

# 13 Plant–Plant Interactions in Coastal Dunes

M.L. MARTÍNEZ and J.G. GARCÍA-FRANCO

## 13.1 Introduction

Biotic interactions among plants have long been recognized as important in determining community structure and dynamics (Pickett 1980). Interactions range from negative to positive and function simultaneously. The result is a balance among mechanisms that cause a gradient of potential effects. In general, it is accepted that as the abiotic stress increases, so will the importance of positive interactions, and the opposite occurs when physical stress is reduced, and the importance of competition is expected to increase (Bertness and Callaway 1994). In coastal dunes, in particular, high environmental heterogeneity generates the possibility of the occurrence of a wide variety of interactions among plants. The number of studies on plant–plant interactions in these environments has increased during the last decades (see Table 13.1) and has shown that both positive and negative interactions are important, although the abiotic environment exerts an important control as well. However, although the successional gradients and dynamics have been widely studied in these environments (for example, Cowles 1899; Yarranton and Morrison 1974; Lichter 2000), there have been few studies of the relative impact of the different interactions during different successional stages. In this chapter we will focus on the most studied plant–plant interactions of the literature on coastal dunes: facilitation, competition, and epiphytism. We will review the information reported in the literature and will include our own data, to test the prediction that positive interactions are more frequent during the environmentally harsh early successional stages, when the sand is highly mobile, while competition and epiphytism become more frequent as the system stabilizes and the plant cover increments.

**Table 13.1.** Chronological survey of the literature on plant–plant interactions studied in dune communities throughout the world, including successional stage, location and nature of the study. (The list is not exhaustive but merely suggestive.) Unlike field experiments, field data refer to observations without previous manipulation

Authors	Interaction	Successional stage	Location	Type of study
Barbour (1970)	Competition	Early	USA	Greenhouse
Yarranton and Morrison (1974)	Facilitation	Stable	Canada	Field data
Pemadasa and Lovell (1974)	Competition	Early to stable	United Kingdom	Greenhouse
Mack and Harper (1977)	Competition	Stable	United Kingdom	Greenhouse
Silander and Antonovics (1982)	Competition, facilitation	Early to stable	USA	Field experiments
De Jong and Klimkhamer (1988)	Facilitation	Early	The Netherlands	Field experiments
Ehrenfeld (1990)	Competition	Early to stable	Worldwide	Literature review
Barros-Henriques and Hay (1992)	Competition	Early to stable	Brazil	Field experiments
Kellman and Kading (1992)	Facilitation	Stable	Canada	Field experiments
Olf et al. (1993)	Competition	Early to stable	The Netherlands	Field experiments
Jungerius et al. (1995)	Competition	Early	The Netherlands	Field data
Alpert and Mooney (1996)	Facilitation	Early	USA	Field data
García-Franco (1996)	Epiphytism	Stable	Mexico	Field data
García-Franco and Rico-Gray (1996)	Parasitism	Stable	Mexico	Field data
García-Franco and Rico-Gray (1997)	Parasitism	Stable	Mexico	Field data
Veer (1997)	Competition	Early to stable	The Netherlands	Field experiments
Kooijman et al. (1998)	Competition	Early to stable	The Netherlands	Field experiments
Vázquez et al. (1998)	Facilitation	Early	Mexico	Greenhouse
Lammerts et al. (1999)	Competition, facilitation	early to stable	The Netherlands	Field experiments
Lichter (2000)	Competition	Early to stable	USA	Field experiments
Shumway (2000)	Facilitation	Early	USA	Field experiments
Martínez et al. (2001)	Facilitation	Early	Mexico	Field data

## 13.2 Facilitation

Facilitation occurs when the establishment of a plant is enhanced by the amelioration of the environmental extremes provided by previously established plants. Because of the frequent disturbance events in the form of sand deposition, and because of the environmental harshness (drought, low nutrients, temperature extremes, intense solar radiation) experienced by dune plants, such positive interactions are expected to occur in these communities. Studies that examine facilitation in coastal dunes are scarce and have shown these interactions to be frequent but not always present. This interaction has been demonstrated for dunes from different latitudes (Canada, The Netherlands, USA and Mexico) (Table 13.1). In general, facilitation seems to occur mostly during the early stages of succession, although it has also been observed during late successional stages, when the dunes are covered by forests (Table 13.1). Descriptive field data and field experiments have demonstrated that beneath the canopy of established plants, late colonizers show better establishment of seedlings (Yarranton and Morrison 1974; Kellman and Kading 1992). In general, the result of these facilitative interactions is a spatial aggregation of the interacting species (Yarranton and Morrison 1974; Kellman and Kading 1992; Callaway 1995).

