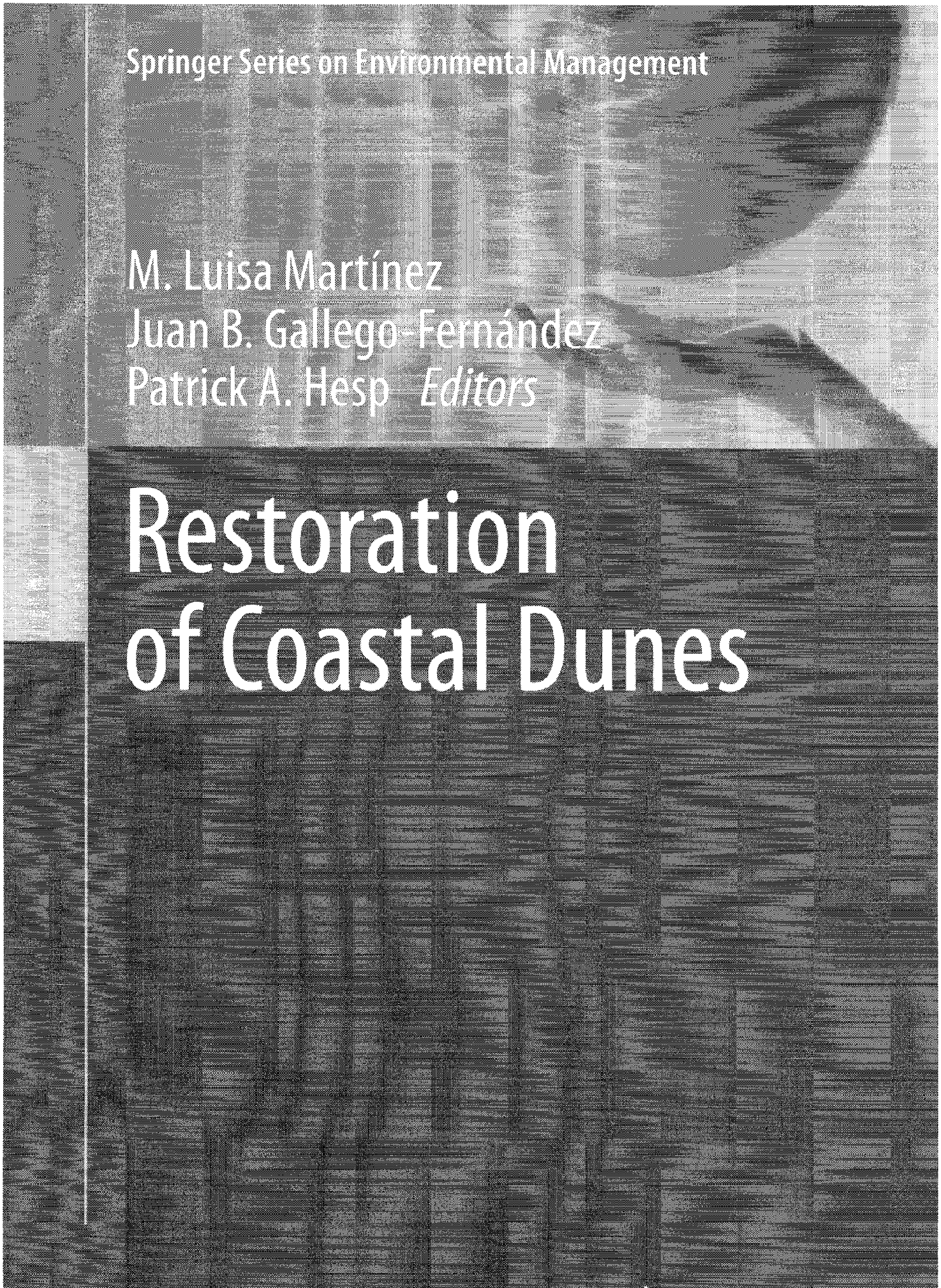

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Restoration of Coastal Dunes

