nitrogen availability and plant density. The most significant improvements required for models to achieve the next step in realism are a full account of phosphorus nutrition, and the biological effects of rotations (Section 3 in Chapter 21; Sadras and Roget, 2004).

A systematic approach that integrates sensing technologies into decision-making in agriculture could be generalised as a sequence of five steps (as adapted from Hammer, 2000):

1. *Understand the system and its management*: It is essential to understand its dynamics and opportunities for management intervention, that is identify decisions that could influence desired system's behaviour or performance.
2. *Understand the impact of climate variability*: It is important to understand whether climate variability has a role in determining the expected changes in spatial responses to changes in management.
3. *Determine the opportunities for tactical management in response to seasonal forecasts and sensed stresses*: Climate prediction and sensing technologies are continuously evolving. Having access to a seasonal forecasting system of sufficient predictive skill and lead time will be as important as being able to identify spatial patterns of stress before economic responses could be quantified.
4. *Evaluate the worth of tactical decision options*: The quantification and clear communication of the likely outcomes, for example economic or environmental, and associated risks of changing a management practice are key to achieving adoption of the technology.
5. *Work with decision-makers:* this generates valuable insights and learning throughout the entire process, that is identifying relevant questions and problems and devising suitable technologies and tools.

The profitable management of the spatial variation of crop performance across paddocks and farms will rely increasingly on the availability of rapid, accurate and affordable techniques to spatially monitor the condition of crops and predict the likely economic responses to tactical interventions and strategic business plans. As farmers learn more about the productive capacity of fields in space and time, and the economic returns from site-specific adjustment of inputs, it is possible that the use of land within a farm and catchment will change. Highly productive land and soil units will be increasingly used for intensive cropping and livestock programmes, while land of lower capability which shows consistent negative financial return will be considered for low-value production options, or, increasingly, to generate environmental dividends including re-vegetation or carbon sequestration. This raises many questions in relation to the shape, size and continuity of land of low production potential. While remote sensing tools can help identify and quantify the value of these areas, deciding how to use them or integrate their environmental value in a farm or catchment context will require a further layer of integration between physiologists, agronomists, ecologists and systems modellers.

We have discussed how a systems approach to integrating sensing and predictive technologies offers considerable opportunities to improve decision-making in many farming systems; however, more functional and interdisciplinary approaches will be required in the future to develop solutions for the sustainable economic growth of our primary industries.

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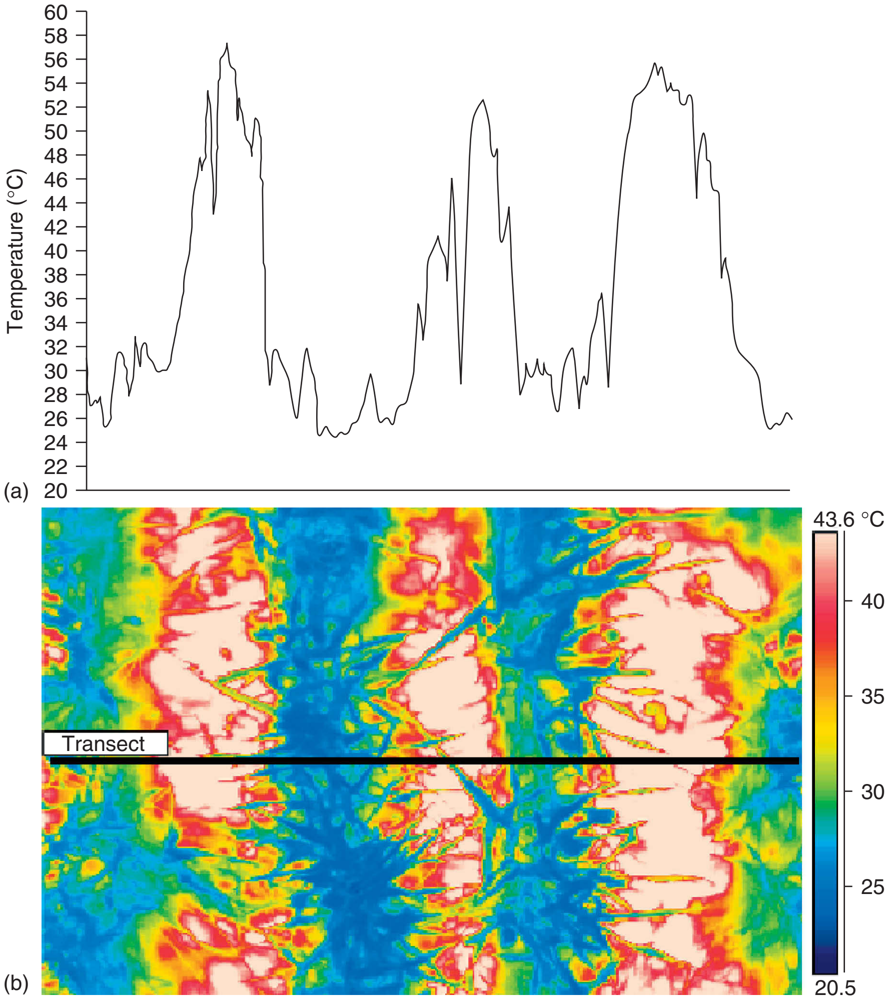


PLATE 3

(a) Profile of crop and soil temperatures derived from (b) a digital thermal image of a wheat canopy taken at 3 m above ground level at Zadoks stage 31 (first node). (Source: Rodriguez et al., 2005.) (see Fig. 1 of Chapter 19)

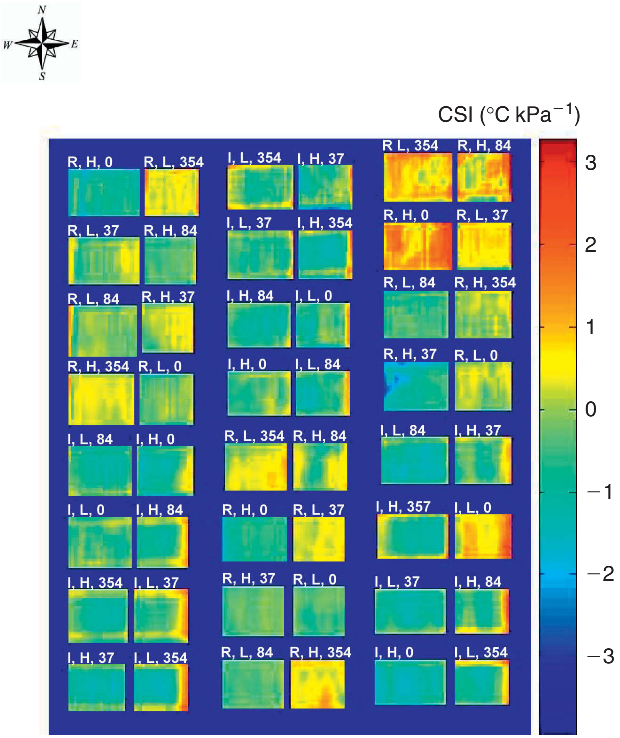
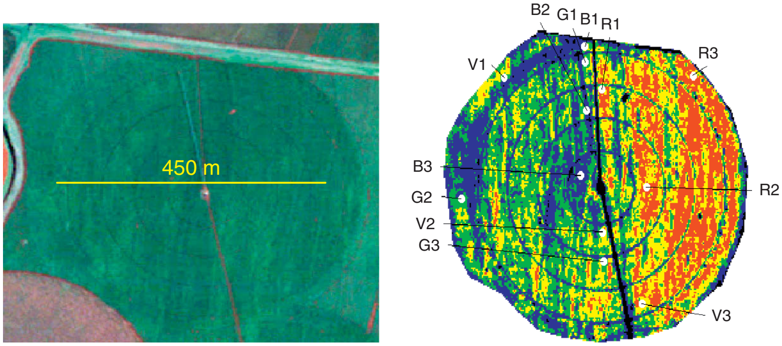
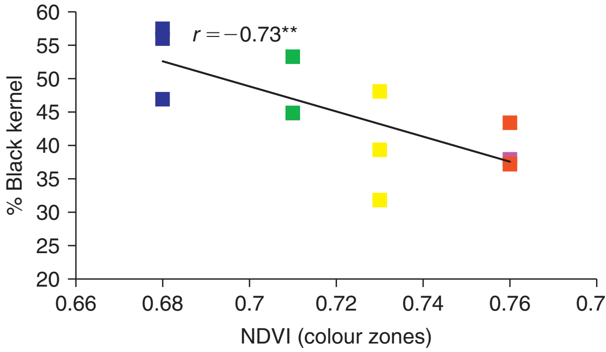


PLATE 4

Canopy stress index (CSI, C° kPa^{-1}) from an aerial digital thermal image taken on 10 October 2004 at noon over a trial at Horsham (36.65°S, 142.10°W), Victoria, Australia. Labels indicate: R and I – rainfed and irrigated plots, H and L – high and low plant densities, and 0, 16, 39 and 163 are kg N ha^{-1} at sowing. (Source: Rodriguez et al., 2005.) (see Fig. 3 of Chapter 19)



(a) True colour (b) Unsupervised classification



(c) Correlation between NDVI (colour zones) and % black (mature) peanut pods.

PLATE 5

*(a) True colour and (b) unsupervised classification of irrigated pivot (cv. VB-97) (area = 17.6 ha), where the red regions indicate high IR reflectance, followed by yellow, green, blue and black indicating decreasing IR reflectance. Labelled points indicate growth sample locations. (c) Relationship between NDVI and percentage of mature (black) pods (**P ≤ 0.01) (see Fig. 7 of Chapter 19).*

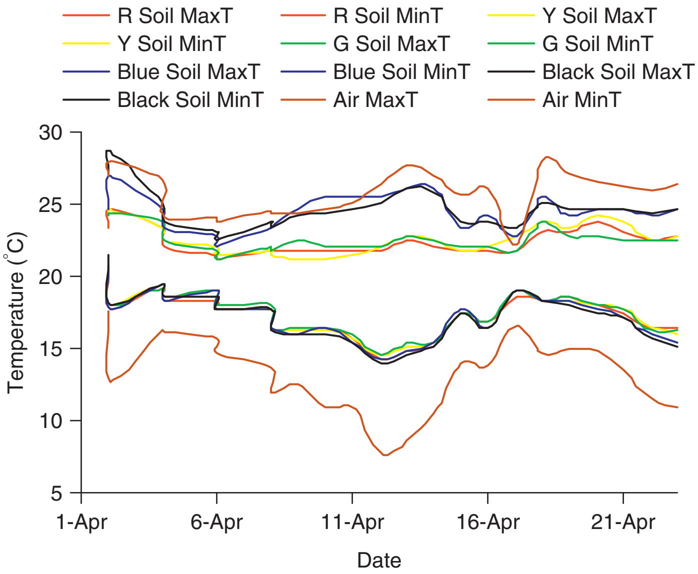


PLATE 6

Measured soil temperature in different colour zones. Ambient temperature recorded during the same period is also shown. AirMaxT = maximum air temperature, AirMinT = minimum air temperature, SoilMaxT = maximum soil temperature, SoilMinT = minimum soil temperature, and the codes for colour correspond to the soil temperature in the NDVI zones identified in the images of Figure 7: R = red, Y = yellow, G = green, B = blue and BL = black (see Fig. 8 of Chapter 19).

Crop Physiology, Modelling and Climate Change: Impact and Adaptation Strategies

Senthold Asseng, Weixing Cao, Weijian Zhang and Fulco Ludwig

1. INTRODUCTION

The global climate is changing, and agriculture will need to adapt to the changes to ensure sustainability and survival. Due to the complexity of agricultural systems and the complex nature of climate change, crop models are often used to understand the impact of climate change on agriculture and to assist in the development of adaptation strategies. Crop models integrate the understanding of crop physiology gathered from many years of laboratory and field experimentations. This chapter describes the application of crop physiology in climate change impact and adaption research through the application of physiology-based crop models. Agriculture will also have to contribute to the mitigation of climate change, with crop models playing a role – mitigation (including aspects related to methane and N oxides) is not considered in this chapter. Likewise, we will not consider other important agricultural issues related to climate change, such as soil carbon, land-use patterns, high-level trophic relations (e.g. crop–insect, crop–pathogen), plant-to-plant competition (crop–weed, plant–plant in mixed cropping or pastures) (e.g. Section 6 in Chapter 17; Betts et al., 2007; Bhattacharyya et al., 2007; Cerri et al., 2007; Chakraborty et al., 1998; Falloon et al., 2007; Kamoni et al., 2007).

This chapter focuses on crop models which consider the various aspects of climate change as drivers (including atmospheric CO_2 and ozone) and capture the main crop physiological functions and other bio-physical aspects of crop–soil–atmosphere systems to address production and natural resource management issues at a paddock level.

2. CLIMATE CHANGE

The global climate has been changing, and further changes are inevitable regardless of efforts to reduce global emissions (IPCC, 2007).

2.1. Realised trends

The climate has changed significantly over the last century. Atmospheric CO_2 has increased from a pre-industrial concentration of 280 to 379 ppm in 2005 (IPCC, 2007). Global temperatures have increased in the past 100 years by an average of 0.74 °C (IPCC, 2007), with minimum temperatures increasing faster than maximum temperatures (Easterling et al., 1997). Some rainfall changes in the past have shown significant differences in agricultural regions. One contrasting example of realised change in climate is the rainfall decline by 20% in the wheat belt of Western Australia over the past decades (Smith, 2004; Cai and Cowan, 2006) versus the rainfall increases by 100–200 mm over the last century in the Argentinean Pampas (Viglizzo et al., 1995). While there is some evidence suggesting that some of the rainfall trends are the result of human influences (Cai and Cowan, 2006), this evidence is less convincing than is the case with the increases in temperature (Nicholls and Collins, 2006). In general, rainfall in the high latitudes of the Northern Hemisphere has increased, while rainfall in eastern Asia, Australia, the Sahel and the Pacific region has declined, with rainfall variability increasing almost everywhere in the world (Dore, 2005).

Many studies have indicated a reduction in the amount of solar radiation reaching the earth's surface (Chameides et al., 1999; Stanhill, 1998; Stanhill and Cohen, 2001; Liepert, 2002; Liepert and Kukla, 1997). This global dimming is probably caused by a combination of increased cloud cover and higher atmospheric concentrations of aerosols (Stanhill and Cohen, 2001) impacting, either positively or negatively, on plant photosynthesis and respiration. The impact of dimming will also be different between the Northern and the Southern Hemisphere, usually due to less direct radiation with more cloud cover in the Northern Hemisphere (Philander et al., 1996). As the total radiation has declined in recent decades, there is an accompanying effect of a higher diffused light fraction (Farquhar and Roderick, 2003).

Other important elements often not considered in climate change impact studies are evaporative demand (ETo), vapour pressure deficit (VPD) and wind, which when considered might overwrite existing assumptions about crop system responses. For instance, ETo is a typical complex variable which will increase or decrease depending on the relative changes of its components (Chattopadhyay and Hulme, 1997; Cohen et al., 2002; Roderick and Farquhar, 2002; 2004). However, in general, less information is available on these variables that makes it difficult to include them in impact studies. Furthermore, in some parts of the world, ozone now frequently increases to concentrations harmful to plants and negatively affecting crop growth (Ewert et al., 1999).

2.2. Future projections

A further accelerating increase of CO_2 concentration in the atmosphere is one of the most certain aspects of global change over the coming decades, and as recent reports indicated, carbon dioxide is accumulating in the atmosphere faster than previously expected (IPCC, 2007). Future atmospheric CO_2 increase will be about 2 ppm year^{-1} (IPCC, 2007). Atmospheric CO_2 is fundamental to the growth and productivity of terrestrial vegetation, as well as critical for the radiative properties of the atmosphere and hence climate. Therefore, the changing atmospheric concentration of CO_2 will have far-reaching effects on agricultural production. Other projected climate changes, such as more severe and frequent droughts (e.g. Hennessy et al., 2008), increasing temperatures and reduced solar radiation and increased ozone concentrations (IPCC, 2007), will affect agricultural systems in particular. Maximum and minimum temperatures are likely to increase at different rates, often with a faster increase in minimum temperature than maximum temperature (Easterling et al., 1997; Vose, 2005; Nicholls, 1997), reducing the diurnal temperature range (Easterling et al., 1997). Nevertheless, projected reduced rainfall with less cloud cover might increase the frost risk frequency in some regions. In addition, an increase in the frequency of extreme high temperatures could result in more severe potential damage to crops than a small average increase over the year (Van Herwaarden et al., 1998; Stone and Nicolas, 1996; Spiertz et al., 2006). Table 1 summarises the main climate changes and their recent and future trends, and the likely general impacts of these changes on crop production.

Future climate change scenarios are usually generated using global circulation models (GCMs). It is important to acknowledge that climate change scenarios produced by GCMs have a large range of uncertainties arising from three sources: (i) the modelled processes within the GCMs themselves, (ii) initial conditions and (iii) future greenhouse gas emissions (IPCC, 2007). Downscaling GCM scenarios to local scales (e.g. paddock) usable for crop simulation modelling adds another dimension of uncertainty (Wilby et al., 2004). However, the reliability of such downscaling can be critical for the outcomes in terms of crop impact. For

Table 1 Summary of Climate Change Factors and General Impact on Crops

Climate Variables		Realised Trends	Projected Trends	General Impact on Crop Growth
CO$_2$		1.4 ppm year^{-1} (379 ppm in 2005)	1.9 ppm year^{-1} (450 ppm by 2050)	Increased net photosynthesis rates, plant biomass production and transpiration use efficiency Reduced transpiration Increased canopy temperature Reduced crop nutrient concentration
Temperature	Max	0.56°C (2005) since 1906		Increased heat stress
	Avg	0.74°C (2005) since 1906	0.02°C year^{-1} (1.3–1.7°C in 2050)	Increased photosynthesis rate, crop growth, phenology
	Min	0.92°C (2005) since 1906		Reduced frost risk
Rainfall		0.11 mm year^{-1}	Variable changes across the globe, in general rainfall increase at high latitude and decrease at low latitude	Positive or negative, depending on the direction and other factors
Solar radiation		Reduced solar radiation and increased diffused light fraction (1365 W m^{-2} in 2005)	Reduced solar radiation and increased diffused light fraction	Photosynthesis could increase in response to increased fraction of diffused light and could decrease in response to reduction in total radiation. The net result depends on the relative changes in each component of the radiation environment and crop type.
Ozone	Troposphere	0.5–2.5% year^{-1} (50 ppb[a] in 2000)	0.5–2.5% year^{-1} (60–100 ppb[a] by 2050)	Increased foliar injury, decreased growth and yield
	Stratosphere	−0.6% year^{-1} (265DU in 2000)	0.1–0.2% year^{-1} (275–286DU by 2050)	Reduced leaf expansion and biomass accumulation

Source: IPCC (2007).