In South Wellfleet, Massachusetts (USA), Shumway (2000) observed that the two herbaceous sand dune species (*Solidago sempervirens* and *Ammophila breviligulata*) grew larger, were more likely to flower, produced a larger number of seeds and were in better physiological conditions (higher midday water potentials, tissue nitrogen and photosynthetic efficiency) beneath the nitrogen-fixing shrubs of *Myrica pensylvanica* than beyond its shade. Similarly, Martinez (2003) found that in the tropical coastal dunes of La Mancha (central Gulf of Mexico), the shade (with significant lower temperature and sand accretion) of the also nitrogen-fixing shrub *Chamaecrista chamaecristoides* was beneficial for seedling establishment of two tall perennial grasses, *Schizachyrium scoparium* and *Trachypogon plumosus* (Table 13.2). Although survival in the shade only was significantly different for *T. plumosus*, in both species the only individuals that reached a mature state and reproduced were those growing beneath *C. chamaecristoides*. Furthermore, adult long-term survival was greater beneath the shade of the shrub than beyond it and reproduction was exclusive to the shade (Table 13.2). As a result of these positive interactions, the studied grasses plus an additional annual (*Triplasis purpurea*) and a herbaceous perennial composite (*Pectis saturejoides*) were significantly closer to *Chamaecrista* than expected by chance (Table 13.3). This spatial aggregation was maintained throughout the seasons of the year: winter (with strong winds), dry and rainy seasons, except for the annual *Triplasis purpurea*, in which the facilitative interaction was not observed when this species was only present in the seed bank during the rainy

**Table 13.2.** Environmental conditions and seedling survival in two contrasting locations: exposed sand and protected sites beneath the facilitative shrub, *Chamaecrista chamaecristoides* (*P* significant differences between the two conditions after a t-test; – not tested statistically)

	Exposed	Protected	<i>P</i>
<b>Environment</b>			
Maximum midday photosynthetic active radiation ( $\mu\text{mol s}^{-1} \text{m}^{-2}$ )	1964	996	0.05
Maximum temperature on the sand surface ( $^{\circ}\text{C}$ )	64	53	0.05
Maximum temperature in the air ( $^{\circ}\text{C}$ )	39	39	n.s.
Nitrates in the sand (mg/l)	0.14	0.16	n.s.
Phosphates in the sand (ppt)	2	2.6	n.s.
Organic matter (%)	0.16	0.12	n.s.
Water content in the sand (mg/g)	70	66	n.s.
Maximum gusts of wind (km/h)	120	90	–
Maximum sand accretion (cm)	22	7	0.05
<b>Seedling survival</b>			
<i>Schizachyrium scoparium</i> (%)	1	6	n.s.
<i>Trachypogon plumosus</i> (%)	0	6	0.01
<b>Long-term adult survival</b>			
<i>Schizachyrium scoparium</i> (years)	1	3	–
<i>Trachypogon plumosus</i> (years)	0	3	–
<b>Reproductive effort (at age 1 year)</b>			
<i>Schizachyrium scoparium</i> (spikes per individual)	0	4	0.05
<i>Trachypogon plumosus</i> (spikes per individual)	0	3	0.05

season. In both examples, the areas beneath benefactors were environmentally improved, resulting in beneficial effects on the surrogate species. The areas beneath the canopies of the shrub were more shaded, had lower temperatures on the surface of the sand, and registered a decreased impact of disturbances by substrate mobility. Additional studies focused on facilitation in coastal dunes have demonstrated that the sand in the vicinity of early mobile dune colonizers had higher nutrient and moisture levels (McLeod and Murphy 1977; De Jong and Klinkhamer 1988; Alpert and Mooney 1996), which were probably also beneficial for late colonizer species.