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Chapter 14
The Impacts on Natural Vegetation Following the Establishment of Exotic *Casuarina* Plantations

Patricia Moreno-Casasola, M. Luisa Martínez, Gonzalo Castillo-Campos and Adolfo Campos

14.1 Introduction

Casuarina equisetifolia Forst. (Casuarinaceae) (hereafter referred to as *Casuarina*) also called Australian-pine or beach she-oak, is a nitrogen-fixing, medium to large evergreen tree, 15–30 m or more high and with a diameter at breast height (DBM) of up to 50 cm. It is native to the tropical and subtropical coastlines of Australia, Southeast Asia, Melanesia, Polynesia, and New Caledonia. However, it has become pantropical as its native range has expanded through its introduction and later naturalization, because of its ability to reproduce in dense stands from abundant self-seeding and its high tolerance to extreme environmental conditions, such as drought and low nutrient availability. It is also tolerant to burial by sand. In Mexico, the natural expansion of *Casuarina* on coastal dunes seems to be limited, but nevertheless in the past decades this species was widely planted, and nowadays it is considered as an invasive in the national invasive species inventory (March-Mifsut and Martínez-Jiménez 2007).

Casuarina plantations have frequently been used outside its distribution range in order to stabilize coastal dunes in Senegal (Mailly and Margolis 1992) and Mexico; for coastal protection (Mascarenhas and Jayakumar 2008); and in coastal dune restoration projects (meaning revegetation) in India (Homji 1995), Cuba (Izquierdo et al. 2005), Puerto Rico (Parrotta 1995), and Mexico (Espejel and Ojeda 1995).

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These introductions have had a strong negative impact on local soil attributes, as well as on the population, community, and ecosystem levels (Gordon 1998).

14.1.1 Impact of Casuarina on Soil Attributes

Casuarina is an actinorhizal species that is able to grow in nutrient-poor soils, mainly because of its ability to fix N_2 in the root nodules through a mutualistic symbiosis with the actinomycete *Frankia*, and by its capacity to develop mycorrhizae (Gordon 1998). Because of this, *Casuarina* plantations may largely modify soil characteristics, especially in coastal dunes.

Sand dune soils have high leaching rates, with a resulting low level of nitrogen. When nitrogen fixers form large stands, local nitrogen cycling may be altered significantly (Vitousek 1986), resulting in higher phosphorous and nitrogen concentrations in leaves as well as enriched soil-nutrient levels (Versfeld and van Wilgen 1986). This enriched soil has been observed in *Casuarina* stands too. Leaf and branch litter beneath *Casuarina* trees can be 5–10 cm thick (Fernald and Barnett 1991), with organic matter accumulating at rates that are similar to those recorded in boreal and subalpine forests (Mailly and Margolis 1992; Izquierdo et al. 2005).

14.1.2 Impact of Casuarina on Vegetation

The high rates of litterfall accumulation and nutrient accumulation beneath *Casuarina* stands can have contrasting effects at the community level. On the one hand, it has been observed that a higher nutrient content in the soil (organic matter and nitrogen) can actually facilitate natural regeneration and thus catalyze succession in deforested and degraded sites (Parrotta 1995). However, contrasting patterns have also been observed by Bond (1993); Duever et al. (1986); Gordon (1998); and Abdel Wahab (1980). These authors found that *Casuarina* plantations can also suppress recruitment of other species, although the mechanisms causing inhibition or shifts in recruitment patterns have not been investigated in detail. Evidence suggests that because *Casuarina* trees reduce light availability, and have higher evapotranspiration rates than the native vegetation (Gordon 1998), they are likely to modify competitive interactions and can out-compete native species (Abdel Wahab 1980; Gordon 1998), by suppressing seedling growth and establishment. Because very few plants grow beneath the canopy of *Casuarina*, Bond (1993) has named this tree a "keystone weed".