[a] *ppb – parts per billion (10^{-9}).*

example, an increase in average maximum and minimum temperatures during the cool period of a crop season may be positive for growth, while an increase of several degrees in maximum temperature during an already hot period (e.g. during grain filling of temperate cereals) for even a few days might be devastating for a crop (Van Herwaarden et al., 1998). In addition, the change in diurnal temperature range can have a significant impact on crop yields (Lobell, 2007). Such detail in future climate change scenarios is often not available or has significant uncertainty (e.g. Lobell, 2007). These uncertainties and limits in downscaling need to be considered when studying the impact of climate change. One way of dealing with these uncertainties is to use a range of possible future climate change scenarios, rather than a single projection, to assess climate change impact.

Nevertheless, to assess the likely impact of these changes will require well-validated simulation models which consider these changes as drivers and capture the main crop physiological functions and other biophysical aspects of crop–soil–atmosphere systems (Jamieson et al., 2008).

3. CROP RESPONSE TO CLIMATE CHANGE

Different aspects of climate change such as higher atmospheric CO_2 concentration, increasing temperature and changed rainfall (reduced or increased) all have different impacts on plant production and crop yield. In combination, these effects can either increase or reduce plant production, and the net effect of climate change on crop yield depends on the interactions between these factors.

3.1. Elevated atmospheric CO_2 concentrations

Elevated CO_2 has two main effects on crop growth. It increases the intercellular CO_2 concentration, leading to increased net photosynthesis rates, and at the same time reduces stomatal conductance, resulting in reduced transpiration (Farquhar et al., 1978). Many experiments have shown that higher CO_2 increases plant biomass production and yield (Tubiello et al., 2007; Morison, 1985; Drake et al., 1997; Garcia et al., 1998; Yang et al., 2006a; Ma et al., 2007). C_3 species (e.g. wheat, soybean, potatoes, sunflower) and C_4 species (e.g. maize, sorghum, millet) have a different degree in response to elevated CO_2. On average, doubling CO_2 concentrations increases photosynthesis by 30–50% in C_3 species and by 10–25% in C_4 species (Tubiello et al., 2007). Increases in crop yield are lower than the photosynthetic response; however, at 500–550 ppm, grain yields of C_3 crops still increase by 10–20% while C_4 crop yields are up to 13% higher (Tubiello et al., 2007; Yang et al., 2006a). Lobell and Field (2008) summarised the CO_2 effect from a number of open-top chambers and free air carbon dioxide enrichment (FACE) experiments, with 0.07% grain yield increase in wheat per ppm CO_2 increase.

The impact of elevated CO_2 on plant production depends on water and nutrient availability. The highest response to elevated CO_2 is found under water-limiting conditions (Kang et al., 2002; Manderscheid and Weigel, 2007) because higher CO_2 concentrations increase leaf and plant water use efficiency (WUE) (Wu et al., 2004). Low nutrient availability can reduce the yield benefit of elevated CO_2 (Kimball et al., 2001; Yang et al., 2006b). The impact of elevated CO_2 at field and farm levels is probably lower than those estimated in well-controlled experimental conditions, due to production-limiting factors such as low nutrient availability, pests and weeds (Tubiello et al., 2007). An important indirect effect of higher atmospheric CO_2 is reduced plant nutrient concentrations (e.g. Yang et al., 2007a, c) which can result in lower grain quality (Rogers et al., 1996; Kimball et al., 2001; Yang et al., 2007b; Wu et al., 2004).

An indirect effect of elevated atmospheric CO_2 increase will be an increase in canopy temperatures via the reduction in stomatal conductance. There is evidence in both wheat and cotton that selection for improved grain yields in breeding programs has been associated with selection for high stomatal conductance, resulting in 'heat avoidance' through evaporative cooling in hot environments (Section 6.2 in Chapter 15; Amani et al., 1996; Lu et al., 1994; Radin et al., 1994). Reduced stomatal conductance due to atmospheric CO_2 increase might therefore have additional effects on crop growth and development similar to an increase in temperatures.

3.2. Temperature

Temperature affects most plant- and crop-level processes underlying yield determination and hence the complexity of the final yield response. Where certain crops are grown near their limits of maximum temperature tolerance, heat spells can be particularly detrimental (Ferris et al., 1998). Conversely, in cooler regions such as the northeast of China, increased annual mean temperatures since the 1980s have contributed to the reported increase in agriculture production (Yang et al., 2007d).

Higher temperatures can negatively impact plant production indirectly through accelerated phenology (Menzel et al., 2006; Sadras and Monzon, 2006; Section 3.1 in Chapter 12), with less time for accumulating biomass

(Amthor, 2001; Asseng et al., 2002). Menzel et al. (2006) analysed phenological data of 125,000 time series of 542 plants in 21 European countries. For the period 1971–2000, they found that 78% of all leafing, flowering and fruiting events advanced. Sadras and Monzon (2006) modelled in detail the effect of realised changes in temperature on the phenological development of wheat, and found earlier flowering, but unexpectedly, no changes in the duration from flowering to maturity due to the shift of flowering to 'cooler' parts of the season.

As a result of climate change, not only average temperature will increase but extreme temperatures will also occur more often than expected, based on the average increase (IPCC, 2007). These extreme temperature events can have large negative impacts on plant growth and yield as shown for wheat by Van Herwaarden et al. (1998). In wheat, temperature increases around anthesis can reduce potential grain weight and therefore yield (Calderini et al., 2001). Higher average temperatures can reduce frost damage due to a reduced frequency of frost (Baethgen et al., 2003). However, indirect effects of temperature may lead to the paradox of increasing frost risk in some systems (Sadras and Monzon, 2006; Belanger et al., 2002). Sadras and Monzon (2006) showed that shifting of flowering to 'cooler' parts of the season due to accelerated phenology with higher temperatures could potentially increase the risk of frost at flowering. Belanger et al. (2002) indicated that increased temperature could reduce cold hardening in autumn and protective snow cover for forage crops during the cold period in continental climates, hence increasing the exposure of plants to killing frosts, soil heaving and ice encasements. In cool climates and at higher altitudes, higher temperatures can increase the length of the potential growing season.

The impact of increasing temperatures can vary widely between crop species. The optimum temperature for leaf photosynthesis and plant growth is higher for C_4 plants than for C_3 plants (Goudriaan and Van Laar, 1994). Species with a high base temperature for crop emergence, such as maize, sorghum, millet, sunflower and some of the legumes such as mung bean and cowpea (Angus et al., 1981), could benefit from increasing temperatures in cool regions. Most of the small-grain cereals, legumes such as field pea and lentil, linseed and oilseed *Brassica* spp. with a low base temperature (Angus et al., 1981) could result in an advanced phenology with increased temperatures. For example, Sadras and Monzon (2006) showed that the modelled date of wheat flowering in different environments is advanced about seven days per degree increase in temperature.

When maximum and minimum temperatures change differently with climate change (Nicholls, 1997), the changes in diurnal temperature range can impact differently on various crops. Lobell (2007) analysed the historical yield data of wheat, rice and maize from the leading global producers and showed that an increase in diurnal temperature range was associated with reduced yields of rice and maize in several agricultural regions worldwide. This reflects the non-linear response of yield to temperature, which likely results from greater heat stress during hot days (Lobell, 2007). Peng et al. (2004a) suggested that rice yields declined by 15% per degree Celsius in minimum temperature due to wasteful night respiration, but this interpretation was challenged in subsequent studies (Sheehy et al., 2006a, b).

An indirect effect of global warming can be a higher plant water demand due to increased transpiration at higher temperatures, which can potentially reduce plant production (Lawlor and Mitchell, 2000; Peng et al., 2004b). In dry-land agriculture, this can directly limit plant growth, while in irrigated systems, increased temperatures could result in higher irrigation water demands in combination with increased losses through evaporation. However, if future temperature changes are similar to the changes in the last 50 years, during which global minimum temperatures have generally increased twice as fast as maximum temperatures, resulting in a reduced diurnal temperature range (Folland et al., 2001), the impact of increasing temperatures on VPD and therefore on atmospheric evapotranspiration would be very small (Roderick and Farquhar, 2002). In addition, higher atmospheric CO_2 concentrations can partly compensate for the increased water demands due to higher temperatures, through a lower stomatal conductance that reduces transpiration (Kimball et al., 1995; Garcia et al., 1998; Wall, 2001). Reduced leaf transpiration as a consequence of higher CO_2 will also increase leaf temperature, with an increased chance of plant damage due to heat stress. Plants grown at higher atmospheric CO_2 tend to have a higher leaf water potential which results in reduced drought stress (Wall, 2001).

Temperature changes can also affect yield quality as shown for the grain protein content (Spiertz and Ellen, 1977; Triboi et al., 2003; Zhao et al., 2008) and the dough quality of wheat (Randall and Moss, 1990; Wrigley et al., 1994). For some crops, night temperatures are critical for grain quality, as shown for fatty acid composition in sunflower (Izquierdo et al., 2002). Chapter 16 deals in detail with the environmental, genetic and G × E drivers of the quality of grains, with emphasis on oil and protein.

3.3. Rainfall and rainfall variability

Global warming is likely to change precipitation amounts and patterns differently across the globe. Total annual rainfall tends to increase at higher latitudes and near the equator, while rainfall in the sub-tropics is likely to decline and become more variable (Giorgi and Bi, 2005). Changing rainfall amounts can have both negative and positive impacts on agricultural production. For example, in (semi-)arid environments, higher rainfall could increase growth, whereas less rainfall could further limit plant production. In contrast, in high-rainfall zones, too much rainfall can result in soil waterlogging, which damages crop growth (Dracup et al., 1993; Jiang et al., 2008) or results in nutrient leaching in sandy soils (Anderson et al., 1998), and reduced rainfall on these soils could limit the negative impacts of waterlogging and nutrient leaching.

Not only the total rainfall amount but also the rainfall distribution plays an important role for determining crop yields. Rainfall around anthesis ensuring water supply during the grain set and grain-filling periods is particularly critical for yield in annual crops (Passioura, 1977; Sadras and Connor, 1991; Fischer, 1979). Changing future in-season rainfall distribution will therefore have an impact on crop growth and yield. Balancing growth and water use before and after anthesis is one of the tools to manage uneven rainfall distribution and scarce irrigation water (Section 3 in Chapter 6). Management options to change the seasonal water use of crops include sowing time, nutrient management, plant density and cultivar choice (Chapters 2 and 3; Passioura, 1977; Sadras and Connor, 1991; Fischer, 1979).

Another specific aspect of future rainfall change is increased rainfall variability through an increase in extreme events. Extreme events could include a higher drought frequency (Hennessy et al., 2008) with long-term effects on farm variability that could reduce crop production and yields below what is expected, based on the average climate change (Easterling et al., 2007; IPCC, 2007). Particularly critical are changes in rainfall intensity and the distribution of small versus large rainfall events, which can have significant consequences for crop production via the impact on soil infiltration depth, run-off, deep drainage, soil mineralisation and crop WUE (Sadras, 2002; Sadras et al., 2003; Sadras and Rodriguez, 2007).

3.4. Solar radiation

Reduction in solar radiation can potentially have a considerable negative impact on agricultural production (Stanhill and Cohen, 2001), which can be partially or completely compensated by the associated increase in the diffused light fraction (Farquhar and Roderick, 2003). Plant production is primarily driven by sunlight, as plant cells transform solar energy into sugars. Hence, a reduction in solar radiation can potentially reduce photosynthesis and growth. However, photosynthesis is often limited by nutrient and/or water availability. Lower solar radiation also reduces potential evaporation (Roderick and Farquhar, 2002). In water-limited environments, this can increase plant-available water and thus increase plant production. Reduced evapotranspiration can also increase drainage and nutrient leaching, which can have large negative ecosystem impacts.

A reduction in solar radiation is usually accompanied by an increase in the diffused light fraction (Farquhar and Roderick, 2003). An expected decrease in photosynthesis with less radiation assumes light-saturated photosynthesis is critical for photosynthesis, but this could be overridden by the canopy light distribution that could be favoured by dimming (Gu et al., 2003; Farquhar and Roderick, 2003; Rodriguez and Sadras, 2007; Sinclair et al., 1992). Section 6.1 in Chapter 7 further discusses the effect of the radiation evironment, including diffuse radiation, on crop photosynthesis.

3.5. Ozone

Ozone (O_3) is a form of oxygen that is an atmospheric pollutant at ground level. Most of the O_3 in the atmosphere (about 90%) is in the stratosphere, the remaining being in the troposphere. The ozone in the troposphere and the stratosphere has different effects on life on the earth, depending on its location. Stratospheric ozone plays a beneficial role by absorbing solar ultraviolet radiation (UV-B) from reaching the earth's surface. Increased levels of UV-B have been measured with a general erosion of the stratospheric ozone layer in the past decades (World Meteorological Organization (WMO), 1995). These increased levels of UV-B have shown to reduce leaf expansion and biomass accumulation in plants (Ballare et al., 1996) and could impact on plant–herbivore interactions by increasing plant resistance to insects (Izaguirre et al., 2003).

Ozone is a strong oxidiser; therefore ozone closer to the earth's surface is potentially destructive to plants. In crops, ozone can create reactive molecules that destroy rubisco, an enzyme crucial for photosynthesis, and makes crop leaves age faster (Giles, 2005). In general, elevated CO_2 can stimulate crop growth, but increasing O_3 levels at ambient CO_2 results in a decline in crop yield in many species (Fuhrer and Booker, 2003). This negative effect results from a limitation of photosynthetic C assimilation due to a reduction in the activity and amount of rubisco (Lehnherr et al., 1987), associated with accelerated leaf senescence (Grandjean and Fuhrer, 1989). Moreover, ozone impairs source-to-sink translocation of photosynthates (Grantz and Yang, 2000). In addition to its effect on crop yield, O_3 affects yield quality. For example, Pleijel et al. (1999) reported that grain N concentration generally increased with increasing O_3, leading to a better baking quality of the flour in spring wheat. However, increasing O_3 had a negative impact on the tuber quality of potato (Vorne et al., 2002). In general, elevated O_3 has negative effects on crop growth and influences the magnitude of the yield enhancement by elevated CO_2.

3.6. Combined impact of climate change

Changes in temperature, rainfall and CO_2 concentrations do not act independently but interact with each other. To develop climate change adaptation strategies so that crop production can remain stable in a changing climate, it is important to understand the interactions between different aspects of climate change. This is shown in few field experiments for CO_2 and water supply interactions with wheat (Kimball et al., 1995), and CO_2 and temperature interactions with a grass-legume pasture (Lilley et al., 2001). Wheeler et al. (1996) showed that a positive yield effect in wheat from 700 ppm CO_2 in the UK could be offset by an increase in mean seasonal temperatures of 1–1.8 °C. It is important to understand the interactions before developing climate change adaptation strategies because, for example, adaptations to higher temperatures may be different from adapting to reduced rainfall (Tubiello et al., 2007; Ludwig and Asseng, 2009).

4. CROP MODELS FOR CLIMATE CHANGE

Chapter 10 outlines common modelling approaches and fundamental components of crop models with emphasis on genetic, environmental, management and G × E × M drivers of grain yield. With a deeper and narrower focus, other chapters discuss modelling approaches for capture and efficiency in the use of radiation (Chapter 7) and aspects of grain quality (Chapter 16). Here we deal with modelling approaches emphasising grain yield and climate change.

Crop modelling is one of the approaches of combining the complexity of climate change with the complexity of physiological functions and other bio-physical aspects of crop–soil–atmosphere systems. The first crop simulation models were developed in the 1980s and used to simulate wheat growth, using conservative crop physiological functions. These models were ARCWHEAT1 (Porter, 1984; Weir et al., 1984), the Dutch models SUCROS (van Laar et al., 1992) and SWHEAT (van Keulen and Seligman, 1987) and five crop models from the ARS Wheat Yield Project, of which the CERES-Wheat (Ritchie and Otter, 1985) and WINTER WHEAT (Baker et al., 1985) were the most prominent. One common feature of these models was that all operated on a daily time step, either approximating or aggregating processes that operate on shorter time steps (Jamieson et al., 2008). The models differed in detail in which physiological processes were aggregated and which production constraints addressed. The widely used Australian APSIM-Nwheat model (Keating et al., 2001), was initially largely based on CERES-Wheat. Substantial changes were then made to the model to improve its performance and to account for a wider range of growing conditions (Keating et al., 2001; Asseng and Van Herwaarden, 2003; Asseng et al., 2001a, b; Asseng et al., 2002). There are a number of other wheat models that have been developed. Some of these are summarised in a GCTE Focus 3, 1996 report and a special issue of the *European Journal of Agronomy* on crop models (Van Ittersum and Donatelli, 2003). Models have also been developed for other crops, for example, for rice (Confalonieri and Bocchi, 2005; Kropff et al., 1993), maize (Jones and Kiniry, 1986), soybean (Sau et al., 1999), velvet bean (Hartkamp et al., 2002), chickpea (Robertson et al., 2002; Soltani et al., 2006), canola (Farre et al., 2002), sugar cane (Keating et al., 1999), potato (Peralta and Stockle, 2002), mung bean, peanut (Robertson et al., 2002), lupin (Fernández et al., 1996; Farre et al., 2004), lucerne (Dolling et al., 2005), sunflower (Villalobos et al., 1996) and cotton (Milroy et al., 2004), with some of these and other crops being described with the same modelling framework (e.g. Jones et al., 2003; Stockle et al., 2003; Keating et al., 2003).