Facilitation has also been demonstrated in forests that have developed on dunes during late successional stages. In the Wasaga Beach dunes, Ontario (Canada), Kellman and Kading (1992) found that the establishment of pine seedlings of *Pinus strobus* and *P. resinosa* was enhanced beneath the pre-established oak trees *Quercus rubra*. Similarly, at La Mancha, Muñiz (2001) registered seedlings of 18 tropical rain forest tree species growing in the shade of isolated *Diphysa robinoides* leguminous trees that were separated (by at least 20–30 m) from the nearest tropical rain forest patch. No seedlings were

**Table 13.3.** Comparison of observed and expected mean distances (cm) ( $\pm$  standard error) from different species to the nearest shrub of *Chamaecrista chamaecristoides* in a mobile area in coastal dunes located on the Gulf of Mexico. Distances were measured during three seasons: nortes (see text), dry and rainy; – no data; *P* represents significant differences between observed and expected distances; t-test)

	<i>N</i>	Observed	Expected	<i>P</i>
Winter with strong winds				
<i>Schizachyrium scoparius</i>	58	50.0 $\pm$ 4.5	87.7 $\pm$ 10.6	<0.001
<i>Trachypogon plumosus</i>	65	52.5 $\pm$ 2.6	87.7 $\pm$ 10.6	<0.01
<i>Triplasis purpurea</i>	200	51.7 $\pm$ 2.4	87.7 $\pm$ 10.6	<0.001
<i>Pectis saturejoides</i>	113	43.1 $\pm$ 2.9	87.7 $\pm$ 10.6	<0.001
Dry				
<i>Schizachyrium scoparius</i>	54	58.1 $\pm$ 4.1	110.1 $\pm$ 10.12	<0.001
<i>Trachypogon plumosus</i>	31	63.8 $\pm$ 7.8	110.1 $\pm$ 10.12	<0.001
<i>Triplasis purpurea</i>	8	44.0 $\pm$ 8.1	110.1 $\pm$ 10.12	<0.01
<i>Pectis saturejoides</i>	135	51.7 $\pm$ 3.6	110.1 $\pm$ 10.12	<0.001
Rainy				
<i>Schizachyrium scoparius</i>	36	38.97 $\pm$ 4.8	100.3 $\pm$ 9.8	<0.001
<i>Trachypogon plumosus</i>	51	52.5 $\pm$ 4.01	100.3 $\pm$ 9.8	<0.001
<i>Triplasis purpurea</i>	–	–	–	–
<i>Pectis saturejoides</i>	129	46.6 $\pm$ 2.8	100.3 $\pm$ 9.8	<0.001

found in the surrounding grassland. The above suggests a facilitative phenomenon although other factors such as predominant seed dispersal beneath these leguminous trees could be playing an important role rather than establishment.

In summary, the evidence described above indicates that facilitation is a frequent (but not necessarily obligate) (see Houle 1997) interaction in the dune environments. The literature focused on facilitation in dunes has shown that they occur during early and late successional stages, as well as between different growth forms: annuals and perennials, and even between different tree species.

### 13.3 Competition

Competition is the mutually adverse effect of organisms on one another, because they are striving for a common resource. Although the literature on competition between plants is vast, relatively few studies have focused on dune environments. In general, competition increases as the system becomes naturally covered by vegetation (Table 13.1) and also as a result of human

management. Not all authors agree with this statement. For instance, Barros-Henriques and Hay (1992) have argued that because resources are limited during early succession, competition is expected to occur during these stages, as niche overlap is high, while Lichter (2000) concluded that dune succession is best explained by differential colonization and competitive abilities of plants.

Some general trends observed as a result of competition are: decreased plant weight, cover and growth of individual species (Mack and Harper 1970; Silander and Antonovics 1982; Pemadasa and Lovell 1974); and restrictions in the distribution of species such as *Cakile* spp. due to competitive exclusion by *Ammophila arenaria* (Barbour 1970). It has also been observed that competition for light occurs in late successional stages (Olf et al. 1993). Furthermore, in early successional stages, the initial colonizers are gradually replaced by alleged competitive interactions with late colonizers (Silander and Antonovics 1982; Martínez et al. 2001). Probably, competition for light is also important in this case.