14.1.3 Impact of Casuarina on the Fauna

Introduced *Casuarina* plantations also affect the native fauna. For example, when these trees are planted on foredunes they fall over easily during strong winds, making nesting habitat inaccessible to sea turtles (*Caretta caretta*) (Schmid et al. 2008). In addition, the removal of *Casuarina* plantations was favorable to the skink (*Eutropis bibronii*) in India, increasing its population, probably because of the availability of more suitable space for basking activity. It was also attributable to the regeneration of *Spinifex littoralis* at sites previously occupied by *Casuarina*, since skinks were found to be associated with this plant (Subramanean and Vikram Reddy 2010).

In their native distribution range *Casuarina* stands may have both negative and positive impacts on the bird community. Arnold (1988) found that the total number of birds was lower in *Casuarina* forests than elsewhere (*Eucalyptus wandoo* open forest and *E. accedens* open forest with *Dryandra sessilis*). In addition, because *Casuarina* provides little food for most nectar-feeders, their densities are usually lower in *Casuarina* forests than in other communities (Arnold et al. 1987). On the other hand, Frith (1979) studied the ecology of land birds in Aldabra Atoll and found that many endemic birds were closely associated with *Casuarina*. In southeastern Queensland Bentley and Catterall (1987) found that *Casuarina* corridors and linear remnants of forests were used by birds to move between forest fragments.

In brief, *Casuarina* is usually considered an invasive species outside its native distribution range, with a negative impact on the population, community, and ecosystem functioning, generally resulting in arrested natural succession. Because it is oftentimes used in Mexico to stabilize coastal dunes and increase vegetation cover.The goal of this chapter was to analyze the impact of *Casuarina* stands on the natural regeneration process occurring beneath the canopy of this tree. We also wanted to explore whether local conditions modify the impact of this species in terms of passive restoration and natural regeneration on tropical dunes in Mexico. We asked: is it possible to recover the natural coastal dune vegetation after reforestation with these exotic–invasive *Casuarina* trees?

14.2 Study Site

The study site is located to the north of the port of Veracruz, in the outskirts of the city (Fig. 14.1). The area is being actively transformed because of the growing infrastructure for commercial activities in the Port. This area is an extensive sand plain where the river Río Medio drains. Nowadays the site is mostly urbanized (Fig. 14.1).

The coastline is oriented in an almost east-west direction, and faces north-west. Sand is transported both by ocean currents and by wind, and extensive dunefields