Most crop models simulate the dynamics of crop development, growth, water and nitrogen in an atmosphere–crop–soil system, driven by daily weather information on rainfall, maximum and minimum temperatures and solar radiation. Pests, diseases, frost and heat damage, phosphorus nutrition, biological effects of rotations and lodging that may affect crops are usually not considered (Section 3 in Chapter 21 revises these and other modelling gaps). These models calculate a yield for a specific environment, as the maximum yield reached by a crop in a given environment is limited only by temperature, solar radiation, day-length (Evans and Fischer, 1999), and include water and nitrogen supply. This maximum yield is also called the resource plateau by Sinclair (1997). Thus, the maximum yield will be higher in high-radiation and long-season environments than in water-limited and short-season growing conditions. Under the latter growing conditions, high yields are not necessarily linked with higher nitrogen input, due to the interaction between N-induced growth and its effect on water use and water availability for grain filling (Fischer, 1979).

4.1. Modelling CO_2 effect

Elevated CO_2 has two main effects on crop growth. It increases the intercellular CO_2 concentration, leading to increased net photosynthesis rates, and at the same time reduces stomatal conductance and transpiration per unit leaf area (Farquhar et al., 1978). While the increased net photosynthesis rates directly affect radiation use efficiency (RUE), the increased net photosynthesis under reduced crop transpiration increases transpiration efficiency (TE). To include these effects in crop models (e.g. APSIM), a relationship as described by Reyenga et al. (1999) has been considered.

$$\Phi_p = \frac{(C_e - \Gamma)(C_{350} + 2\Gamma)}{(C_e + 2\Gamma)(C_{350} - \Gamma)} \qquad (1)$$

where Φ_p is the ratio of the light-limited photosynthetic response calculated according to Goudriaan et al. (1985) at the enhanced CO_2 concentration compared with the current level (350 ppm; assumed to be the CO_2 concentration when the model was developed) for scaling RUE. C_{350} is the CO_2 concentration when most models were initially developed (=350 ppm), and C_e is elevated CO_2 concentration (ppm). The temperature-dependent CO_2 compensation point (Γ) is calculated as $\Gamma = (163 - T)/(5 - 0.1T)$, where T = temperature (°C), according to Bykov et al. (1981).

TE (=shoot biomass per unit crop transpiration) is often linearly scaled by a factor that increases linearly from 1 to 1.37 when the CO_2 concentration increases from 350 to 700 ppm, according to Gifford and Morison (1993). This scaling of TE captures, though not explicitly, the effects of elevated CO_2 on the ratio between internal and external CO_2 concentrations.

Other models (e.g. CERES and EPIC) employ a constant multiplier (lower for C_4 than C_3 crops) for daily total crop production under elevated CO_2 (Tubiello et al., 2007). Tubiello and Ewert (2002) give a comprehensive summary of modelling approaches for simulating elevated CO_2.

4.2. Modelling temperature effect

Temperature in many crop models causes developmental rates to vary, and thermal time is commonly used to predict development (Cao and Moss, 1997; Jamieson et al., 2008). In the context of the developmental model, thermal time is the time integral of the temperature response function based on daily maximum and minimum air temperatures. Temperature response functions used in crop models include segmented linear models with base, optimum and maximum temperatures (Weir et al., 1984) and various curvilinear versions that cover similar temperature ranges (Jame et al., 1999; Streck et al., 2003; Xue et al., 2004). Some crop models also include vernalisation (a crop- and cultivar-specific requirement for cold-temperature accumulation) to slow the accumulation of developmental time (e.g. CERES-Wheat, Ritchie and Otter, 1985; Cao and Moss, 1997). Chapter 12 discusses in detail the genetic and environmental controls of crop development.

Dry matter production in most crop models is a function of RUE, solar radiation, leaf area index (LAI), a temperature response curve, water and nitrogen stress (Jamieson et al., 2008). Thus changing temperatures would have accelerated growth rate and biomass accumulation in crop plants. In some crop models, heat stress is partially considered, with maximum temperatures above 34 °C accelerating senescence and hence enhancing maturity (Keating et al., 2001). If minimum temperature increases faster than maximum temperature (Easterling et al., 1997), the simulated VPD in some crop models (e.g. Keating et al., 2001) will result in no changes in evaporation demand in such a simulation, as observed by Roderick and Farquhar (2002). If minimum and maximum temperatures increase at a similar rate as reported for a location in Germany by Wessolek and Asseng (2006), such temperature change would also lead to an increase in the ETo and higher water use. In general, most models ignore the impact of changes in the diurnal temperature range on grain yields (Lobell, 2007).

Temperature effects on yield quality are considered in some models, for example, for wheat grain protein content (Asseng and Milroy, 2006) and different wheat grain protein fractions (Martre et al., 2006). Early models for grain legumes and oilseed crops that consider oil content did not include temperature as a factor (Robertson et al., 2002), but advances in this area resulted in algorithms, modules and whole models where oil concentration and the profile of fatty acids account for temperature (Section 3 in Chapter 16).

4.3. Modelling rainfall and rainfall variability effect

The state of water in the soil on any particular day depends on the state of the previous day, and any additions (precipitation and irrigation) and subtractions (evaporation, transpiration, drainage, run-off) that occur throughout the day. Methods for estimating daily evapotranspiration as combinations of diffusion and energy balance equations have been in existence since the late 1940s (Penman, 1948), with slightly more (Monteith, 1965) or less (Priestley and Taylor, 1972) complex variations developed thereafter (Jamieson et al., 2008). These equations are used to estimate the upper limit of evapotranspiration demand (potential evapotranspiration). Many simulation models use variations of the Ritchie (1972) model that allows both plant and soil factors to reduce actual evapotranspiration below the potential. Plant factors are mostly related to canopy size and how it limits the interception of energy to drive the transpiration process. Soil factors are considered in crop models when the rate that the soil can supply water is less than the demand. Evapotranspiration will proceed at a rate limited by either the available energy or water transport through the system. Differences among models are mainly about how they calculate constrains to the rate of water uptake, and how they then calculate and apply indices of stress to reduce canopy expansion, biomass partitioning and growth, and account for temporary reductions in water use, such as canopy folding, wilting or stomatal closure (Jamieson et al., 2008).

Water shortage stress is generally simulated by using a stress index that can be the ratio of supply rate to demand rate, constrained to a maximum of 1 (Ritchie and Otter, 1985; Porter, 1993) or a fraction of available soil water in the rooted soil (Stapper, 1984; Amir and Sinclair, 1991; Keating et al., 2001). The stress index is applied in various ways to reduce biomass production by limiting leaf area expansion or accelerating leaf senescence, and to reduce the photosynthetic rate or RUE (Hu et al., 2004).

4.4. Modelling solar radiation effect

There have been two main approaches in simulating RUE. One group of models (AFRCWHEAT2, SWHEAT, SUCROS2) calculates the daily growth rate from photosynthesis equations, integrated over a layered canopy at sub-day intervals. The other group uses an aggregated RUE approach based on the analysis of Monteith (1977). These models include CERES-Wheat and its derivatives such as APSIM-Nwheat (Keating et al., 2001), the model of Amir and Sinclair (1991) and Sinclair and Amir (1992), and Sirius (Jamieson et al., 1998a, b).

As diffused light can be an important component for determining photosynthesis (Sinclair et al., 1992), some models consider the fraction of diffused light, for example CERES (Ritchie et al., 1985) and the APSIM-Wheat model (Keating et al., 2001), while other models ignore it (e.g. Robertson et al., 2002).

Day-length is often used for modelling photoperiod effects on phenology (e.g. CERES and APSIM models).

4.5. Modelling ozone effect

Ewert et al. (1999) extended the AFRCWHEAT model (Porter, 1993) and the more detailed LINTUL model (Spitters and Schapendonk, 1990), to account for the effects of ozone. Both models assumed that ozone damage is caused by ozone uptake. In AFRCWHEAT, ozone reduces the light saturation rate of leaf photosynthesis and induces a short-term response that is reversible or not depending on the leaf age. In LINTUL, ozone decreases the rubisco concentration and increases the costs of detoxification and repair processes. In both models, the plant response to ozone depends on plant development (Ewert et al., 1999).

4.6. Model validation

Simulation models have been tested against measured data under various growing conditions (e.g. for wheat models: Ritchie et al., 1985; Otter-Nacke et al., 1986; Savin et al., 1994; Toure et al., 1994; O'Leary and Connor, 1998; Keating et al., 1995; Probert et al., 1995, 1997; Jamieson et al., 1998a, b; Asseng et al., 1998a, b, 2001a, b). Figure 1 illustrates one example of model validation as simulated grain yields versus observed grain yields for a wide range of management options and growing environments.

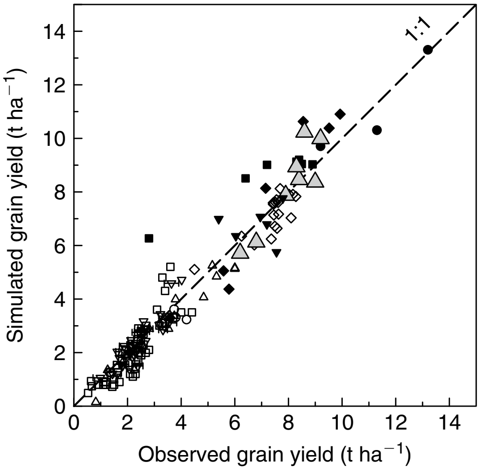


FIGURE 1

Simulated versus observed wheat grain yield for Western Australia data set I (▽); Western Australia data set II (□); New South Wales (○); Gatton, Queensland (△); Lincoln, New Zealand (◆); Xiangride, China (●); FACE experiment, Arizona, USA (large ▲); Obregon, Mexico (▼); Polder and Wageningen, The Netherlands (◇); and plant density experiment, The Netherlands (observed after Darwinkel, 1978) (■). (Source: Asseng, 2004.)

Several models have been tested under climate change conditions including elevated atmospheric CO_2 with data from the Maricopa FACE experiment in Arizona, USA (e.g. Grant et al., 1995; Kartschall et al., 1995; Tubiello et al., 1999a; Jamieson et al., 2000; Grossman-Clarke et al., 2001; Asseng et al., 2004) (Figure 1) and experiments with elevated CO_2 in open-top chambers (Ewert et al., 1999; Rodriguez et al., 2001). While most of this work concentrated on the elevated CO_2 aspect of climate change, a few models have been tested with different intensities and durations of water stress periods (e.g. Jamieson et al., 1998a, b; Asseng et al., 2004) and one model has in addition been compared with field data under severe terminal water limitations and rising air temperatures (Asseng et al., 2004).

Some specific aspects of crop models, for example the approach of modelling elevated CO_2 impact on crop growth, have been evaluated independently, by comparing the calculated RUE and TE using the Reyenga et al. (1999) functions with measured RUE and measured TE (Asseng et al., 2004). Linear regression of observed versus calculated RUE with intercept set to zero indicated no significant bias ($y = 1.022x$; Mallows C_P statistic = 1). For the FACE experiment conducted at Maricopa, enhancement of ambient concentration of CO_2 by 200 ppm increased TE by 26% for the Dry treatment and 25% for the Wet treatment in 1993–1994 whereas according to the study by Reyenga et al. (1999) for a CO_2 level of 550 ppm the increase in TE function was 21% (Asseng et al., 2004). In addition, TE estimated using the physiological model of Farquhar and Caemmerer (1982) (assuming an average daily reduction of stomatal conductance with elevated CO_2) was similar to the TE under elevated CO_2 estimated with the approach of Reyenga et al. (1999), lending further support to this widely applied approach.

Ewert et al. (1999) tested the AFRCWHEAT and the LINTUL models with wheat growth data from open-top chambers with 2× ambient CO_2 and 1.5× ambient ozone. They reported underestimations of the CO_2 effect on biomass with AFRCWHEAT, but overestimations of the CO_2 effect on biomass with LINTUL. Both models closely predicted the biomass production with increased ozone, but the LINTUL model was less accurate for LAI and intercepted radiation. Both models simulated well the observed interaction effects of CO_2 and ozone on biomass (Ewert et al., 1999).

Long et al. (2006) argued that current modelling efforts have overestimated the impact of increasing CO_2 on future crop yields, because crop models used in these studies were parameterised with data obtained from earlier 'enclosure studies' and not from more sophisticated FACE experiments. Although these models are parameterised with data obtained from earlier 'enclosure studies', the same models have also been successfully tested with data from FACE experiments (e.g. Grant et al., 1995; Kartschall et al., 1995; Tubiello et al., 1999a; Jamieson et al., 2000; Grossman-Clarke et al., 2001; Asseng et al., 2004), as both experimental methods are shown to be consistent (Tubiello et al., 2007; Ewert et al., 2007; Ziska and Bunce, 2007).

5. IMPACTS OF CLIMATE CHANGE ON CROP PRODUCTION

Climate change can have a considerable impact on agricultural production, especially if the amount and distribution of rainfall changes. Rising temperatures and elevated atmospheric CO_2 concentrations (Van Ittersum et al., 2003; Amthor, 2001), increases in ozone concentration (Ewert et al., 1999) and reduced radiation reaching the earth (Stanhill and Cohen, 2001) will affect agricultural production. Elevated atmospheric CO_2 almost always increases plant production (Amthor, 2001; Poorter and Perez-Soba, 2001). Higher temperatures can potentially increase or decrease grain yields (Van Ittersum et al., 2003; Peng et al., 2004b).

5.1. Past trends

An analysis of trends in on-farm rice and wheat yields in the Indo-Gangetic Plains, starting from the 1980s using CERES models, revealed that reduced radiation and increased minimum temperatures have caused a decline in the simulated potential yields in several places (Pathak et al., 2003).

Since the mid-1970s a significant decline in winter rainfall has been experienced in the Mediterranean and the semi-arid region of Western Australia (Smith et al., 2000). This decline in rainfall was associated with, and probably caused by, a large-scale change in global atmospheric circulation during the mid-1970s with anthropogenic forcing contributing to about 50% of the observed rainfall decline (Cai and Cowan, 2006). The drop in rainfall by up to 20% has had significant negative impacts on the water sector in Western Australia. For example the water inflow into dams surrounding Perth has declined by about 50% (Power, et al., 2005). While the impact of the drying trend on the water sector is very clear, the impacts on the agricultural sector are less well understood. As most of the agriculture in Western Australia is rainfall limited, it has been assumed that a drying trend would also have a negative impact on crop production. However, despite low rainfall, observed farmers' average wheat grain yield in the Western Australian wheat belt increased from 1.0 t ha^{-1} in 1970 to about 1.7 t ha^{-1} in 2000 (Turner and Asseng, 2005).

When examining trends in historic grain yield data (e.g. Hamblin and Kyneur, 1993), it is difficult to separate the effect of climate change on crop production from the effects of changes in land use, crop varieties and crop management (Magrin et al., 2005). Ludwig et al. (2009) used the APSIM model in combination with historic climate data to study the impact of past rainfall reductions on wheat yield, deep drainage and nitrate leaching against a constant background of cultivars and management. Unexpectedly, this study revealed that despite the large decline in rainfall, simulated yields based on the actual weather data did not fall. At the same time, simulated drainage and nitrogen leaching decreased by up to 95%. These results were due to rainfall reductions mainly occurring in June and July, a period when rainfall often exceeds crop demand, and large amounts of water are lost by deep drainage. These simulated findings will have significant implications for estimating future climate change impacts in this region, with rainfall reduction causing non-proportional impacts on production and externalities like deep drainage where proportionality is often presumed (Ludwig et al., 2009) (Figure 2).

In Sardinia, Italy, also a Mediterranean environment, a similar decrease in winter rainfall over the last 20 years translated into a reduced simulated occurrence of waterlogging, which improved yield on waterlogged soils (Bassu et al., 2009). This decrease in winter rainfall was also associated with a slight increase in spring rainfall, contributing to additional yield increase in this environment (Bassu et al., 2009).