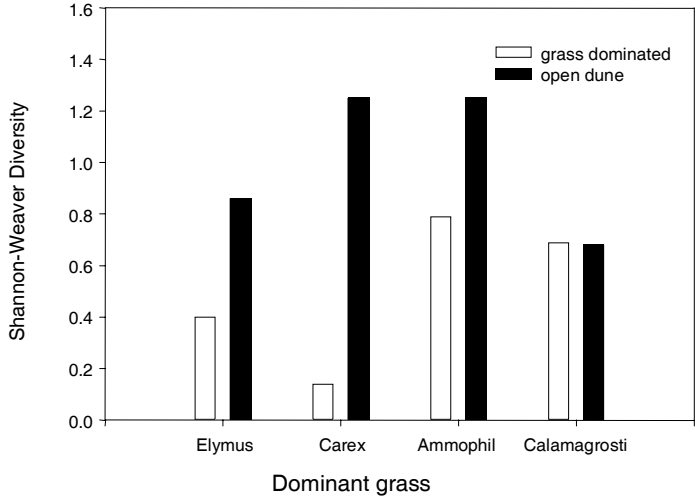
Specific and well-known examples of competition between plants growing on coastal dunes are grass encroachment and the invasion of exotic plants. In both cases it is argued that species are replaced by competition (Kooijman et al. 1998).

### 13.3.1 Grass Encroachment

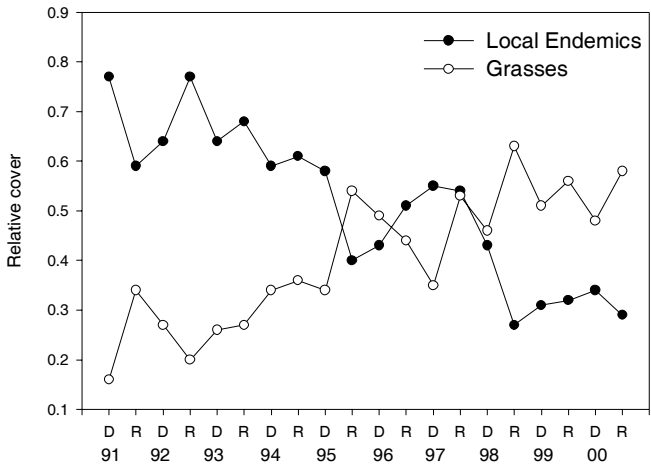
The encroachment by grasses occurs when aggressive and competitive grasses (e.g. *Elytrichia atherica*, *Calamagrostis epigejos*, *Ammophila arenaria*, *Schizachyrium scoparium*) (Kooijman and Haan 1995; Martínez et al. 2001) spread on dune areas, leading to the dominance of a few tall grass species over formerly species-rich communities. This process has been observed under varying circumstances: atmospheric Nitrogen deposition (beneficial for the grasses) or a reduced disturbance regime due to a decreased recreational use or a few or no herbivores (such as rabbits) that initiate small-scale substrate mobility (Kooijman and Haan 1995; Martínez et al. 2001). In particular, grass encroachment is considered problematic on the coasts of The Netherlands, Belgium, Germany and certain parts of France, because of drastic reductions in diversity due to the dominance of grasses (Fig. 13.1; Veer 1997). In The Netherlands, habitat management techniques such as mowing or grazing have been used to re-initiate substrate mobility, which stimulates the growth and development of locally lost pioneer vegetation, and combats grass encroachment in the dune areas (Jungerius et al. 1995). However, caution must be taken before destabilizing dunes for management purposes, since this can lead to a mobile dune field with serious erosive problems.

The paucity of evidence for grass encroachment in tropical dunes is due to the lack of studies in these latitudes. In an ongoing 10-year-long study at La

**Fig. 13.1.** Decreased species diversity in sites dominated by different grass species in The Netherlands. (Modified from Veer 1997)



**Fig. 13.2.** Decreased relative cover of local endemics as grass cover increases in Mexican sand dunes during a ten year period (1991–2000). Plant cover was registered every 6 months during the dry (D) and rainy (R) periods. (Modified from Martínez et al. 2001)