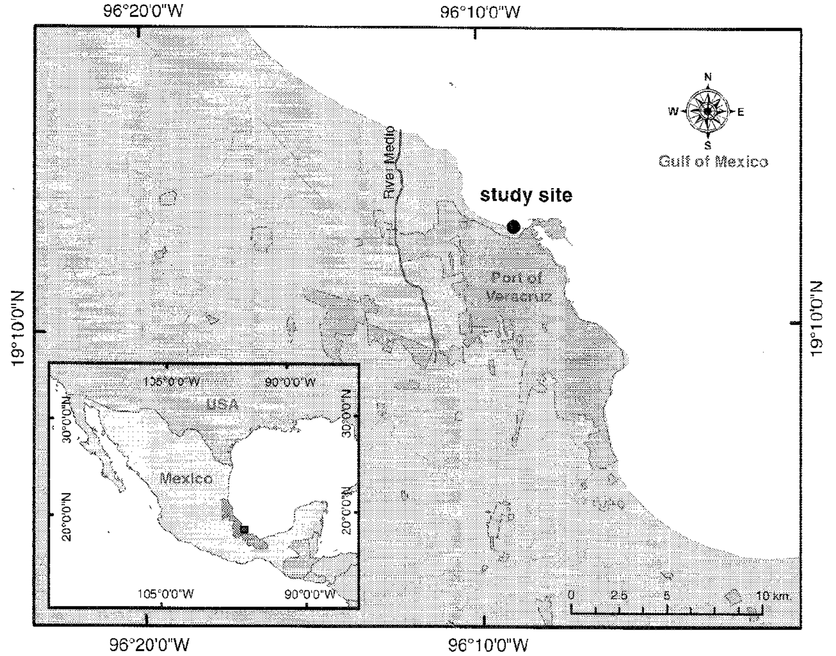

Fig. 14.1 Location of the study site

with transgressive and parabolic dunes can be found in the region (López-Portillo et al. 2011). Long-term (40 years) means that annual precipitation is 1,500 mm, and mean monthly temperatures range from 17 °C in January to 33 °C in June. Eighty percent of the rain falls between May and October and the dry season occurs from November to April.

In 1885, Ignacio Ochoa Villagómez, an agronomist, constructed an artificial dune at the study site with the basic idea that it would protect urban infrastructure by stopping the sand blowing from nearby mobile dunes, until the trees and grasses that were introduced stabilized the sand. Australian sea-pines (*C. equisetifolia*) were planted, since they tolerate considerable sand accretion and the low nutrient and moisture conditions of sand dunes. This plantation largely prevented the sand from blowing into the neighboring city and then became protected and remained a cornerstone for the local inhabitants (Siemens et al. 2006). It was known as "*La Pinera*" (the pine grove), until the present century when the port began to expand: *La Pinera* was partially cut down and its surface contracted to less than 50 % of its original area.

14.3 Methods

14.3.1 Vegetation

The *Casuarina* artificial forest was subdivided into three stands with different mean trunk width. Diameter at breast height (DBH; approximately 1.50 m) was measured in five 10-m × 10-m plots in each of these three forest stands, allowing us to define them as young (smallest DBH values), mature, and old *Casuarina* plots (largest DBH values). These *Casuarina* stands were planted on different dates and in rows parallel to the coast. In each of these different-aged stands two transects of five 10 × 10 m adjacent quadrats were marked, parallel to the shoreline, so that we could observe changes in the community composition in each of these stands. In each quadrat, species were collected for identification, and plant cover per species was estimated with the Westhoff and van der Maarel (1978) scale. For comparison, the same type of sampling took place in a coastal tropical dry forest growing on sand dunes further inland, on a slope of the same dune system, but where *Casuarina* trees had not been planted. Finally, another set of ten 10 × 10 m quadrats was sampled on a foredune area stabilized with *Casuarinas*, 5 km north of the study site, with a DBH structure similar to the mature stand (referred to here as *Casuarina*). For each stand Shannon's diversity index was calculated. In all cases, once species were identified, the type of fruit was determined, either from herbarium species or from the literature and then a dispersal syndrome was assigned to each species. A matrix was built with the species cover values and analyzed with a principle component analysis (PCA) ordination using the program PCOrd (McCune et al. 2002).

14.3.2 Soil Attributes

Soil profiles 1 m deep were excavated at two sites in each stand, close to the quadrats where floristic composition was sampled. In each horizon soil samples were collected and transported to the laboratory. Samples were air dried and sieved (up to 2 mm) before chemical analyses were performed. The following analyses were carried out following standard procedures as described by Sparks (1996): pH in water was measured using a 1:2 relation, total organic carbon (Walkley and Black 1934), total nitrogen using the Kjeldahl method, exchangeable cations (Ca, Mg, Na, K) through soil lixiviation with ammonium acetate 1 N pH 7, $CaCO_3$ percentage was calculated using the neutralization method of HCl with a known concentration and a posteriori titulation of the excess acid with NaOH. In a saturation extract the following chemical properties were determined: electrical conductivity (dS m^{-1}), calcium (mg L^{-1}), magnesium (mg L^{-1}), potassium (mg L^{-1}), sodium (mg L^{-1}), chloride (mg L^{-1}), bicarbonates (mg L^{-1}), and sulfates (mg L^{-1}). The saturation extract is an important aqueous solution because many soil properties, such as the composition of soluble salts and electrical conductivity, are related to the plant's response to salinity.