An opposite rainfall trend has been observed in Argentina. Annual rainfall in the Argentinean Pampas has increased by 100–200 mm over the last century, with statistically significant rainfall increases in the months of December and January (Viglizzo et al., 1995). Based on a simulation study using the CERES-type models,

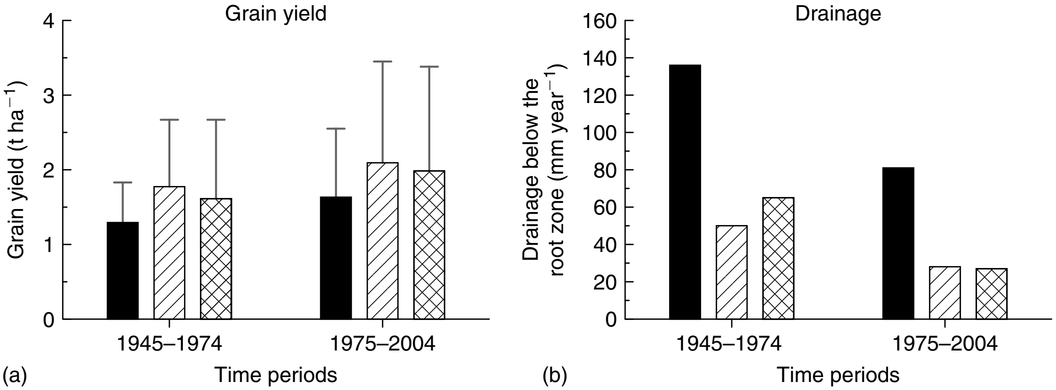


FIGURE 2

Simulated average (a) wheat grain yield and (b) annual deep drainage below potential root depth for sand (filled bars), loamy sand (diagonal lines) and duplex soil (cross bars) at Mingenew, Western Australia. (Source: Ludwig et al., 2009.)

summer crops like soybean have mostly benefited, with a 28% increased yield from the increased summer rainfall in the period 1971–1999, when compared to the period 1950–1970 in the current cropped region (Magrin et al., 2005). In another study with CERES-Wheat and CROPGRO-Soybean, Monzon et al. (2007) showed that the actual increase in average October–December temperature between 1971 and 2003 ($0.038\,°\mathrm{C\,year^{-1}}$) accelerated simulated wheat development and advanced harvest ($0.15\,\mathrm{days\,year^{-1}}$) with no impact on yield. This allowed for earlier sowing of double-cropped soybean, which together with more favourable temperature increased simulated soybean yield ($26.2\,\mathrm{kg\,ha^{-1}\,year^{-1}}$). Chapter 3 (Sections 3.2.2 and 5.2) highlights the significance of anticipating sowing for double-cropped soybean in these farming systems. Simulations using APSIM indicated that the additional rainfall in the Pampas of Argentina has increased the attainable yield of wheat grown over winter in the currently cropped region, but less than expected from the large amount of additional rainfall. The higher attainable yield from additional rainfall would allow extension of wheat cropping into currently non-cropped areas, where the attainable wheat yield increased on average from 1 to $2\,\mathrm{t\,ha^{-1}}$ over the last 70 years. However, the poor water-holding capacity of the sandy soils that dominate the region outside the current cropping area limits the potential use of most of the increased summer rainfall. Nevertheless, the higher yield potential indicates that the region is suitable for future cropping (Asseng et al., 2009).

These simulation studies highlighted that yield is often non-linearly related to climate change. Also the complexity of the change, the rainfall distribution, soil water storage and crop water use, and system aspects which are usually incorporated into a crop model, should be considered for a realistic assessment of climate change impacts.

5.2. Future scenarios

To generate future impact scenarios for agriculture, crop physiology often imbedded in models is linked with climate projections. However, the climate change information required for such impact studies is of a spatial scale much finer than that provided by GCMs with resolutions of hundreds of kilometres. The most straightforward means of obtaining projections of higher spatial resolution is to apply coarse-scale change projections to a high resolution observed baseline – the 'change factor method' (Wilby et al., 2004). However, this approach does not consider any potential changes in rainfall distribution or intensity. Fine resolution climate information can also be obtained via more sophisticated statistical downscaling, assuming that the present day climate is valid under the different forcing conditions of possible future climate. It is also important to recognise that increased precision of downscaling does not necessarily translate into increased confidence in regional projections. Statistical downscaling is usually based on a single GCM output, while comprehensive impact studies must be founded on multiple GCM outputs to overcome some of the uncertainties associated with each individual GCM. The reliability of future rainfall scenarios in terms of rainfall distribution and intensity will be particularly critical for understanding the impact of future rainfall changes on crop production (Sadras and Rodriguez, 2007; Mearns et al., 1997). Other issues with statistical downscaling from GCMs that are not yet resolved, and which also apply to the change factor method, include the handling of extreme events and potential local feedbacks, for example by vegetation (Wilby et al., 2004).

In studies of climate change impact at global and regional scales, GCM outputs have been directly linked with physiological knowledge (e.g. relative yield response to elevated CO_2) (Olesen and Bindi, 2002; Pielke et al., 2007) or crop models (e.g. CERES, EPIC) that are based on physiology (Wu et al., 2007; Tao et al., 2008). Physiology-based crop models have been extensively used to analyse the impact of climate change on regional or local production of wheat (e.g. Seligman and Sinclair, 1995; Mearns et al., 1996; Wolf et al., 1996; Reyenga et al., 1999; Reyenga et al., 2001; Weiss et al., 2003; Aggarwal, 2003; Richter and Semenov, 2005; Luo et al., 2005; Wessolek and Asseng, 2006; Asseng et al., 2004; Anwar et al., 2007) and other crops (e.g. Aggarwal and Mall, 2002; Mall et al., 2004; Tsvetsinskaya et al., 2003; Chipanshi et al., 2003; Holden et al., 2003; Reilly et al., 2003; Trnka et al., 2004; Mall et al., 2007; Olesen et al., 2007; Abraha and Savage, 2006). Jamieson and Cloughley (2001) used the Sirius model (Jamieson et al., 1998a, b) to assess the impact of several climate change scenarios (un-specified temperature and CO_2 increase) on both irrigated and dry-land wheat production in New Zealand through to 2100. The simulations indicated that although maturity would be advanced by 10–20 days, the associated CO_2 fertilisation would still raise yields by 15–30% on a base yield of $10\,t\,ha^{-1}$.

Wheat crop models were amongst the first to show the importance of the impact of climate variability and extreme events on production (Semenov and Porter, 1995; Porter and Semenov, 1999) and showed that changes in temporal rainfall distribution may be part of the cause of increased risk of crop failure (Porter and Semenov, 1999).

Simulations in India showed a general increase in rice yields in a scenario including 400–750 ppm CO_2, 1–5 °C temperature increase and irrigated crops with no change in rainfall (Aggarwal and Mall, 2002) and a decrease or increase, depending on the region and scenario, in soybean yields (Mall et al., 2004). In Botswana, Chipanshi et al. (2003) modelled a scenario assuming doubling CO_2, 2–3 °C increase in temperature, and increase or decline in rainfall depending on the location and month. Simulations with CERES-Wheat and CERES-Maize indicated a reduced growing season and yield declines from 4 to 30% depending on the soil type. For Africa and Latin America, by 2055 (based on IPCC 2001, non-specific atmospheric CO_2, temperature and rainfall changes), maize production is predicted to decline by an average of 10%, based on a simulation study with CERES-Maize but with large regional and soil type dependent variations, and therefore large variations in potential negative socio-economic consequences across these continents (Jones and Thornton, 2003).

Global warming can lead to an increase in extreme temperature events that are extreme in a physiological sense (Porter and Semenov, 2005). However, the risk of extreme high temperature might also be reduced through accelerated phenology shifting inherently sensitive stages (e.g. flowering) to cooler months (Sadras and Monzon, 2006). Baenziger et al. (2004) studied extreme temperature events by examining for late frosts occurring after spike formation, which can be a yield-limiting consequence of global warming.

The apparent yield-enhancing effect of elevated atmospheric CO_2 might not come without additional costs. Jamieson et al. (2000), analysing and extending work from the Maricopa FACE wheat study (Kimball et al., 1999), showed that extra N fertiliser was required to realise the potential yield gains from elevated atmospheric CO_2 concentrations (550 ppm), although minimum leaf N concentrations were slightly less under elevated atmospheric CO_2 (Sinclair et al., 2000). Hungate et al. (2002) have shown that ecosystem demand for N will increase with increasing atmospheric CO_2 concentrations. As plant N nutrition can become yield limiting under elevated CO_2, simulating feedbacks through N cycling will be critical for modelling elevated CO_2 impact assessments on crop production. Nutrients other than N, often not considered in crop models, can also become yield limiting under elevated CO_2. Models lacking these feedbacks are likely to overestimate the yield-enhancing impact of elevated CO_2 (Hungate et al., 2002).

Some crop modelling studies simulated the individual effects of higher temperatures and CO_2 by artificially constructing climate change scenarios (Wang et al., 1992; Van Ittersum et al., 2003). Ludwig and Asseng (2006) simulated individual effects of increased temperature (2–6 °C), increased CO_2 (525, 700 ppm) and reduced rainfall (by 10–60%) on wheat in Australia with specific focus on how different aspects of climate change interact with each other. In a simulation study by Van Ittersum et al. (2003) in the Mediterranean environment of Western Australia, elevated CO_2 concentration (400–700 ppm) increased wheat yields, particularly if nitrogen fertilisation was sufficient and conditions were relatively dry. This and other simulations showed that higher temperatures could increase plant production (e.g. Van Ittersum et al., 2003; Ludwig and Asseng, 2006). In Mediterranean environments, where crops are grown in winter, plant growth is often limited by low temperatures, and global warming could potentially have a positive effect on crop yields (Van Ittersum et al., 2003; Ludwig and Asseng, 2006). It has been shown that higher temperatures had non-linear effects, with initial (up to 3 °C) benefits for better water-holding clay soils, and not for poor water-holding sandy soils, but with higher temperature yields will decline substantially (Van Ittersum et al., 2003). A similar benefit for yield from a temperature increase of up to 3 °C (and 460 ppm CO_2) has been simulated for irrigated and dry-land wheat in India (Attri and Rathore, 2003). Differences in crop response to climate change depending on the soil type have also been shown in other simulation studies (Chipanshi et al., 2003; Jones and Thornton, 2003). Elevated CO_2 concentrations (400–700 ppm) and increased temperatures (+3 °C) both decreased grain protein, but in financial terms this was more than offset by the increase in yield in most cases. If, in addition, precipitation was decreased, financial returns dropped below present levels, particularly in the low precipitation regions (Van Ittersum et al., 2003).

Deep drainage as the main cause of dry-land salinity (George et al., 1997) tended to be slightly higher under elevated CO_2 concentrations (400–700 ppm) but when higher average temperatures (1–7 °C) were also simulated this was reversed. Deep drainage was greatly reduced in the low precipitation scenarios (Van Ittersum et al., 2003). Hence, climate change is likely to affect not only productivity but also deep drainage and dry-land salinity in some cropping regions. The impact can vary in direction such that both 'win-win' and 'lose-win' outcomes may occur, particularly depending on the relative change in precipitation (Van Ittersum et al., 2003; Ludwig and Asseng, 2006; Aggarwal, 2003; Mall et al., 2004).

From a global point of view crop modelling studies have estimated a positive impact from climate change on agricultural production in the temperate regions up to a temperature increase of about 2–3 °C. However, with more severe warming, production is likely to be negatively affected by climate change (Easterling et al., 2007; Tubiello et al., 2007). In tropical and semi-arid regions, with temperature increases of only 1–2 °C, climate change has already exhibited a negative impact on food production.

While crop models are an important tool for understanding the complexity of climate change impact on agriculture, results from such studies still need to be considered as an 'initial estimate'. Most of these models have been tested under a wide range of growing conditions with varying temperatures and rainfall, and some have been compared with elevated CO_2 data from FACE experiments. However, some of the simulated interactions of, for example, CO_2 and temperature have never been tested with measurements.

6. ADAPTATION TO CLIMATE CHANGE

Due to past emissions of greenhouse gases, the world is already committed to a warming of 0.1 °C per decade for at least the next 50 years. To reduce the negative impacts of climate change on agriculture, and to benefit from any possible positive impacts, it is necessary to focus on adaptation (Howden et al., 2007). For example, relatively small changes in farm management and selection of different crop varieties can significantly reduce any negative impact of moderate climate change. However, to adapt to more severe changes in climate, significant adaptation is needed, for example switch to new crops and varieties, or even change land use.

6.1. Management

This section outlines a few selected topics to illustrate the challenges and opportunities for adaptive management in future climates, namely the effects of CO_2 on protein concentration and management of fertiliser, opportunities for increasing cropping intensity, trade-offs and externalities related to changes in rainfall patterns and rainfall by soil interactions, management of timing of flowering through sowing date, and the role of seasonal forecast and diversification to deal with rainfall variability.

The beneficial effect of elevated CO_2 concentrations on crop yields depend on soil nutrient availability, as elevated CO_2 reduced grain protein concentration (Van Ittersum et al., 2003; Ludwig and Asseng, 2006; Amthor, 2001). To fully benefit from the positive impact of higher CO_2 concentrations and to minimise negative impacts on grain quality, it is necessary to adjust N fertiliser inputs by a relatively small amount under high CO_2 environments (Jamieson et al., 2000; Van Ittersum et al., 2003; Ludwig and Asseng, 2006).

Increasing average temperatures will create new opportunities to increase cropping frequency in some farming systems (Evans, 1993). For example, a simulation study by Monzon et al. (2007) showed that recent temperature increases favoured wheat–soybean double cropping in the southern Pampas. Increasing cropping intensity via multiple cropping is critical to the financial performance and viability of diverse cropping systems worldwide (Section 3.2.2 and 5 in Chapter 3; Section 3 in Chapter 5).

Trade-offs between crop production and externalities under climate change need consideration. In the temperate climate of northeast Germany, Wessolek and Asseng (2006) explored the trade-off between grain yields and groundwater recharge management through variable N inputs, for future climate change scenarios. Groundwater recharge in this region is important for urban water supply, irrigation, forestry and peat protection. The simulations indicated that in this environment a trade-off between deep drainage and grain yields can be potentially controlled through N management. However, such control was more effective under current climate conditions than under future climate, and on better water-holding silt soils compared to poor water-holding loamy sand. The authors suggested that under future climates, areas with poor water-holding soils should be managed extensively for groundwater recharge harvesting, while better water-holding soils should be used for high input grain production (Wessolek and Asseng, 2006). In other regions where rainfall will increase and/or with more extreme rainfall events, measures should be taken to reduce waterlogging, erosion and nutrient leaching (Howden et al., 2007).

Higher average temperatures can reduce frost at current flowering windows, but might increase frost risk with earlier flowering due to accelerated development (Sadras and Monzon, 2006). In many temperate environments, management of winter crops has to be balanced between early flowering, and associated risk of frost, and late flowering with associated risk of heat stress and/or water deficit (Section 3.1 in Chapter 2). In practice, flowering date is manipulated by combining management, i.e. sowing date, and cultivar phenology (Section 6.2). Howden (2003) showed that by adapting sowing dates to recent reduced frost risks in northeast Australia, gross margins of wheat cropping systems could be doubled. In a simulation study for Bulgaria, bringing sowing dates forward for wheat and maize was suggested as an adaptation measure to reduce yield loss with future temperature increases (Alexandrov and Hoogenboom, 2000). In Italy, 10–40% yield losses were predicted with future climate change for a range of crops using the CropSyst model (Tubiello et al., 2000). Based on simulations, sowing summer crops earlier and using slower-maturing winter crops was shown to be effective to maintain yields at current levels (Tubiello et al., 2000) (Figure 3).

Under the current climate, agricultural production is significantly affected by climate variability. Changes in variability in future climates are still uncertain (Nicholls and Alexander, 2007), but rainfall variability typically

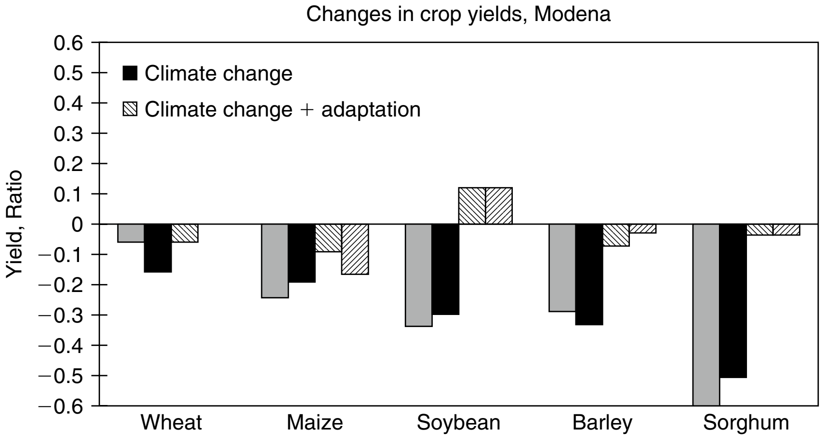


FIGURE 3

Simulated changes in crop yield in Modena, Italy. Ratio of climate change scenarios with and without adaptation, to baseline yields. Within each category (with and without adaptation), results both for GCM I scenario (left) and GCM II scenario (right) are shown assuming a doubling of CO_2*, a 4°C temperature rise and an increase in rainfall of about 10% in all months with GCM I and up to 30% rainfall decrease in some spring and summer months with GCM II. (Source: Tubiello et al., 2000.)*

increases as mean annual rainfall decreases (Nicholls and Wong, 1990). Using CERES-Wheat, Mearns et al. (1997) have shown that if the variance of temperature and rainfall changes in addition to changes in the means, this could have consequences on yield. For example, the positive effect of increased rainfall on yield can be lost through an increased variance of rainfall. A reduction in yield due to a decline in rainfall could be enhanced through a decrease in rainfall variance (Mearns et al., 1997). In some farming systems, perceptions about climatic risk and uncertainty about rainfall in the forthcoming season have led to conservative, low input management approaches that aim to reduce the losses in dry seasons. However, such low input approaches usually fail to capitalise on the benefits of climatic variability, that is the good rainfall seasons (Meinke and Stone, 2005). Management of climate variability using a combination of models and forecasting tools is important to reduce fluctuations in agricultural production and manage risk (Hammer et al., 1996, 2001; Hansen, 2002, 2005; Jones et al., 2000; McIntosh et al., 2007; Moeller et al., 2008). For example, Moeller et al. (2008) showed simulation-based management strategies linked to specific seasonal rainfall forecasts in the Mediterranean environment of Western Australia (Figure 4). Although annual rainfall variation in some regions of the world, including the Pampas of Argentina, the east of South Africa, Australia and parts of India, is influenced by ENSO (5–25%) (Peel et al., 2002), the predictability of ENSO is inherently uncertain (Jones et al., 2000). Nonetheless, advances in the application of climate prediction in agriculture have been made in regions affected by the ENSO, such as northeast Australia (e.g. McIntosh et al., 2005; Everingham et al., 2002) or South America (e.g. Podesta et al., 2002; Hansen et al., 1996). Chapter 3 (Section 4) and Chapter 19 (Section 4) further illustrate the use of modelling in risk management. Linking GCMs as seasonal forecasting tools with crop models has been recently suggested as the next step to better manage increased seasonal rainfall variability in dry-land agriculture.