Mancha, tall grasses (*Schizachyrium scoparium* and *Trachypogon plumosus*) have been gradually increasing their cover, while the Mexican endemics (*Chamaecrista chamaecristoides* and *Palafoxia lindenii*) are becoming locally extinct (Fig. 13.2; Martínez et al. 2001). This extremely rapid stabilization and species replacement has probably been enhanced by the removal of cattle since 1988 (M.L. Martínez, unpubl. data) when the dune system became a nature reserve under protection. Interestingly, the rabbit population has also started to increase, and appears to gradually reverse this situation by reducing the density of the dominant grasses. It has been quantified that in the 480-m<sup>2</sup> dune area monitored during 10 years the maximum plant cover of the domi-

nant grass *Schizachyrium scoparium* was 60 % before rabbits were observed, and decreased to 45 % 2 years after these herbivores had increased their population noticeably (M.L. Martínez, unpubl. data), resulting in larger areas of exposed sand and rendering the sampled area more mobile. Slowly, local endemics started to increase their cover since the dominant grasses became less abundant and apparently their competitive impact had decreased. In this sense, herbivores may greatly affect the end result of plant–plant interactions.

### 13.3.2 Invasive Plants

The introduction of exotic species to stabilize mobile sand was a common practice in the past. For instance, because of its high tolerance to burial, the European marram grass (*Ammophila arenaria*) was widely used for this purpose. In many occasions, the grass became naturalized, and spread widely, replacing the native sand binders, such as the endemic *Desmoschoenus spiralis* (New Zealand) and the native Tasmanian species *Festuca littoralis*, *Spinifex hirsutus* and *Acaena novae-zelandiae*. In the west coast of North America it replaced the native *Ammophila breviligulata* (van der Maarel 1993a, b).

Conifers have also been introduced to stabilize dune systems in Europe. The large-scale introduction of pines to dune systems has resulted in the shading out of most of the dune flora, including rare species, and the lowering of the water table through a combination of an increased transpiration and artificial drainage. Some additional woody invasive species that eliminate native and endangered species through competition are: *Hippophae rhamnoides*, *Acer pseudoplatanus*, *Lupinus arboreus*, *Pinus* spp., *Rhododendron ponticum* (van der Maarel 1993a). In The Netherlands, common Reed (*Phragmites australis*) overgrows native and characteristic slack species such as the tussock forming sedge (*Schoenus nigricans*) and the grass (*Parnassia palustris*) resulting in the local extinction of such species and thus, in biodiversity loss (Grootjans et al. 1991).

Recent studies have demonstrated that the introduction of alien and exotic species is not necessarily needed for stabilization, since indigenous dune species can be used successfully to stabilize the shifting substrate (Carter 1991). Thus, the current new trends in management policies prevent further unwanted species invasions and employ an ecological approach using the available indigenous species.

Because of the frequent disturbance events, coastal dunes are also prone to natural invasions by species from other communities. Castillo and Moreno-Casasola (1996) found that throughout the coastal dunes located along the Gulf of Mexico, 71 species (10.83 %) were considered coastal, while the remaining 89.8 % (573 plant species) were either ruderal/secondary species or from other nearby communities. These natural invasions poten-



tially lead to an increased biological diversity of the dune communities. However, when the invaders exert a negative impact on the community they displace native species by competing for resources, interfering with successional processes, altering disturbance regimes and disrupting food chains. Thus, dune conservation should aim at preserving the natural dynamics of these systems, where both coastal and non-coastal species coexist, maintaining species diversity.

## 13.4 Epiphytes

### 13.4.1 Non-Parasites

Approximately 23,000 of all plant species are epiphytic. They are taxonomically widespread among vascular plants (Kress 1989), although more than half of them are orchids, ferns, bromeliads, or cacti (Benzing 1990). Typically, the ecological interaction between non-parasitic epiphytes (named epiphytes hereafter) and their host woody plants has been described as commensalism. Epiphytes obtain support and adequate environmental conditions without a metabolic relationship, while host plants (phorophytes) are neither benefited nor damaged (Lütte 1989). Nevertheless, in some cases a high epiphyte infestation results in competition for light and nutrients. It also generates high mechanical pressure that breaks the branches and stems, creating microenvironmental conditions that could promote the establishment of host pathogens (Benzing 1990).