14.4 Results

14.4.1 Vegetation

The three *Casuarina* stands (young, mature, and old) were dominated by *C. equisetifolia* trees, but these showed very different DBH sizes (Fig. 14.2). Although they could not be correlated with planting date or age class (because we could not find that information in the local archives), they showed a different size structure, and thus it could be assumed that they were planted at different times.

A total of 100 species were collected in the area, and eight species were not identified. Species richness and diversity varied among stands (Fig. 14.3). Species richness and diversity were very low in the *Casuarina* plots growing on the dry sand of foredunes. These values increased considerably on the young *Casuarina* plots in humid areas, where several herbaceous, shrub, and tree species begin to appear. With increasing age, species richness, and diversity beneath *Casuarina* continued increasing (Fig. 14.3). Highest diversity and mean species richness were recorded in the tropical dry forest and in the old *Casuarina* plots. The highest belong to the tropical dry forest, which represents the original vegetation, or at least the less disturbed vegetation at the site.

The plant community structure was also different between the study sites (Fig. 14.4). For comparison, trees, shrubs, and woody lianas were grouped into a single class, and herbs and creepers into another. In the *Casuarina* plots located in the drier area, the only tree species that we found was the Australian pine, with only three herbaceous species (Fig. 14.4a). Young and mature plots showed an

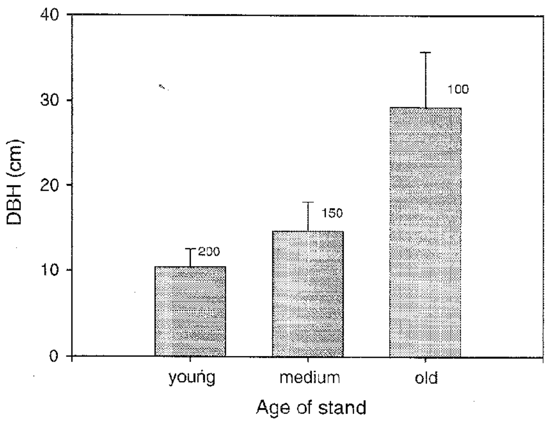

Fig. 14.2 Mean diameter at breast height (DBH) and standard deviation of *Casuarina* trees, in a *Casuarina* plantation growing on coastal sand dunes. Numbers above bars indicate total number of individuals measured in ten 10-m × 10-m plots. The first diameter class was interpreted as a young stand, the medium-sized class as a mature stand, and the larger-stemmed trees as the oldest plantation

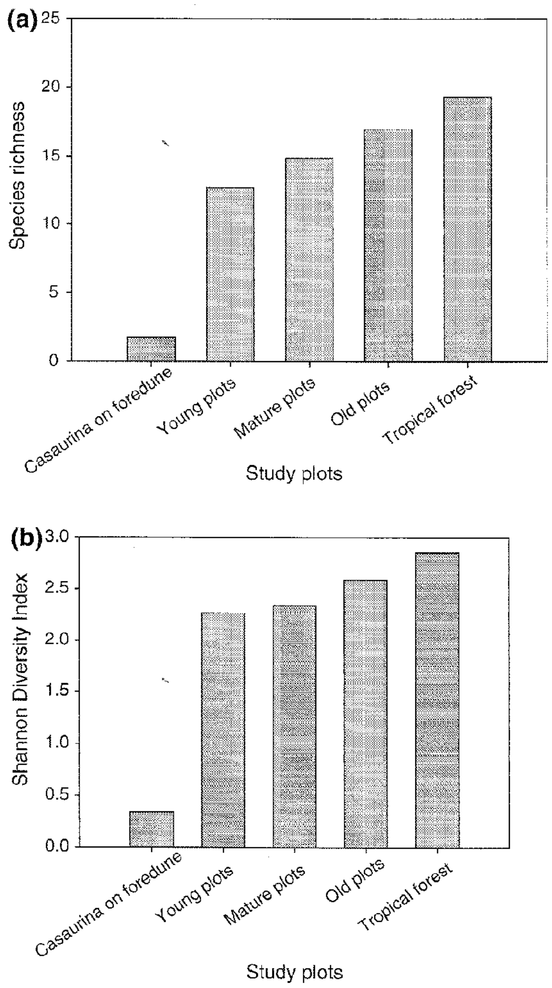

Fig. 14.3 **a** Species richness and **b** diversity values (Shannon diversity index) for the five stands. Highest diversity and species number were found in the tropical dry forest and in the older *Casuarina* plots