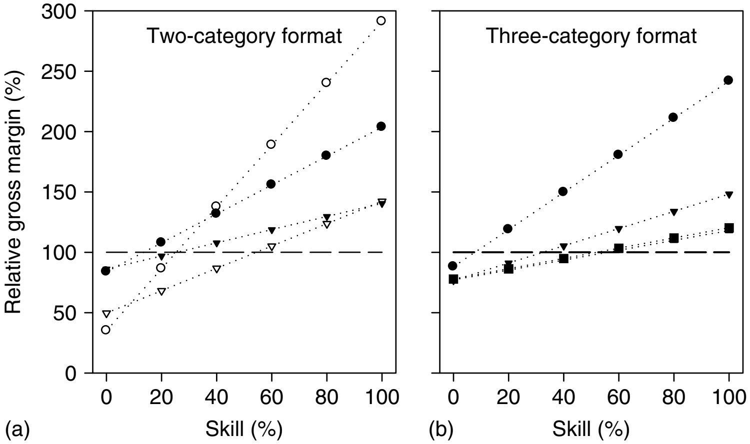


FIGURE 4

Effect of skill of hypothetical balanced (a) two- and (b) three-category forecasts on relative average gross margin (GM) from 105 years of simulated wheat yields for clay soil at four locations in Western Australia. In this Mediterranean-type environments, N fertiliser is often applied conservatively to limit growth and water use before flowering to allow for soil water during the grain filling period. Results of the conditional nitrogen (N) fertiliser strategies are expressed as percentage of average GM obtained with a fixed N rate and sowing strategy in all years. Fixed management in all years (--); two-category (above and below average rainfall categories) format (a): Merredin, fixed (●) and flexible sowing (○); Buntine fixed (▼) and flexible sowing (▽); three-category (above, average and below average rainfall categories) format (b): Merredin, fixed sowing (●); Buntine, fixed sowing (▼); Wongan Hills, fixed sowing (■); Mingenew, fixed sowing (▲), Only those cases are presented where, at a skill level of 100%, the forecast distribution of GM was significantly different from that associated with forecast knowledge. (Source: Moeller et al., 2008.)

In addition to seasonal forecasts, diversifying farming systems can be used as an adaptation measure for projected dryer climates in some regions. There are a range of options which can be explored with crop models to diversify systems; for example, using different varieties, varying planting dates, using different crops or agro-forestry. Also combining livestock and crops can be a risk-spreading diversifying strategy in some regions, while in some very dry regions the negative impact of livestock on soil cover for erosion control might prohibit livestock in a farming mix.

6.2. Breeding

Breeding new varieties is often cited as a possible adaptation to climate change (Salinger et al., 2005; Humphreys et al., 2006). However, only few experimental studies have tried to quantify the benefits from cultivar differences under elevated CO_2 (Slafer and Rawson, 1997; Manderscheid and Weigel, 1997). Trait-based adaptation strategies were modelled by Ludwig and Asseng (2009). They showed that traits related to early vigour for environments with terminal water shortage (e.g. Mediterranean-type) can potentially increase production in future warmer and dryer climates (Figure 5). However, the rainfall seasonality in terms of water availability before and after flowering, the soil water storage capacity and nutrient supply will all influence the benefits from early vigour (Asseng et al., 2002). For example, on sandy soils in Mediterranean-type environments, early vigour will be most beneficial as yields are often limited by biomass

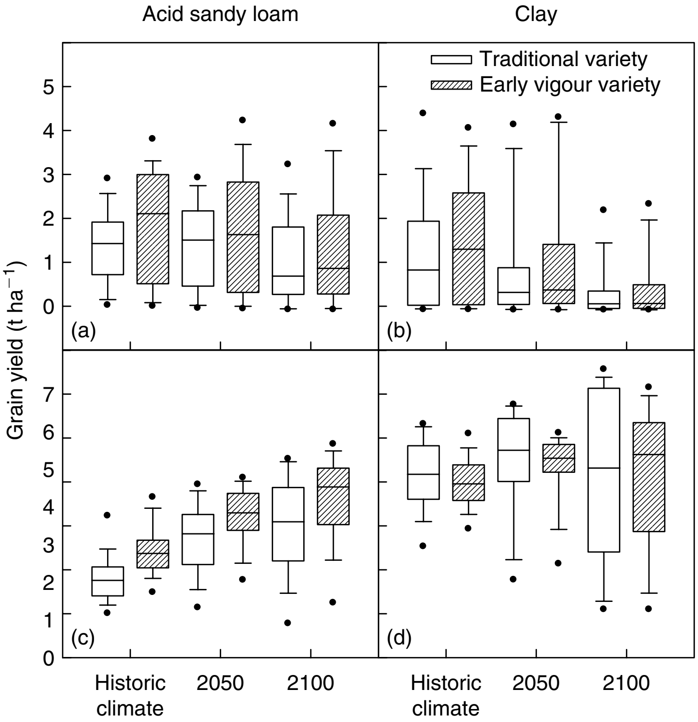


FIGURE 5

Simulated grain yields for (a, b) Kellerberrin (annual rainfall <350 mm) and (c, d) Kojonup (annual rainfall >450 mm), Western Australia for year 2050 with 525 ppm [CO_2], +2°C and −15% rainfall and for year 2100 with 700 ppm [CO_2], +4°C and −30% rainfall. Open bar represents the standard current cultivar and the bar with pattern represents the variety with early vigour trait as an adaptation option. Box plots represent 5 (dot), 10 (upper error bar), 25 (upper box edge), 50 (line in box), 75 (lower box edge), 90 (lower error bar) and 95 (dot) percentile probability of exceedance. (Source: Ludwig and Asseng, 2009.)

accumulation at flowering (Asseng et al., 2002). In other environments vigorous early growth can deplete stored soil water too early, resulting in small grains with low yields (van Herwaarden et al., 1998). Increased WUE under elevated CO_2 will reduce some of the latter negative effect. Breeding varieties with slower development in warmer climates, also depending on the changes in rainfall pattern, could be necessary to reduce the negative impacts of increasing temperatures (Ludwig and Asseng, 2009). Fine-tuning phenotype characteristics of crops for future climate scenarios might require models that link phenotypes to their underlying genetics – such models are currently under development (e.g. Hammer et al., 2006; Chapter 10).

Breeding in warm, dry environments should focus on improving agricultural production under even warmer, and more water scarce situations, and how to benefit from higher CO_2 concentrations. For example, wheat genotypes have been selected for higher TE using carbon isotope discrimination as a screening technique (Condon et al., 1992; Richards, 2006). Breeding should also consider that elevated CO_2 will increase both photosynthesis and TE in the future, hence the more restricted benefits of putative improvement in these traits under future climates (Box 1 in Chapter 9). Improving heat stress tolerance during grain filling of wheat (Spiertz et al., 2006) is another important adaptive trait. Most of the negative impacts of climate change associated with higher average temperatures in temperate regions are related to accelerated development and less time for biomass accumulation. Simple adaptation measures such as using varieties with more thermal time and vernalisation requirements, or increased photoperiod sensitivity could delay development to counteract these negative impacts. Understanding the genetic and environmental controls of crop phenology (Chapter 12) and using this in gene-to-phenotype models (Chapter 10) may assist breeding to adapt to these changes.

In high-latitude and high-altitude environments, where agriculture has not been suitable due to low temperatures and short growing seasons but become suitable with global temperature rise, crop simulation models could be used to explore the varietal needs for these potentially new agricultural regions, as discussed in Chapter 4 (Section 5).

7. CONCLUSIONS AND KNOWLEDGE GAPS

Physiology-based crop simulation models have been a key tool in extrapolating the impact of climate change from limited climate change-related field and controlled experiments to other climatic zones, soils, management regimes, crops and climate change scenarios. The impact of the individual climate change components and the combined effect of climate change scenarios on crop production and externalities have been explored with such models. To counteract negative impacts of climate change and to capture some of the new opportunities of these changes, management options have been investigated. Breeding options have received much less attention.

While these models are a simplification of the reality, they allow a first assessment of the complexity of climate change impact and adaption options in agriculture. Nevertheless, the simulation outcomes should always be evaluated critically and sometimes require further ground-truthing via field experimentations for specific conditions (Ziska and Bunce, 2007). For example, most of the models used for climate impact studies have been successfully tested with FACE experiments of up to 550 ppm CO_2 (Ewert et al., 2007). However, some of these models, which assume a linear relationship between elevated CO_2 and crop response, have been used for scenarios with CO_2 levels above 550 ppm (e.g. Van Ittersum et al., 2003), but only few models have been tested with CO_2 up to 700 ppm (Ewert et al., 1999). In an experimental field study with potatoes, the crop response from ambient to 550 ppm atmospheric CO_2 was relatively higher than the response between 550 and 680 ppm CO_2 (Fangmeier et al., 2002).

There are a number of other knowledge gaps that require attention to improve physiological-based crop models and their application in climate change impact and adaptation studies. These include issues related to interactions between different climate factors, interactions of climate with the environment, the impact of specific climate factors on water relations, specific crop feedbacks like sink–source relations, and extreme events, which are briefly discussed here.

Elevated CO_2 leads to stomata closure, reduction of transpiration and less canopy cooling. The interaction between CO_2 and temperature is therefore important, for example it may increase pollen sterility in rice (Ziska and Bunce, 2007), but it is often not considered in crop models. As the frequency of extreme high temperatures (>35°C) during the growing season will increase, the interactions with elevated CO_2 need to be understood and considered (Attri and Rathore, 2003). Amthor (2001) indicated a reduction of yield with elevated CO_2 in combination with warming for wheat, compared with elevated CO_2 alone. Alonso et al. (2008) found a higher photosynthetic temperature optimum in wheat under elevated CO_2. No such interactive effects have been reported for soybean (Boote et al., 2005). Crop models need to be tested with such data sets of interactive effects to ensure their validity for climate change scenarios. Similarly, interaction effects of elevated CO_2 and flooded conditions, salinity (Ziska and Bunce, 2007) or soil constraints like soil compactions, sub-soil toxicity or transient waterlogging are unknown, but need to be considered (Probert and Keating, 2000). Due to the interactive effects and feedbacks that emerge when climate factors are combined, experiments in which only single factors are manipulated are likely to be inadequate to fully predict the impacts of future climate change (Dermody, 2006).

Furthermore, studies with elevated CO_2 and warming at very low water supply, specific rainfall patterns and a range of soil water-holding capacities have been simulated in climate impact scenarios, but these models have never been tested with experimental data with such interactions as treatments. However, the combination effect could be very different to the sum of the single effects. For example, the net primary production response of grassland to interactive global changes (increased atmospheric CO_2, temperature, rainfall and nitrogen deposition) differed greatly from simple combinations of single factor responses (Shaw et al., 2002). In addition, genotype by CO_2 interactions (Slafer and Rawson, 1997; Manderscheid and Weigel, 1997) are usually ignored in simulation studies, mainly due to the lack of experimental data, but different cultivars are often used for various regions and might respond to elevated CO_2 differently. Linking crop models with the genetic underlying structure of crops might help to adapt crops to future climate change through genetic improvements (Chapter 10). Little is known about CO_2 acclimatisation of crops and hence this is ignored in simulation studies.

Nitrogen is considered in most crop models. Other nutrients such as potassium and phosphorus can also become growth-limiting factors under elevated CO_2 conditions (Hungate et al., 2003; Ziska and Bunce, 2007), but are usually not considered in crop models or in climate impact studies. Nutrients could also become limiting when climate change alters soil factors, for example by restricting root growth for nutrient uptake (Brouder and Volenec, 2008).

Quality aspects of yield are often affected by climate (Wu et al., 2004; Rogers et al., 1996; Kimball et al., 2001; Yang et al., 2007b) but are not, or are less well simulated than yield itself (e.g. protein composition, oil content), and simulation studies on the impact of climate change will require a better understanding of the physiology of yield quality and its incorporation into crop models (Chapter 16).

Specific changes in climate could become critical in determining the impact on crops. For example, the importance of minimum temperature, rather than just mean temperature, for grain yield determination in wheat and rice needs more attention and might require modifications on how crop models respond to changes in minimum temperature (Fischer, 2007). Also, if the frequency of dry winds with high VPD increases with climate change in some regions, the potential damage to crops demands further study as dry winds are ignored in current crop models (Fischer, 2007).

Physiological processes such as sink–source relationships of grain yield, correctly or incorrectly represented in crop models (Sinclair and Jamieson, 2006; Fisher, 2008), could be differently affected by elevated CO_2 and increased temperature (Triboi et al., 2006; Ziska and Bunce, 2007; Jifon and Wolfe, 2005). For example, wheat grain yield has been reported to be reduced under elevated CO_2 in sink-manipulated shoots, implying that a high source:sink ratio may result in a down-regulation of photosynthetic capacity that more than offsets the direct stimulating effect of elevated CO_2 (Uddling et al., 2008).

One of the challenges in climate change impact research is how to deal with extreme events like heat stress, frost and flooding. While the frequency of extreme events is often predicted to change in the future, predicting the timing of extreme events is still poor (IPCC, 2007). However, the timing of critical events is crucial in determining the crop impact as the impact often depends on the crop phenological stage (e.g. frost and flowering of cereals) (Section 3.2.2 in Chapter 15).

Despite these many knowledge gaps, crop models that integrate crop physiological understanding with soils hydrology, soil carbon and nutrient dynamics have improved our understanding of the impacts of climate change on many aspects of local and world food production. The application of these models stimulates investigations into climate change adaptation and assists in communication with the public and policy makers that continued climate change could have a devastating impact on food supply. Continually improving crop models with further physiological understanding will help to improve our appreciation of future climate change impact and adaptation options in agriculture.

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CHAPTER 21

Whither Crop Physiology?

Antonio Hall and Victor Sadras

1. INTRODUCTION

In his introduction to ‘Crop physiology: some case histories’, Evans (1975) outlined a brief history of the discipline. Citing Balls, he wondered whether its role might not be restricted to retrospective explanation of results obtained by breeders. Some might be tempted to add the results obtained by agronomists to that category. Since then, Simmonds (1991) included crop physiology in his list of ‘bandwagons’. Currently, a lot of emphasis is placed on the expectations aroused by molecular approaches to, say, yield improvement and stress tolerance (Chapter 14; Hammer et al., 2006; Struik et al., 2007). A further issue is privately funded, and largely unpublished, research on functional genomics and other ‘omics’, the results of which remain outside the public domain (Struik et al., 2007). In addition, growing concerns about humankind’s impact on the environment have led to a much greater emphasis on global and regional ecosystem functioning. These changes in research foci have created a whole new scenario for crop physiology.

So, is crop physiology committed to irreversible decline, overtaken by alternative research perspectives, shunted to one side by emerging new fields, after having promised more than it could deliver and having, even in its prime, only provided retrospective explanations? We believe the answer to these questions is ‘no’. Our reasons include:

- the number of important, crop-level issues that still await systematic study from a crop physiological perspective before they can be reduced to a usable corpus of knowledge linked to frameworks that can help breeders and agronomists, among others;
- the importance of crop physiological information and knowledge for the formulation of modelling tools to quantitatively explore matters such as agro-ecosystem functioning and projected impacts of climate change (Chapters 4 and 20), the complexity of genotypic, environmental and G × E control of crop yield (Chapter 10) and grain quality (Chapter 16), the design of crop rotations for risk management, greater yield and profit, more effective resource utilisation and reduced environmental impact (Chapters 2–4 and 19);
- the value of crop physiological principles in the design and execution of agronomic and breeding experiments, targeting phenological adaptation (Chapter 12), improved water- and nitrogen-use efficiencies (Chapters 8, 13 and 15), yield and grain quality (Chapters 15 and 16);

- the need for understanding and integrating potential impacts of the crop-centred products of functional genomics (Chapters 10–16; Hammer et al., 2006; Struik et al., 2007; Yin et al., 2004).
- the need to estimate fluxes of carbon, water and reactive nitrogen linked to the functioning of the agro-ecosystems which cover large areas of the planet. Adequate understanding of global biogeochemistry cannot emerge without good knowledge of crop functioning.

According to Boote and Sinclair (2006), early efforts in physiological studies had a narrow cell or individual plant focus (e.g. nitrate reductase) that shifted to a crop-oriented perspective in the 1960s, and then back to the current narrow focus on specific genes influencing behaviour at molecular level. This latest shift is, they argue, unwise in that 'the gains in understanding the whole-plant response is not given full consideration' and they contend that the cycle of focus will return to the challenge of integrating understanding at the crop level.

In what follows, we present a selection of topics, drawn from a much broader range of potentially interesting issues, to illustrate some of the very many gaps in current knowledge about the physiology of crops. Our illustrations of gaps emphasise the importance of crop-level studies carefully linked to crop development as essential to deal with the issues. We also discuss the present status of the interfaces between the discipline and modelling, breeding and agronomy. We close with a very personal view of the present status of the discipline and its future prospects. Readers will note that although we refer to some of the chapters of this book, we have made no attempt at systematic coverage of their contents.

2. CROP PHYSIOLOGY'S UNFINISHED BUSINESS

In crop physiology, as in many other disciplines, degree of understanding varies across fields. Patchiness in the coverage of any particular field becomes more obvious as the limits of the selected field are broadened, and judgements as to relative progress when comparing fields can become highly subjective. Some of this patchiness results from an inherent difficulty in methods (e.g. root systems, Chapter 13) but most of it stems from current perceptions of the relative importance of different fields in plant and crop sciences. For instance, studies on photosynthesis are much more abundant than studies on partitioning of biomass. A rough interrogation of Web of Science returned a 5:1 ratio of papers in these two categories, which does not match their relative importance in driving progress in crop yield (Chapter 15).

In this context, we have elected to establish canopy net carbon exchange (NCE) in C3 crops as a reference field against which progress in other fields of crop physiology may be contrasted (Boote and Sinclair, 2006). We then consider three fields that are both important and especially patchy due to a combination of conceptual reasons and lack of proper methods, that is root morphology and function, biomass partitioning and crop responses to extreme temperatures.