Epiphytic plants are distributed worldwide, although vascular epiphytes are more abundant in tropical or sub-tropical subtropical latitudes. There are only a few reports of epiphytes for coastal dune systems. Australia has only one epiphytic species recorded, while six vascular epiphytes and one non-vascular epiphyte have been reported for Europe (Table 13.4). The American Continent is the best-known region, with 32 vascular epiphyte species recognized from different coastal ecosystems (Table 13.4). In terms of epiphytes, La Mancha, Mexico, is the best-studied place.

Because epiphytes are dependent on phorophytes, an advanced successional stage with woody plants established is critical for epiphyte colonization in the dune systems. According to García-Franco (1996), these host trees and shrubs should first have growth of heavy branches, a clumped distribution, and a relatively long time of exposure so that the seeds from the epiphytes can be dispersed onto these branches. Secondly, epiphyte seed dispersal should occur during the season when seeds can be better dispersed by wind (winter season for bromeliads, orchids, and ferns; García-Franco 1996) or by birds (dry season for aroids and hemiparasites; López de Buen and Ornelas 2001).

And thirdly, the distance between the sources of epiphyte seeds and the dune system should be such (ca. 50 m) that successful establishment of phorophytes is favored while individuals are dispersed (García-Franco 1996).

In addition, environmental harshness, (drought, light intensity, strong wind speed, nutrient limitation and constant salt spray) can limit epiphyte distribution and diversity (García-Franco 1996). For example, vascular epiphytes, such as *Tillandsia concolor*, *Tillandsia ionantha*, and *Tillandsia paucifolia*, considered as full or nearly full sun-plants and xerophytes (sensu Benzing 1990), endure drought and are able to establish in the young forests and shrubs at La Mancha, Mexico. In contrast, other species such as *Brassavola nodosa*, *T. usneoides*, and *T. schiedeana* resemble full sun and xerophytic plants, but they are less tolerant to the dune environment and grow in the tropical rain forest established on stabilized dunes at the same dune system (García-Franco 1996).

**Table 13.4.** Epiphytes and parasites species recorded on coastal dune systems of different regions of the World. *p* Parasite, *e* epiphyte. (Survey from Davy and Costa 1992; Dillenburger et al. 1992; van der Maarel 1993a, b; Rhoades 1995; García-Franco 1996)

Geographic location	Family	Species
Africa (Kenya, W. Africa, Senegal)	Scrophulariaceae	<i>Striga gesneroides</i> (p)
America (Brazil, Cuba, Galapagos, Mexico, USA)	Araceae	<i>Anthurium scandens</i> (e) <i>Philodendron bipinnatifidum</i> (e)
	Bromeliaceae	<i>Aechmea bracteata</i> (e) <sup>a</sup> <i>A. recurvata</i> (e) <i>Hohembergia peduncularis</i> (e) <i>Tillandsia aëranthos</i> (e) <i>T. concolor</i> (e) <sup>a,b</sup> <i>T. ionantha</i> (e) <sup>a,b</sup> <i>T. paucifolia</i> (e) <sup>a,b</sup> <i>T. recurvata</i> (e) <sup>a</sup> <i>T. schiedeana</i> (e) <sup>a,b</sup> <i>T. streptophylla</i> (e) <sup>a</sup> <i>T. usneoides</i> (e) <sup>a,b</sup> <i>T. utricularia</i> (e) <sup>a</sup> <i>T. xerographica</i> (e)
	Cactaceae	<i>Hylocereus undatus</i> (e) <sup>a</sup> <i>Lepismium cruciforme</i> (e) <i>Rhipsalis baccifera</i> (e) <i>Selenicereus testudo</i> (e) <sup>a</sup>
	Cuscutaceae	<i>Cuscuta acuta</i> (p)
	Cytinaceae	<i>Bdallophyton americanum</i> (p) <sup>a</sup>
	Lauraceae	<i>Cassytha filiformis</i> (p)
	Moraceae	<i>Ficus aurea</i> (e)
	Loranthaceae	<i>Psittacanthus caliculatus</i> (p) <sup>a</sup> <i>P. shiedeana</i> (p) <sup>a</sup> <i>Struthanthus venetus</i> (p)