2.1. C3 crop canopy net carbon exchange: a 'gold standard' reference for crop physiology?

Correct estimation of canopy NCE requires appropriate description of light distribution across leaf elements within the canopy, of the variation in photosynthetic capacity of those leaf elements, of the respiratory load associated with both the leaf elements and the supporting structures (e.g. petioles, stems) and of the responses of both photosynthesis and respiration to the main factors affecting canopy function, that is plant water, nitrogen and carbohydrate status, radiation, temperature, water vapour pressure deficit (VPD), CO_2 concentration of the air and so on (Section 6 in Chapter 7). Starting from early approximations based on responses to light of leaf photosynthesis and simple descriptions of canopy structure (Loomis and Williams, 1969), it is now possible (e.g. Boote and Pickering, 1994) to model canopy NCE (at least for C3 crops) starting from leaf A/Ci curves (Farquhar, 1982) and using simple or more complex (e.g. hedgerow canopies) models of canopy structure to describe profiles of light distribution (Boote and Pickering, 1994; Goudriaan, 1988; Sinclair and Horie, 1989). These sorts of model allow for good description of canopy responses to light, temperature and CO_2, and it should be possible to broaden them to incorporate the effects of VPD and leaf energy balance (Box 1 in Chapter 7, Collatz et al., 1991) and nitrogen distribution profiles within the canopy and their variation across the crop season (Section 3.3.3 in Chapter 8). Use of 3D canopy modelling may capture subtler aspects of light distribution and leaf photosynthesis within the canopy (e.g. Evers et al., 2007; Maddonni et al., 2001). Uncertainties as to the nature of root-signal control of stomatal aperture (Ren et al., 2007), of how to estimate non-lamina respiratory loads, and how to link variations in plant carbohydrate status (source/sink balance) to rubisco regeneration, on the effects of stomatal closure on Ci/Ca ratios (Xu and Hsiao, 2004), and the impact of phosphorus deficiency on leaf photosynthesis and its within-canopy variation are some of the hurdles remaining before a fuller description of canopy NCE dynamics across the crop season and under variable environmental conditions becomes feasible. Accounting for these processes will not necessarily improve the already high predictive capacity of current models, but would allow for better linkages with both the genetic and environmental drivers of carbon exchange in crop canopies.

In spite of the imperfections noted above, current status of C3 crop canopy NCE modelling shows how it has been (or might be) possible to link basic photosynthesis processes (rubisco activity and electron flow), consideration of optical properties of leaves and descriptions of canopy architecture to scale from the chloroplast to the canopy in a meaningful, connected fashion. Equivalent bodies of structured knowledge are, as yet, unavailable for other important crop resource-capture systems and processes. To go no further, equivalent frameworks for canopy photosynthetic responses in C4 (Lizaso et al., 2005) and CAM species are more rudimentary or lacking.

2.2. Root system structure and function

Roots are essential structures for capture of water and nutrients (Chapters 6–8 and 13) and anchorage (Ennos et al., 1993; Goodman et al., 2001; Sposaro et al., 2008). Owing largely to methodological constraints, our understanding of crop root system dynamics and functioning is sketchy (Chapter 13; Kirkegaard et al., 2008; Passioura, 2002; Wang and Smith, 2004) and far from comparable to that of canopy dynamics and functioning. Ideally, a full understanding would lead to a capacity to quantify root structure and function throughout the life of a crop. This would involve, throughout the crop season, the dimensions of rooting depth, distribution of root length density (apparent and effective, see below) in the soil profile and potential (i.e. not restricted by availability) root capacity for the capture of water and nutrients.

Modellers have, out of necessity, been in the forefront of attempts to tackle the issue and have generated frameworks to capture variations with depth and ontogeny of root morphology and functionality (Wang and Smith, 2004; Yang and Midmore, 2005). One framework is based on root biomass distribution in the profile and resulting root length density profiles (e.g. King et al., 2003) or alternative approaches to generate dynamic 3D root distribution in the profile (e.g. Dunbabin et al., 2002). Some explorations of intra- and inter-specific variability for root biomass have been made (Dunbabin et al., 2004; Manschadi et al., 2006, 2008; Waines and Ehdaie, 2007) and the assumption (with some experimental support, e.g. Section 4 in Chapter 13) put forward that more biomass means a more active root system. A second framework uses an empirical approach based on the dynamics of water uptake rates in layers of the soil profile (Dardanelli et al., 2004; Meinke et al., 1993; Monteith, 1986; Robertson et al., 1993). Important products of the work used to develop the two frameworks include thermal time approximations to the description of the dynamics of rooting depth or water extraction front during the emergence-anthesis phase, definition of the likely volume-of-influence of individual root axes and recognition of the importance of soil structure on root axis clumping (Passioura, 1980, 1988; Ritchie, 1985). Root clumping implies that effective root length density is less than the apparent one, resulting in poor estimates of water uptake rates. However, frameworks for the description of root axis functionality dynamics and the spatial distribution thereof are rudimentary or non-existent (Wang and Smith, 2004). This could be particularly critical for the description of crop functioning after anthesis, because both the root biomass and the empirical approximations to root functioning have a limited capacity to deal with this phase.

Models that use biomass, and the resulting root length density, as an indicator of root functionality (King et al., 2003; Ritchie, 1985) need to deal with root senescence as the dominant process driving the dynamics of root biomass stock during grain filling (Hall et al., 1990; Sadras et al., 1989). On the other hand, the technique used to develop empirical functions (which lump together root biomass, root functionality and root clumping) to describe root water uptake capacity for different soil layers (Dardanelli et al., 2004; Meinke et al., 1993; Monteith, 1986; Robertson et al., 1993) has been mostly applied during the pre-anthesis phase of the crop cycle and, by its very nature, the estimation of the empirical water uptake functions for each soil layer takes too long for reliable measurements to be made over the relatively short grain-filling interval.

The importance of understanding, modelling and manipulating the dynamics of root systems after anthesis in annual crops is emphasised by the yield benefits associated with uptake of water and nitrogen during this phase (Section 4 in Chapter 13). Indeed, water uptake after flowering has a strong influence on harvest index (HI), yield and water-use efficiency (Section 3.1 in Chapter 6), and root nitrogen absorption after anthesis is an important component of the stay-green trait associated with nitrogen-use efficiency and tolerance to both water and heat stress (Section 3.4. in Chapter 8 and Section 3.2.3. in Chapter 15).

Both the above-mentioned frameworks view root functionality as a static property, that is as a function of achieved root length density for a given layer of soil, or as a function of a measured descriptor of root water uptake dynamics. Neither of these approaches can handle seasonal or sub-seasonal variations in specific potential root uptake rates, and currently there is no framework to handle the crop-level description of the attribute. Recent work using DNA techniques (Brunner et al., 2001; McNickle et al., 2008) suggests that we may stand at the threshold of substantial advances in determining functional root biomass distribution in the soil profile and its dynamics during the season. Short-term variation in root uptake capacity, associated with plant development and nutritional status (Imsande and Touraine, 1994; Muller and Touraine, 1992), is another area that begs for attention.

Owing to the difficulties of characterising root systems in realistic field conditions, many studies have used simplified systems, for example seedlings and sand culture. These simplifications ignore important attributes of root systems influenced by soil properties (Passioura, 2002, 2006). This simplified approach also overlooks root recognition of self- and non-self-associated morphological responses (Hess and De Kroon, 2007; Raper and Barber, 1970) and higher-order consequences for communal versus individual plants (Section 5 in Chapter 9) and crop-weed interactions (Section 6.2 in Chapter 18). In some cases, root traits characterised in oversimplified systems bear little resemblance with field conditions. In others, artificial growing conditions may still provide relevant information as shown in studies of root angles in cereals in Japan and Australia. These studies showed cultivar-specific root angle is under strong and relatively simple genetic control, root angle correlates with depth of root systems in the field, and that root depth as driven by root angle is adaptive, for example selection for yield has favoured shallow root systems in dry environments with small rainfall events or environments prone to waterlogging, and deep root systems have been favoured in dry environments where crops rely on stored soil water (Manschadi et al., 2008; Oyanagi, 1994; Oyanagi et al., 1993). Chapter 13 (Section 5) discusses shallow branch root angle in bean as a trait associated with capture of surface phosphorus in highly weathered soils.

Another, potentially important, issue is that the root system may be constructed of at least two categories, which for species of Cactaceae have been termed 'permanent' (long-lived) and 'rain' (ephemeral and appearing and disappearing in flushes following a rainfall event) (Palta and Nobel, 1989a, 1989b). This is yet to be studied in crop species, but the sudden appearance of superficial roots shortly after the end of a dry spell is easily observed in both maize and sunflower (A.J. Hall, unpublished). Tap and secondary root generation and growth in *Arabidopsis* show different responses to substrate nitrogen availability (Zhang and Forde, 2000), again suggesting that not all roots are equal. Yang and Midmore (2005) have suggested possible ways of dealing with some of these issues. The root systems of cereals and legumes, at similar root length densities, exhibit different water uptake capacities (Gallardo et al., 1996; Hamblin and Tennant, 1987), yet we know little of the underlying morphology and physiology of these differences, the degree to which they exist for other crops or their genetic and environmental regulation. Advances in the genetics and molecular aspects of aquaporins may help understanding some of these whole-plant observations, as reviewed by Bramley et al. (2007). Aquaporins can control water flow across membranes by changes in their abundance in the membrane, by opening and closing the channel (gating) or both; hence the analogy with stomata. In some cases, there is a good correlation between expression of aquaporins and physiological traits, for example aquaporin expression follows a day/night cycle consistent with the daily changes in root hydraulic conductivity coupled with transpiration. In other cases, for example up- and down-regulation in response to stresses, the patterns are less clear, partially due to post-transcriptional regulation. In the next 5–10 years aquaporins may play a role in gene-to-phenotype modelling (Chapter 10) of root hydraulic conductivity.

2.3. Biomass partitioning

Increased HI has been an important component of the raising yield potential of some crops, notably rice and wheat, during most of the twentieth century (Chapter 15). A back-of-the-envelope calculation by Austin (1980) suggested an upper limit of 0.62 for HI in wheat, which seems to hold after an updated evaluation (Table 1 in Chapter 15). Foulkes et al. (Section 3.2.1. in Chapter 15) concluded that a feasible strategy for future, modest, improvements in HI is to continue reducing structural stem dry matter while accounting for the trade-off with lodging risk, something fraught with unknowns in itself (Berry et al., 2004; Sposaro et al., 2008).

Advances in the understanding of improved HI in grain and tuber crops includes genetic (e.g. role of Rht genes in wheat), hormonal (e.g. gibberellic acid, GA) and enzymatic control of plant partitioning of carbohydrates (Sonnewald et al., 1997), anatomical and physiological aspects of phloem loading and unloading (Boote and Sinclair, 2006; Patrick, 1994, 1997), plant- and crop-level factors that affect grain number and grain size, and crop-level photomorphogenic control of plant resource allocation (Boccalandro et al., 2003). The general impression is one of fragmentary coverage of the topic, where appropriate but not necessarily reasonably robust empiricisms, sometimes illuminated by the results of some key experiments and principles (Loomis and Connor, 1992) are used to make up for a lack of fundamental understanding and the absence of an appropriate general framework. Again, a long way from canopy photosynthesis models.

The role of Rht genes has been assessed in terms of both their primary effect on tissue expansion as related to GA sensitivity and their consequent effects on plant height, radiation-use efficiency, biomass production, floret survival, kernel number and size and HI (Borrell et al., 1991; Gale and Youssefian, 1985; Miralles et al., 1998; Miralles and Slafer, 1995). The role of photothermal conditions during the grain number determination phase, together with its connection to plant and inflorescence size or growth rates in several crop species has been established (Section 5 in Chapter 12; Section 3.2.2 in Chapter 15). Currently, advances are being made on the possible role of inter-plant uniformity in determining crop, as against individual plant, HI (Borrás et al., 2007; Maddonni and Otegui, 2006). Recent comparisons across crop species of grain size responses to variations in source:sink relationships (Borrás et al., 2004) have provided a more robust understanding of the controls of grain size, a field related to earlier work on the links between post-anthesis water availability and pre-anthesis labile carbohydrate reserves (Section 3 in Chapter 6) and their influences on grain growth. The current conceptual model of determination of grain yield components assumes no developmental overlap between the phases of determination of grain number (pre-anthesis) and grain size (post-anthesis). This model is based on the observation that actual grain size strongly depends on growing conditions after anthesis, which affect rate and duration of grain filling (Egli, 2006; Sadras and Egli, 2008). Potential grain size, however, is largely defined before fertilisation. In wheat, barley, triticale, maize, soybean and sunflower, maternal tissues developed during early reproductive stages set an upper limit for grain size (Aguirrezábal et al., 2003; Calderini et al., 1999a, 1999b; Calderini and Reynolds, 2000; Cantagallo et al., 2004; Duggan and Fowler, 2006; Egli, 1990; Gambin et al., 2007; Kiniry and Otegui, 2000; Lindstrom et al., 2006; Ugarte et al., 2007). The concurrent determination of grain size and number demonstrated by Gambin et al. (2006) in maize is consistent with the evolutionary proposition of plants adjusting number of offspring to allow for environmental conditions, and the maintenance of a narrow range of seed size maximising maternal fitness (McGinley et al., 1987; Sadras, 2007). Also, consistent with the notion of maternal control of maximum grain size, Borrás et al. (2004) showed a strongly asymmetric response: size was reduced, particularly in maize, when source:sink ratio was reduced, but increasing source:sink ratio increased grain size modestly and the response tended to plateau, particularly in wheat and maize.

To model this important crop outcome, various empirical approaches have been developed including generic rates of HI increase (Chapman et al., 1993; Spaeth and Sinclair, 1985) or more ambitious frameworks (Dingkuhn and Kropff, 1996; Ng and Loomis, 1984; Villalobos et al., 1996) that describe partitioning with variable coefficients modulated by developmentally activated switches and rules that cover the whole of the crop cycle and partially account for environmental factors (water, radiation, temperature). There remains a need for models to incorporate pre-anthesis effects on grain size (e.g. Calderini et al., 1999a).

2.4. High- and low-temperature stresses

Crops growing in areas to which they are adapted can be subjected to chronic (e.g. salinity, high or low soil pH, high soil aluminium concentration, chronic high temperature) or intermittent stresses (e.g. drought, waterlogging, short exposures to high and low temperatures). Chronic stresses apply throughout the crop cycle, albeit with fluctuating intensity due to variations in, say, soil water content. Intermittent stresses often tend to occur for limited intervals during the crop cycle. The final response of a crop (i.e. yield, quality) to a single stress episode depends on:

- nature of stressor, for example osmotic, thermal, mechanical;
- previous history and acclimation, for example for extreme temperatures (Hubackova, 1996; Schapendonk et al., 2007; Wang and Li, 2006), water deficit (Wikbergi and Ogreni, 2007), waterlogging (Visser and Voesenek, 2005), salinity (Amzallag, 1996; Djanaguiraman et al., 2006) and wind (de Langre, 2008; Moulia et al., 2006);
- developmental timing, intensity and duration of stress (Jordan and Miller, 1980);
- conditions for recovery, including time remaining until the end of the season (McNaughton, 1983; Oesterheld and McNaughton, 1991) and availability of plant meristems (Bonser and Aarsen, 1996; Sadras, 2000);
- background growing conditions, for example availability of resources (Sadras, 1996a) and interactions with other stress factors (Chapin et al., 1987; Mooney et al., 1991).

The complexity arising from the combination of all these factors and the recurrence of stresses during a growing season is in sharp contrast with the oversimplified view whereby all these factors, including the nature of stress, are disregarded on the grounds of common gene action and shared metabolic pathways (Figure 4 in Chapter 1; Vinocur and Altman, 2005). In the case of water stress, two important steps in generating a useful framework have been the recognition of the importance of the timing, and the (as yet imperfect) attempts to build into this scheme the effects of duration and intensity of stress. Much remains to be understood on the physiological, molecular and genetic bases of crop responses to all stresses, including those that have received the greatest attention namely water stress (Reynolds and Tuberosa, 2008) and salinity (Munns and Tester, 2008); and this doubtless will continue to be an active area within crop physiology as discussed throughout most of this book. Understanding crop responses to high and low temperatures is in a much more primitive state than that for drought and salinity, in spite of their importance for agriculture.

2.4.1 High-temperature stress

Anthony Hall and his colleagues (Ahmed and Hall, 1993; Ahmed et al., 1992; Marfo and Hall, 1992; Mutters and Hall, 1992; Ehlers and Hall, 1998; Hall, 1993) have studied cowpea responses to chronic high-temperature stress and its interaction with photoperiod in detail. Furthermore, they have successfully bred varieties bearing genes that mitigate high temperature effects on floral bud formation, seed coat discoloration and on anther and embryo development (Ehlers et al., 2000). Boote et al. (2005) have summarised the effects of chronic high temperature on yield and its components in rice, soybean and peanut. Importantly, they have confirmed that, in general, vegetative processes are much less sensitive to chronic high temperature than reproductive processes (e.g. Jain et al., 2007).