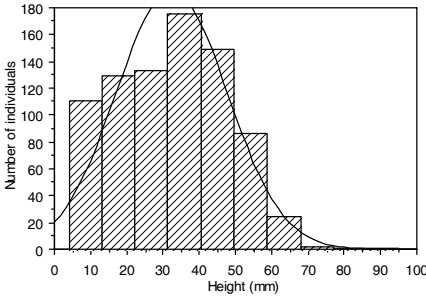
Epiphytes living on relatively ephemeral supports (small branches and stems) frequently fall to the ground due to the wind action (Matelson et al. 1993). This is particularly important in coastal zones, where constant sea-shore winds play a key role in the community dynamics. At La Mancha, Mexico, strong winds occurring during hurricanes and winter storms (both with wind speeds potentially higher than 80 km/h) affect epiphytes. Frequent dramatic population changes could occur when reproductive individuals and juvenile stages growing on the exterior upper branches fall to the ground by the wind action. For example, studies by García-Franco and Martínez (unpubl. data) showed that when strong northerly winds occur, the smallest individuals of *Tillandsia ionantha*, *T. concolor* and *T. balbisiana* are the ones that most frequently fall to the ground (Fig. 13.3). Probably, the loss of the smallest individuals has a demographic impact since recruitment possibilities might be decreased as well.

Geographic location	Family	Species
	Orchidaceae	<i>Brassavola cucullata</i> (e) <sup>a,b</sup> <i>B. nodosa</i> (e) <sup>a,b</sup> <i>B. tuberculata</i> (e) <i>Cattleya intermedia</i> (e) <i>Myrmecophyla tibicinis</i> (e) <sup>a,b</sup> <i>Oncidium cebolleta</i> (e) <sup>a,b</sup> <i>Oncidium pumilium</i> (e) <sup>b</sup>
	Polypodiaceae	<i>Polypodium aureum</i> (e) <i>Polypodium polypodioides</i> (e) <sup>a</sup> <i>Microgramma vacciniifolia</i> (e) <i>Microgramma</i> sp. (e) <sup>a</sup> <i>Vittaria lineata</i> (e)
Asia (Japan, New Guinea)	Viscaceae	<i>Phoradendron tamaulipensis</i> (p) <sup>a</sup>
	Cuscutaceae	<i>Cistanche helipaea</i> (p)
	Lauraceae	<i>Cassytha filiformis</i> (p)
Europe (Croatia, Yugoslavia)	Moraceae	<i>Ficus casica</i> spp. <i>caprificus</i> (e) <i>Parietaria lusitanica</i> (e)
	Polypodiaceae	<i>Polypodium australe</i> (e) <i>Sedum telephium</i> spp. <i>maximum</i> (e) <i>Selaginella helvetica</i> (e) <i>Umbilicus pendulinus</i> (e)
	Non-vascular (liverworts)	<i>Riccia</i> spec. <i>Plur.</i> (e)
Oceania (Australia, New Zealand)	Lauraceae	<i>Cassytha filiformis</i> (p)
	Polypodiaceae	<i>Pyrrosia serpens</i> (e) <i>Amysema preissii</i>

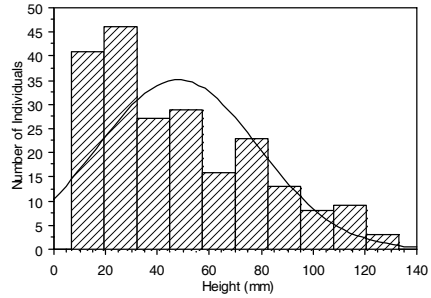
<sup>a</sup> Species recorded for CICOLMA

<sup>b</sup> Species full sun and xerophyte

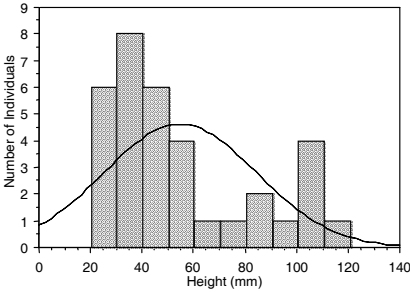
a)



b)



c)



**Fig. 13.3.** Frequency of bromeliads fallen to the ground as a consequence of strong winds (80 km/h) occurring at La Mancha in 2000. Data for: **a** *Tillandsia ionantha*, **b** *Tillandsia concolor*, **c** *Tillandsia balbisiana*

Finally, epiphytes may have an indirect impact on the coastal dune dynamics. Potentially, a medium to heavy epiphyte infestation on the long-lived shrubs established since earlier successional stages (e.g. *Randia laetevirens* at La Mancha) could help reduce wind speed and then sand carry-over as well, promoting dune stabilization and plant colonization.