Brief exposures to periods of high temperature can also reduce yield and grain quality substantially (Jain et al., 2007; Prasad et al., 2001; Rondanini et al., 2006; Savin and Nicolas, 1996; Stone and Nicolas, 1994; Wallwork et al., 1998; Wardlaw et al., 2002), and this is an area that stands in need of much research. Important requirements for progress via experiment include the need to (i) use short (up to several days) exposures to high temperature rather than continuous high temperature, (ii) mimic diurnal temperature dynamics (as against two-level day/night temperature regimes), (iii) avoid the interactions between temperature and VPD that occur when relative humidity rather than VPD is controlled in experiments, (iv) use several temperatures (essential for the generation of response functions) and, (v) identify the physiological causes of alterations in grain number (e.g. pollen and ovule functionality, Gross and Kigel, 1994; Prasad et al., 2001) and grain size and quality (Calderini et al., 1999a; Rondanini et al., 2006; Savin and Nicolas, 1996; Stone and Nicolas, 1994; Wallwork et al., 1998; Wardlaw et al., 2002). Because the effects of stress often exhibit threshold responses, and because the nature of the responses are strongly influenced by the developmental stage at which stress occurs, our capacity to predict the likely outcome of an episode of high temperature will depend strongly on our ability to adequately integrate the influences of intensity, duration and crop developmental stage. Rondanini et al. (2006), building on earlier work by Wardlaw et al. (2002), demonstrated that it was possible to integrate effects of duration and intensity of heat stress on grain yield and oil content in sunflower using developmental stage-dependent functions of cumulative hourly heat load above a threshold temperature to describe grain responses. Thus far, work on point heat stress exposures has been limited to a few species, that is peanut (Prasad et al., 2001), wheat, barley (Passarella et al., 2002; Savin and Nicolas, 1996; Stone and Nicolas, 1994; Wallwork et al., 1998; Wardlaw et al., 2002) and sunflower (Rondanini et al., 2003, 2006). Few of these efforts have attempted to scan a broad range of developmental stages or develop response functions. This is likely to become an active area of research in future, particularly in view of likely increases in mean global temperature and frequency of episodes of high temperature stress associated with climate change (Section 3.2 in Chapter 20). An associated area of research, and one that has received little or no attention, is that of possible acclimation and compensation responses of crops to exposure to short episodes of heat stress. For example, works by Aguirrezábal et al. (2003) and Izquierdo et al. (2006) suggest that sunflower oil composition in the mature grain is influenced by temperatures experienced early during grain filling, while Rondanini et al. (2006) have shown that the linoleic/oleic fatty acid ratio in the same species can recover from brief exposures to stress provided enough time elapses between the end of exposure to stress and physiological maturity (see Chapter 16). Likewise, major interactions between heat stress, water deficit and nitrogen supply remain largely unexplored (Table 1).

Table 1 Symptoms of Heat Stress at Flowering in Wheat (% of Plants with Damaged Ears) Increased with Nitrogen Supply and Sowing Density in Rainfed Crops and were Undetected in Irrigated Crops

Nitrogen Rate (kg ha^{-1})	Rainfed		Irrigated	
	Low Density	Normal Density	Low Density	Normal Density
0	10	22	0	0
16	20	28	0	0
39	27	37	0	0
163	33	60	0	0

Sowing density was 102 kg seed ha^{-1} (normal) and 52 kg seed ha^{-1} (low).
Source: Rodriguez et al. (2005).

2.4.2. Low-temperature stress

The effects of low temperature on crop functioning and yield have attracted and continue to attract attention, particularly for winter and spring cereals. Progress towards a framework for prediction, analysis and management of the effects of frost on the survival of winter cereals has been substantial (Section 1.1 in Chapter 4). In comparison, the effects of late (i.e. from prior to anthesis through grain filling) frosts on cereal yields are much less advanced. It has been shown that winter hardiness in cereals is strongly influenced by development, and that the transition from vegetative to reproductive phase approximately marks the stage at which winter hardening ceases to be possible and irreversible dehardening sets in, even at temperatures which previously favoured hardening. Delay in development, due to low temperatures, vernalisation or photoperiodic requirements, or an increased cultivar requirement for a minimum number of leaves, all serve to widen the developmental window during which hardening is feasible given the right temperature cues (e.g. Fowler, 2008). Cultivar and species differences in threshold induction temperature, rate and duration of the hardening process, and lowest tolerable freezing temperature, all contribute to defining crop freezing tolerance under naturally variable temperatures prior to the transition from vegetative to reproductive (Fowler, 2008). Progress has been made in defining the temperature responses of the dehardening process (both prior to and after the vegetative-to-reproductive transition), and in quantifying the effects of extended exposure to close-to-lethal temperatures on crop frost tolerance (Fowler et al., 1999). Similarly, response functions for the effects of snow cover on frost tolerance mediated by accumulation of toxic metabolites have been developed by Bergjord et al. (2008) (but see Chapter 4 for the protective effects of snow cover and interactions with diseases). While there is still much to be done to uncover the genetic and molecular bases of freezing tolerance in over-wintering crops (Fowler, 2008; Vágújfalvi et al., 1999), the model of Fowler et al. (1999) and its variant by Bergjord et al. (2008) are robust enough to predict the time courses of frost tolerance between sowing and the start of spring growth in crops of several winter wheat cultivars grown under differing conditions. The way forward to improving these models to incorporate factors such as variations in threshold induction temperatures and cultivar variations in minimum leaf number seems fairly straightforward. One factor which may need further study, and which is not explicitly included in either of these models, is frost heaving of the soil and its interaction with cultivar (Section 1.1. in Chapter 4).

The contrast between our current understanding of the effects of frost on wheat crop functioning prior to and after stem elongation is remarkable, in spite of the widespread recognition that late frost can seriously affect wheat yields in temperate and subtropical regions of the world (e.g. Boer et al., 1993). There is some evidence that if ears subjected to radiation frost under controlled conditions reach tissue temperatures of close to −5 °C, damage – measured as loss of spikelet fertility or increase in electrolyte leakage from ear tissues – occurs (Fuller et al., 2007; Marcellos and Single, 1984). However, responses of yield and grain quality to frost can occur at earlier (Whaley et al., 2004) and later (Dexter et al., 1985) developmental stages and at lower or higher temperatures (Rebbeck et al., 2006). Where frost reduces kernel size, grain protein content may increase (Rebbeck et al., 2006). Precise descriptions of damage symptoms, their distribution among ears in the field, and their connection with crop development is still very unsystematic and strongly dependent on observations made after particular frost events (Cromey et al., 1998; Rebbeck et al., 2006; Whaley et al., 2004). Other elements that contribute to the difficulties in capturing the effect of frost in the field include (a) inconsistent correlation between screen- and crop-level temperature (Goldsworthy and Shulman, 1984), (b) a very sharp fall in floret survival after a certain threshold (Marcellos and Single, 1984), (c) a large variability in thresholds for damage depending on growing conditions prior and during the frost event, for example plant carbohydrate status, VPD and wind (Jacobsen et al., 2005; Rapacz, 1999; Snyder and Melo-Abreu, 2005; Vágújfalvi et al., 1999) and (d) growing conditions after the event. In two successive seasons at the same location, for instance, the threshold canopy-level temperature for wheat frost damage shifted from −2.7 to −4.3 °C (Rebbeck et al., 2006). Conditions after the event putatively influence recovery and yield compensation (e.g. late tillering, shift in floret survival to higher positions on the rachilla, increased grain size) after frost damage, but these effects are poorly understood. Table 2 shows, for instance, that the reduction of wheat grain set caused by frost in dominant ear positions (a–b) was partially compensated through cultivar-dependent increase in grain set in lower-order positions (c–e).

Table 2 Partial Grain Set Compensation after Frost Damage in Wheat

Cultivar	Treatment	Percentage of Grains in Floret Position				
		a	b	c	d	e
TPZ 3466	Control	52	36	12		
	Frosted	24	23	23	25	5
Kite	Control	51	41	7	1	
	Frosted	32	32	24	12	1
SUN 20A	Control	51	44	5		
	Frosted	24	25	27	25	
Warigo	Control	56	35	9		
	Frosted	25	18	32	25	

Source: Marcellos and Single (1984).

The time course of frost events, including possible repeat frost on successive days, is often unknown, a condition which can also extend to crop developmental status at the time of frost. An important hurdle to more systematic studies is the difficulty in simulating radiation frost conditions in the field using intact plants. Radiant frost cabinets (which may not exactly duplicate natural conditions) require a lot of ancillary equipment to function and this complicates their use in field trials. Much remains to be done before a broad framework (which should include due analysis of the variations in damage with development, and exploration of the effects of intensity and duration of frost) for the understanding of frost effects on yield and grain quality can be constructed.

3. THE INTERFACE BETWEEN CROP PHYSIOLOGY AND MODELLING

Mathematical models of crop structure and function are essential for integration of otherwise fragmented knowledge. Reciprocally, solid physiological knowledge is critical for models with application in breeding and agronomy. Finally, the exercise of model building has often served to map knowledge gaps. In the previous sections, this dynamic loop between understanding and modelling of physiological processes was illustrated for root systems and HI. Here we outline recent progress and gaps of current crop simulation models.

It is sometimes suggested (e.g. White, 2006) that typical daily time-step models such as CERES, CropSyst and APSIM have reached a plateau and there is little new published about models. While it may be true that the similarities in the approaches to simulating the various soil-crop-atmosphere processes that models attempt to capture have increased considerably over the last two decades, this should not hide significant innovations or the challenges that remain.

Stimulated by the massive growth and fragmentation of information and knowledge on the molecular aspects of plant processes, and the increasing interest in spatial variation and remote sensing technologies, two new types of models are emerging. At the higher end of the scale, daily time-step models of individual crops are being integrated in whole-farm quantitative tools that represent a significant step forward in relation to linear programming for optimisation purposes (Box 1 in Chapter 19). At the other end, there is a shift from crudely empirical parameters to describe genotype-dependent responses (e.g. phenology as modulated by photoperiod) towards parameters that reflect more closely the emerging knowledge on their genetic control, and the integration of this information in the established (e.g. CERES-type) frameworks accounting for soil, climate and management (Chapter 10).

Other recent modelling innovations include the distinction between structural and reserve protein dynamics in the grain of wheat (Section 3.2 in Chapter 16; Martre et al., 2003), the development of row canopy photosynthesis models (Boote and Pickering, 1994) and the first steps in 3D canopy models (Barczi et al., 2008; Maddonni et al., 2001). The need to adapt crop models to the spread of conservation tillage and other changes in agronomic practice (e.g. shift from burning to chopping of leaf and tip biomass in sugar cane fields) has driven improvements to the modelling of surface residue decomposition and of the effects of these residues on crop water balance (Thorburn et al., 2001). The demonstration that photodegradation can be an important component of surface residue decomposition (Austin and Vivanco, 2006) will require further study and changes in this module of crop models.

Some aspects of crop structure and function continue to lack reasonably satisfactory modelling solutions. There are two categories of modelling gaps, namely gaps related to factors that are normally ignored in the models, and elements that are already considered but in need of improvement. Important gaps in the first category are heat stress and frost, soil-borne diseases and other biological 'rotational' effects, and abiotic soil constraints other than water and nitrogen [although these last two are also problematic (Probert and Keating, 2000)]. High on the list of the second category are root morphology and function, biomass partitioning and canopy senescence. Phosphorus nutrition is ignored altogether in some models, rudimentarily considered in others and increasingly important for many agronomic applications. The modelling gaps, particularly in the first category, partially reflect the intrinsic difficulties involved in quantifying some processes such as frost (Section 2.4) and biological 'rotational' effects (Karlen et al., 1994; Kirkegaard et al., 2008; Ryan et al., 2008). Depending on the relative importance of these as yet unresolved or partially solved issues for particular model applications, they can determine the success or failure of attempts to use a model for that application (e.g. Landau et al., 1998). For example, models are commonly used in studies of crop rotations, but they fail to account for major biological effects of rotations; for example wheat-after-wheat yield depression (Section 6 in Chapter 2, Sadras and Roget, 2004). Likewise models are a common tool to probe future climates, but the effect of heat stress is essentially ignored. Hopefully, the future will see progress in developing effective approximations to the filling of these modelling gaps.

In addition, there is the vexed question of the propriety of some of the assumptions about the nature of the physiological processes included in the models (Passioura, 1996). Indeed, models can give the right answer (e.g. reasonable yield estimates) for the wrong reasons that may be more (e.g. compensation between poorly estimated yield components) or less obvious (e.g. assumptions on allocation patterns). Modelling producing seemingly sound answers from concealed wrong assumptions is not unlike drunk driving, in the sense that it may generate an enthusiastic sense of solid understanding, thus becoming an obstacle rather than an aid to knowledge (Sadras and Trápani, 1999).

A topic that continues to be extremely important in modelling is the balance between its various parts (Ritchie, 1991), given that under many circumstances a model is only as strong as its weakest link (Passioura, 1996). In this context, larger mismatches are those arising from the refinement in the treatment of certain processes within a model (e.g. canopy photosynthesis) in contrast with uncertainties about the modelling of other processes (e.g. root functioning) within the same model.

In spite of all the possible caveats (and those noted above are by no means the only ones that could be considered), and the basic fact that a model is a simplification of reality, crop simulations models, prudently applied with a critical appreciation of their limitations, remain essential tools for the exploration of issues which are beyond the reach of experimentation or extrapolation from current experience. Examples include the management of risk in crop production through regional diversification (Section 4 in Chapter 3) or integration of rainfall forecasts and soil variability in fertilisation management (Chapter 19), and quantification of nitrogen leaching and deep drainage in agro-ecosystems (Asseng et al., 2001; Diaz-Ambrona et al., 2005; Sadras, 2002). As a breeding aid, models allow for quantitative environmental characterisation and identification of target environments, identification of plant traits and trade-offs, gene pathways and networks (Chapter 10). Models also provide a useful tool to explore long-term changes in crop production (Bell and Fischer, 1994; Meinke and Hammer, 1995) and soil attributes (Kamoni et al., 2007; Pennock and Frick, 2001), and to analyse climate-driven productivity issues (Rodriguez and Sadras, 2007; Sadras and Angus, 2006; Sadras and Rodriguez, 2007). And, of course, models continue to be the only way to go when trying to predict the effects of climate change on crop productivity (Chapter 20).

4. THE INTERFACE BETWEEN CROP PHYSIOLOGY AND BREEDING

The current status of the interface between crop physiology and breeding, one of the themes of this book, suggests some (slowly) increasing degree of mutual understanding and convergence between disciplines that may grow into more active collaboration in the future. Past attempts by crop physiologists to identify and evaluate drought-tolerance or yield-connected traits that could be of interest for breeders include narrow xylem vessels in wheat (Richards and Passioura, 1989, 1981a, 1981b), osmotic adjustment in wheat and sunflower (Chimenti and Hall, 1993; Chimenti et al., 2002; Morgan, 1995; Morgan and Condon, 1986), anthesis-silking interval (Bolaños and Edmeades, 1996) and spike row number in maize (Otegui and Slafer, 2004), accumulation of ureides as a marker of sensitivity of N_2 fixation under water stress in soybean (Sinclair et al., 2007), carbon isotopic discrimination as a marker of transpiration efficiency in wheat (Condon et al., 2002), stay-green in sorghum (Borrell et al., 2000, 2001; Borrell and Hammer, 2000) and wheat (Christopher et al., 2008) and root attributes improving phosphorus nutrition in bean (Section 5 in Chapter 13).

Richards (2006), Sinclair and colleagues (2004, 2005) and Palta and Watt (Section 5 in Chapter 13) identified, from different perspectives, the conditions for a successful contribution of physiology to plant breeding with emphasis on stress adaptation. Richards (2006) assessed seven selected traits with putative value for yield under water deficits and concluded that successful traits 'directly or indirectly transfer their effects to yield over long time scales by increasing either water use (amount and pattern), water-use efficiency or partitioning of more biomass to grain'. Sinclair and colleagues (2004, 2005) and Palta and Watt (Chapter 13) proposed four elements necessary for physiological R&D that leads to commercially useful germplasm: (i) initial assessment, under realistic field conditions, of the benefit to a crop from modifying a target trait; (ii) development of phenotyping techniques; (iii) forming of multidisciplinary teams with expertise in crop physiology, genetics, breeding and agronomy; and (iv) long-term (12–15 years) commitment to achieving yield increase by both researchers and funding bodies. The development of fast and effective phenotyping is critical not only as step (ii) in this top-down approach, but also in the bottom-up biotechnology model (Xu and Crouch, 2008). Palta and Watt (Table 1 in Chapter 13) identified three root traits that completed the R&D process into effective deployment in commercial varieties, namely resistance to Al and cyst nematodes and improved capture of phosphorus. They highlighted how sharply contrasting germplasm was first identified and rapid phenotypic screens were developed for these traits with strong links to yield in the field; the clear-cut phenotypic screens meant that major genes regulating the underlying mechanisms were identified, and robust markers developed. They also pointed out the importance of extensive training and involvement of breeders with the researchers that originally thought of these traits and phenotyping approaches. Palta and Watt also pointed out obstacles to incorporate otherwise sound root traits in advanced germplasm related to the need for maintenance of disease and quality attributes.

Attempts to bring together physiology and breeding have had a chequered success record, for a variety of reasons, some of which have nothing to do with the intrinsic value of the target traits involved. The traits that have gained some acceptance are those that are easier to select for; for example anthesis-silking interval and spike row number in maize (Otegui and Slafer, 2004). Two hard-to-quantify processes in this slow convergence between disciplines are the influence (sometimes heatedly denied) of crop physiological ideas on breeders' decisions (e.g. erect leaves in maize, Duvick and Cassman, 1999; Fischer, 2004) and a better understanding by physiologists of the need to (a) view any particular trait in the context of appropriate scales of time, level of organisation and background environment, for example scaling-up from stomata to canopy when considering crop water economy (Jarvis, 1995) and (b) understand the limitations a breeder faces when dealing with complex traits and variable environments (Chapman, 2008; Chapman et al., 2002) in a context of a large number of breeding plots and little or no possibility of manipulating the environment in which they grow (Sections 5 and 6 in Chapter 15).

Work continues on a number of traits and management guidelines relevant for yield potential, grain quality or stress tolerance, and much-but not all-of this work has strong roots in the principles of crop physiology. Examples include canopy and root vigour (Chapter 13, Botwright et al., 2002; Rebetzke and Richards, 1999; Richards and Lukacs, 2002), and photoperiodic and thermal control of development with consequences for yield (Section 5 in Chapter 12), grain quality (Chapter 16) and water- and nitrogen-use efficiencies (Chapters 6 and 8).