### 13.4.2 Parasites

A special case of epiphytism are the parasitic interactions (Benzing 1990), where there is physiological communication between the plants by means of the haustorium, resulting in a negative impact on the host while the parasite benefits from the interaction by drawing water and nutrients (Kuijt 1969). According to the level of host dependence, parasitic angiosperms have been divided into hemiparasites (photosynthetic obligate and facultative para-

sites), and holoparasites (non-photosynthetic obligate parasites), and they are further divided into stem and root parasites (Stewart and Press 1990).

Approximately 1 % of all known plant species are parasites (Norton and Carpenter 1998). Parasitic angiosperms are distributed worldwide, and all plant communities contain at least one parasitic species interacting with one or several hosts (Stewart and Press 1990). Despite their wide distribution, there are few parasite records on the coastal dune ecosystems and the ecological studies are fewer. One parasite species has been reported for Africa and Oceania, and two more for Asia (Table 13.2). The American continent has seven parasitic species recorded, most of them from the coastal dunes of La Mancha, Mexico (Table 13.2).

The distribution of parasites is obviously host dependent, but the environmental conditions and the parasite's environmental range also limit their distribution (García-Franco and Rico-Gray 1996). Therefore, parasite establishment on coastal dune systems appears to be restricted to advanced successional stages, and, probably, depends on the presence of some specific susceptible woody plant species. In general, stem hemiparasites as mistletoes are bird dispersed (Howe and Smallwood 1982; van der Pijl 1982; López de Buen and Ornelas 2001) and root holoparasites are primarily mammal dispersed (Kuijt 1969). For example, in the coastal dune system of La Mancha, Mexico, *Phorandendron tamaulipensis*, stem hemiparasite, shows strong preference for *Randia laetevirens* growing on semi-mobile dunes. The overlapping fruiting periods between the host and the parasite coupled with the behavior of *Minus polyglottos* (Passeriforme: Mimidae) which perches and eats fruits from both plant species, enables the seeds of the parasites to be dispersed and deposited on the branches of new hosts (García-Franco 1996). In contrast, in the tropical rain forest developing on stabilized sand dunes at La Mancha, *Bdallophyton americanum* (root holoparasite) is dispersed by mice and ants (García-Franco and Rico-Gray 1997). This parasite always grows on the superficial fine roots (first 10 cm depth and 0.55 cm diameter) of *Bursera simaruba* that develop during the rainy season (García-Franco and Rico-Gray 1996). Dispersers such as mice and ants deposit seeds on the ground close to the host's roots. In general, the seeds from parasitic plants are chemotropic, which means that germination occurs in response to a chemical gradient through the contact with the host's epidermis (Stewart and Press 1990; Kuijt 1969). The environmental clues that trigger the germination of the parasite seeds still remain largely unknown.

### 13.5 Conclusions

Different plant-plant interactions occur throughout the different successional stages of the dune environment. It was generally accepted that early

succession was controlled by environmental factors (i.e. soil nutrient status) and positive interactions, while late succession was controlled by vegetation processes such as competition (Lammerts et al. 1999). Contrary to this hypothesis, our observations and the literature indicate that the interactions mentioned in this review are not restricted to a certain successional stage. For example, facilitation and competition occur during both early and late stages. Epiphytes and parasites are more abundant during advanced successional stages, when woody vegetation is present, although they can also be found in earlier stages and relatively more mobile sites of the dune environment, as long as hosts (woody vegetation) are available. In all cases, plant–plant interactions play a key role in community dynamics, in terms of substrate stabilization and species successional replacement. In many occasions, plant–plant interactions are greatly affected by the activities of animals. Herbivory can reduce plant–plant competition while epiphytes and parasites frequently depend on their dispersal vectors (often animals) in order to colonize a new host.

The importance of plant–plant interactions adds a new dimension to the proper approach to coastal dune conservation and restoration. Frequently, restoration projects aim at the reintroduction of previously existing species. Research to date indicates that interactions and processes should also be restored.

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