A more holistic approach, strongly influenced by crop physiological principles, is that embodied in the use of ideotypes as a guide to breeding, the success or failure of which is hedged about with many practicalities which lie between a 'useful' attribute (or ideotypic set of attributes) and its (their) incorporation into agronomically adapted elite lines. Fischer (2004) and Peng et al. (2008) provide some cautionary insights about the use of ideotypes and the associated hits and misses in the generation of Green Revolution semi-dwarf wheat and New Plant Type rice, respectively. In other cases, for example transcription factors enhancing drought tolerance (Nelson et al., 2007) or the use of transgenics (Rivero et al., 2007) in which crop physiology played a small, or nil, part in identifying the trait, there has been some progress towards applying crop physiology to the understanding of the nature of crop response to the incorporation of the trait. Certainly, crop physiological principles and frameworks will be an integral part of appropriate testing of putatively interesting new traits.

One area in which the crop physiology/breeding interface is active concerns the use of crop physiological principles to inform breeding strategies and decisions. Although still in the early stages, work of this nature is strongly influenced by the need to successfully connect crop (plot) performance, environment and crop development. Examples of this are the work by Chapman et al. (2002) on sorghum, de la Vega and colleagues (2001, 2006, 2001) and Andrade et al. (Section 3 in Chapter 11) on sunflower, Reynolds et al. (2001) on wheat and Messina et al. (Chapter 10) on maize. These efforts are particularly important as they illustrate how crop physiological knowledge, either on its own or incorporated into models, can illuminate and inform traditional plant breeding and, most especially, allow progress in the understanding of genotype × environment (G × E) interactions. It is worth re-stating that G × E interactions, if their origin is not revealed and understood, can constitute an even greater hurdle to the breeder than the more frequently considered (by non-breeders) G effects, largely because they often account for a greater proportion of the observed variance than the genetic effects (Chapman, 2008). These studies also illustrate the magnitude of the limitations on understanding G × E interactions imposed by poor environmental information (soils, weather and management). Use of models combined with extended weather records and good soil profile descriptions can allow for progress, but it is a sobering fact that the vast majority of multi-location field trials lack adequate environmental characterisation. Common sense selection of putative variables (e.g. de la Vega and Chapman, 2001, 2006) and the use of proxy variables (Chapter 15) can help, but in the long run the poor environmental characterisation remains a major obstacle and a rate-limiter for delivery of molecular-based solutions for crop improvement. For example, a recent study on G (QTL) × E, combined highly refined science for characterisation of the G component, whereas E was coarsely characterised with variables such as June–August or September–November rainfall (Kuchel et al., 2007).

Another, and as yet little explored, dimension at the crop physiology/breeding interface is the complexity of the web of genetic controls that are involved in controlling specific crop responses to the environment (Hammer et al., 2006; Struik et al., 2007). An example of this is the study by Ghiglione et al. (2008) who recorded changes in the wheat spike transcriptome between terminal spikelet and anthesis under short-day conditions inducing slower development and higher flower survival than in plants grown under long-day conditions. The authors were successful in categorising the over 2100 expressed genes into six clusters exhibiting contrasting patterns under short and long days, with the two smallest clusters containing over 90 genes;

the physiological interpretation of this study is summarised in Chapter 12 (Box 2). An investigation into the molecular bases of what is a possibly more complex trait, water-use efficiency, by Xue et al. (2006) revealed a similar panorama in terms of the number of genes involved. Resolving the key controlling genes in such a situation using available techniques is a daunting problem. It is possible that strategies that focus on the identification of a limited number or even as little as one transcription factor (e.g. Nelson et al., 2007) that regulates key points in some genetic pathways may provide a way of accessing at least some processes linked to stress tolerance or yield. An alternative, top-down, approach to bridging the gap between plant growth and genes or markers is that of Reymond et al. (2003), who synthesised the intra-specific variability of maize leaf expansion rate responses to temperature, soil water and VPD into a much more manageable, but still important, number of QTLs. Whether the bottom-up, the top-down or some combination of the two approaches will prove to be the best route to progress remains to be seen, but it needs to be emphasised that the works by Ghiglione et al. (2008) and Xue et al. (2006) are unusual in that they attempted to deal with potentially important yield-linked processes, using appropriate experimental models, and covering a range of levels of organisation from the genes to plants or crops growing under field conditions. In sum, the researchers used insights gained from crop physiology to guide their work. Further, if some of these efforts actually impact on breeding programs, experiments designed using crop physiological frameworks will be critical for testing the traits and establishing their limitations, particularly those arising from bottom-up black-box type approaches (e.g. Nelson et al., 2007; Rivero et al., 2007). In this category, improvement of crop yield via enhancement of leaf photosynthesis is the best example where a whole-plant or crop standpoint arrives at radically different conclusions from that of bottom-up perspectives (Box 1 in Chapter 9, Section 5 in Chapter 15).

The above, fairly restricted, overview suggests that activity at the interface between crop physiology and breeding can be expected to increase in the future. This increase can include research into the physiological bases of interesting traits (e.g. root and canopy vigour, osmotic adjustment); in the clarification and strengthening of understanding of G × E interaction, and in the testing and understanding of the function of potentially interesting new attributes to the improvement of crop water and nitrogen economy, drought tolerance and yield. Hopefully, this work will be conducted under the aegis of a more informed understanding of the problems, pitfalls and opportunities that exist for bridging the gaps between functional genomics, crop physiology and breeding (Hammer et al., 2006; Struik et al., 2007).

5. THE INTERFACE BETWEEN CROP PHYSIOLOGY AND AGRONOMY

The connection between crop physiology and agronomy, the other interface that this book has emphasised, exhibits an interesting mix of past successes, unresolved issues and new challenges (Chapters 2–4 and 19; Miller, 2008). At the very least, the existence of these last two categories constitutes an argument in favour of the continued need for research into crop physiology.

The use of critical windows of development for the determination of grain number and grain size, together with the identification of the dominant environmental drivers for each yield component, pioneered by Fischer (1985) in wheat and later extended to other crops including maize, sunflower, soybean and barley has proved immensely useful in understanding genotypic, seasonal, regional and global variations in yield potential (Aggarwal and Kalra, 1994; Cantagallo et al., 1997; Magrin et al., 1993; Ortiz-Monasterio et al., 1994). For example, this framework of sequential determination of yield components (which undoubtedly needs revising, Section 2.3) has been useful for understanding inter-year and inter-season variability of yield in both irrigated (Section 3 in Chapter 6) and rainfed crops (Magrin et al., 1993; Mercau et al., 2001), for the designing of more profitable farming systems (Figure 4 in Chapter 3) and to guide breeding (Section 5 in Chapter 12; Section 3.2.2 in Chapter 15). Use of this basic framework, combined with the downward shift from crop to constituent plant and back up to crop, also underlies the emerging understanding of how heterogeneity in plant size within a stand as generated by disease or insect damage or intra-specific interference can affect yield (Hide et al., 1997; Pagano et al., 2007; Sadras, 1996b; Sadras et al., 1999).

Crop physiological principles and the understanding of the basic processes of crop resource capture and dissipation have proven invaluable in the design of agronomic experiments for evaluating management options, for example in relation to soil depth (Calviño et al., 2003; Sadras and Calviño, 2001), row spacing (Andrade et al., 2002; Calviño et al., 2004), nitrogen fertilisation (Chapter 8), spatial heterogeneity, climate risk and design of rotations (Chapters 3 and 19). Some of this work has involved straightforward mapping of crop performance across environmental gradients and, in others, the use of more or less complex crop models, but crop physiological principles have enriched the agronomic outcome. The driving forces behind this need to ally agronomy and crop physiology are likely to become stronger in the future. With all their current weaknesses, crop simulation models continue to be the best alternative with which to explore regional agro-ecosystem functioning in terms of yield, production, profit and environmental outcomes against the background of continuously changing trends in climatic variables (Section 3). Appropriate research into the many unknowns in our understanding of crop functioning is the unavoidable pre-requisite for better models.

Challenges for agronomy continue to be very large and overcoming them could contribute significantly to humankind's likelihood of providing adequate food security across the globe while preserving fragile ecosystems. Four examples of the nature of some of challenges that need to be overcome can be found in analyses of (i) water-use and (ii) nitrogen-use efficiencies, (iii) the contribution of biological nitrogen fixation to soybean nitrogen balance and (iv) the widespread process of intensification of agriculture and other challenges at the farming system level.

French and Schultz (1984) put forward the idea that it should be possible to establish a limiting value for the slope of the yield/seasonal rainfall relationship for wheat crops in southeast Australia, and that analysis of the downward excursions with respect to that limit should help to establish the causes of limitations, other than water, to yield (Figure 7 in Chapter 2). Although the interpretation of the precise meaning of the limiting boundary is open to criticism and the value of the approach can be substantially improved if crop performance is related to crop evapotranspiration (rather than rainfall) and if observation is combined with modelling (Sadras, 2005; Sadras and Angus, 2006), the over-riding message is that many crops are limited (or co-limited) by factors other than water and under-perform in terms of water use or availability. Some of these responses are attributable to environmental factors outside the control of the farmer, for example evaporative demand or soil condition (Sadras and Angus, 2006), but there are many indications that correct management of soil fertility, weed infestation or crop pathogens offer ways of improving crop use of the water resource (Angus and van Herwaarden, 2001; French and Schultz, 1984; Sadras, 2005; Sadras and Angus, 2006) and, lest it be forgotten in the pursuit of efficiency, yield. There have been some attempts to apply this framework to crops other than wheat (Loss et al., 1997; Zhang et al., 2000; Grassini et al., 2009) but the message remains the same: there are many unused opportunities for increasing yield. At the other end of the water availability scale, it has been shown that water productivity in rice can be markedly increased by agronomically oriented management (e.g. Tabbal et al., 2002). Agronomic work, guided by crop physiological principles, will play an important part in reducing the gap between attainable and actual yields. In the context of scarce R&D funding, the case has been advanced for prioritising agronomic solutions to narrowing the yield gap, particularly in poorer countries, over alternative investments in genetic solutions for drought adaptation (Marris, 2008).

Concerns about the role of nitrogen fertilisers is at the heart of the discussion about how to feed an expanding world population. In spite of certain arguments, meeting global food demand while protecting fragile ecosystems from inappropriate expansion of cropped areas is impossible without artificially fixed nitrogen (Box 2 in Chapter 1). Hence, mitigating the negative impacts of reactive nitrogen leakage outside the currently exploited agro-ecosystems (Cassman et al., 2003) must become a research focus. With current technology, even under the best management, some undesirable leakage and volatilisation of applied nitrogen appears to be inevitable due to the common mismatch between nitrogen availability and crop uptake capacity (Angus, 2001). Nevertheless, many farmers use nitrogen in an unnecessarily inefficient way, often because of insufficient attention to the quantification of indigenous sources of nitrogen (availability at sowing, in-season mineralisation, rainfall) (Chapter 8). Opportunities exist for generation of decision rules and techniques for improving nitrogen management accounting for spatial variation in soil, interaction between water and nitrogen supply and uncertain seasonal rainfall (Chapter 19). The success or failure of these initiatives will be strongly influenced by the approaches selected and the degree to which these are informed by crop physiological principles.

A recent analysis by Salvagiotti et al. (2008) of some 637 data sets for soybean-*Bradyrhizobium* responses (yield, biological nitrogen fixation) to N fertiliser application contains, among several interesting insights and pointers to further research requirements, at least two surprising findings. The first is that it is not possible to estimate, with any degree of confidence, the partitioning ratio of nitrogen between aerial and subterranean biomass. The lack of reliable information as to this ratio means it is not possible to establish whether the nitrogen balance for high-yielding soybean crops is positive, neutral or negative. The second surprise is that it proved impossible to fully explain a range of estimates of fixed nitrogen that ranged between 0 and 337 kg N ha^{-1}. That these uncertainties relate to the functioning of the most widely sown grain legume on the planet speaks volumes for the need for appropriate studies.

World-wide, agriculture faces a set of common challenges, namely the need to increase production and profit with consideration of long-term environmental and social outcomes and food safety issues (Miller, 2008). These high-level challenges acquire particular nuances in specific countries and regions (Chapters 2–5). Intensification of agriculture, through the increase in rates of inputs, the number of crops per year, intercropping or a combination of these elements, appears as an obvious way to increase yearly production rates in robust agro-ecosystems. More intense use of the more productive land could allow for the conservation of resources in less productive, environmentally fragile parts of the landscape (Loneragan, 1997). Implementation of any form of intensification on a strong knowledge base will require research in many issues, some old and others new, ranging from crop characteristics such as duration of crop cycle, competition for radiation, water and nutrients between successive or simultaneous crops, other forms of crop interference not mediated by availability of resources (allelopathy, changes in soil micro-flora and weed communities), on stubble dynamics, through to the optimisation of the mix of crops within cropping systems. A solid set of physiological tools and concepts (e.g. critical periods for grain yield determination, capture and efficiency in the use of resources) on their own or integrated in mathematical models are valuable aids in the design of new cropping systems aimed at exploiting the synergies of tailored cultivars and improved management practices.

6. CONCLUSIONS

The above illustrations of insufficiently explored issues, although clearly incomplete and strongly influenced by personal preference, constitute strong arguments for the need for continued investment in crop physiology. These, and other issues, need to be explored at crop level, in the field, and in the context of the whole crop cycle, from sowing to harvest. Success in this endeavour will require the development of new techniques (e.g. DNA probes for root morphology and functionality) or the systematic application of already available equipment (e.g. radiative frost chambers). Fieldwork will need to be complemented by experiments in glasshouses and controlled environments, but the final reality check will be how well the frameworks developed under those conditions prove useful in the field, across years and sites.

Crop simulation models, improved to incorporate new knowledge about soils, crop physiology and atmospheric processes, will continue to act as powerful tools for integrating information about the many processes underlying the formation and realization of yield. Also, these models will continue to prove irreplaceable in exploring new situations (such as can arise from alterations in agronomic practice) and in providing multi-year and multi-environment perspectives impossible to obtain by direct experimentation.

While it is probable that improvements will continue to be made in model algorithms designed to capture, say, crop development and NCE, it is to be hoped that there will be a much more marked improvement in model capacities to deal with root system functioning and with crop biomass partitioning. These are needed to restore the necessary balance between the elements of current deterministic models, as improvement in our understanding of canopy function prior to anthesis has tended to get ahead of our capacity to describe root functioning. Effective ways of dealing with phosphorus in soil and plant, biological effects of rotations, inter-plant hierarchies with the crop and soil spatial heterogeneity constitute further, potentially important, hurdles. Modellers and crop physiologists should be able to contribute to both issues.

The interdisciplinary connectivity at the crop physiology/breeding interface should continue to improve as practitioners of both disciplines continue to gain a better appreciation of limitations and opportunities on both sides of the interface. Balls' concern about crop physiology as a retrospective science needs to be superseded by a more mature appreciation of mutual benefits. At the very least, his concern was probably based on a static view of crop improvement and farmers' needs. Currently, it is hard to conceive of a breeding programme that does not incorporate some notions of crop physiology. Point successes in identifying easy-to-see attributes which contribute to stress tolerance (e.g. ASI in maize) may show the way to the future, and if molecular markers could be developed for 'invisible' attributes such as osmotic adjustment (Kiani et al., 2007), this interface may become more active in future.

Changes in agronomic practice, driven by the intensification of agriculture, greater concern for the environmental effects of agricultural practices, climate change and the need to ensure sustainability, will all continue to generate new issues requiring attention from crop physiologists. A recent example is the potential effects of direct drilling into stubble on delayed seed germination, more heterogeneous seedling establishment and increased plant susceptibility to root lodging. Another is the development of plant types and management procedures necessary for successful intercropping (Section 5 in Chapter 3). Evaluating the likely effects of increased frequency of high temperature episodes associated with climate change will require the development of reliable species-specific response functions that can handle the effects of timing, intensity and duration of stress episodes (Section 2.4). Mitigation of reactive nitrogen losses from agro-ecosystem will require research to improve the fit between crop nitrogen demand and fertilisation. Improving the domain of applicability of crop models will be an important and necessary by-product of improvement of our understanding and predictive capacity of processes which require extrapolation into future conditions or regional agro-ecosystem coverage.

Over the recent past, redirection of funds and institutional support towards molecular approaches to plant biology and towards ecosystem level studies have had a negative effect on research activity in crop physiology and agronomy, as reflected in changes in institutional structures and budgets. This process, in addition to constituting a substantive threat to continuing progress in the field, is a tragedy of lost opportunities. Thus, in spite of the declared interest in agriculture that prefaces many projects (e.g. Minorsky, 2003) much molecular work is misdirected. Examples are studies of drought tolerance based on germination or on seedling responses to *blitzkrieg* desiccation, aiming at plant survival rather than growth and yield, insufficiently linked to the evolutionary and agronomic realities of crop species, focused on lower levels of organisation with no clear up scaling pathway (Figure 4 in Chapter 1) and overlooking significant trade-offs (Chapter 9). Some thoughtful commentaries on these issues can be found in Passioura (2006), Sinclair et al. (2004), Sinclair and Purcell (2005), Hammer et al. (2004, 2006), and Struik et al. (2007). Lack of balance in research activities across levels of organisation from genes to ecosystems deprives those working at the molecular end of the chain from establishing useful partnerships with those focusing on the crop level [with a very few notable exceptions (Ghiglione et al., 2008; Xue et al., 2006)], and reduces the understanding of agroecosystem processes by those researching at ecosystem and global levels. In these disconnections can be found the seeds of many misdirected efforts (Sinclair and Purcell, 2005) and poorly grounded ideas (Box 2 in Chapter 1; Box 1 in Chapter 9). Crop physiologists will need to seek opportunities to interest administrators, molecular biologists and ecologists in the workings of crops. Crop physiologists are uniquely qualified to work at the crop level, and are uniquely placed to bridge the gaps between crops and upstream and downstream disciplines. There are just too many challenges that need to be faced and too many new exciting tools being developed to step back and allow others to re-discover the wheel.

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