increased number of tree species. Finally, in the old *Casuarina* stand and the tropical dry forest we found that 90 % of the species that we recorded were trees. Interestingly, we found a larger number of trees species in the old *Casuarina* stands than in the tropical dry forest.

Species composition was also different in the study plots. In the young stand, herbs (*Urochloa maxima, Commelina erecta, Palafoxia lindenii*), shrubs and small trees (*Citharexylum ellipticum, Solanum diphyllum, Trixis inula, Lycianthes lenta, Malvaviscus arboreus, Bursera simaruba*), and woody climbers (*Gonolobus barbatus* and Passilfora spp.) were found. Mature stands have a similar number of herbaceous and woody species as the young stand, but species richness and

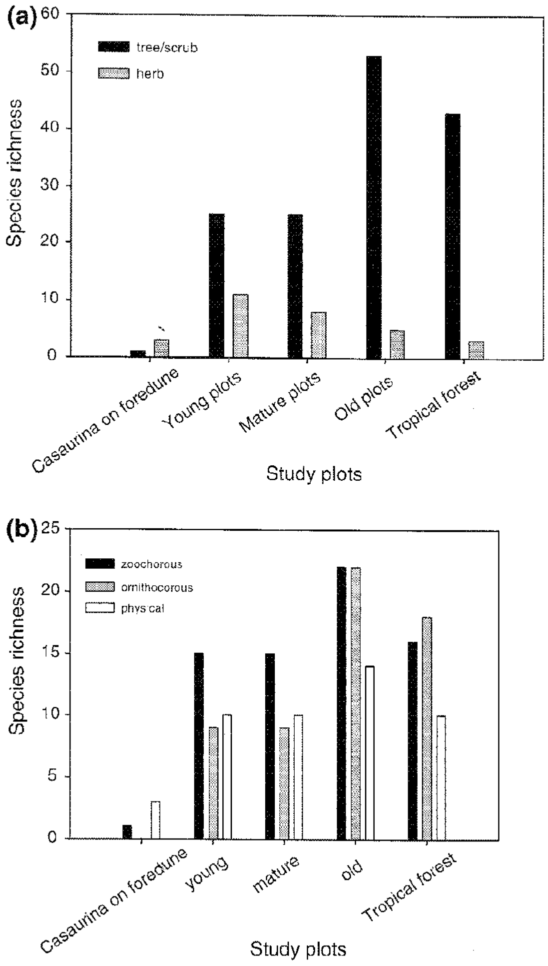

Fig. 14.4 **a** Species number of the different growth forms recorded in each stand. **b** Species number in relation to different seed dispersal syndromes in different stands

diversity was slightly higher (Fig. 14.4a). In the older *Casuarina* plots, the number of woody species increased considerably (*B. simaruba, Sideroxylon celastrinum, Cestrum dumetorum, Chiococca coriacea, Jacquinia macrocarpa, Piper amalago*, and *Passiflora serratifolia)* and were more abundant. In this case, species richness and diversity values were higher and closer to those found for the tropical dry forest. In contrast with the above, the *Casuarina* plantation on a nearby foredune showed a very low species richness, with only one tree species (and besides *Casuarina*) and three typical dune herbaceous pioneers (*Ipomoea pes caprae, P. lindenii, Bidens pilosa*; Fig. 14.4a). In brief, community richness and composition has changed drastically over time (Fig. 14.5).

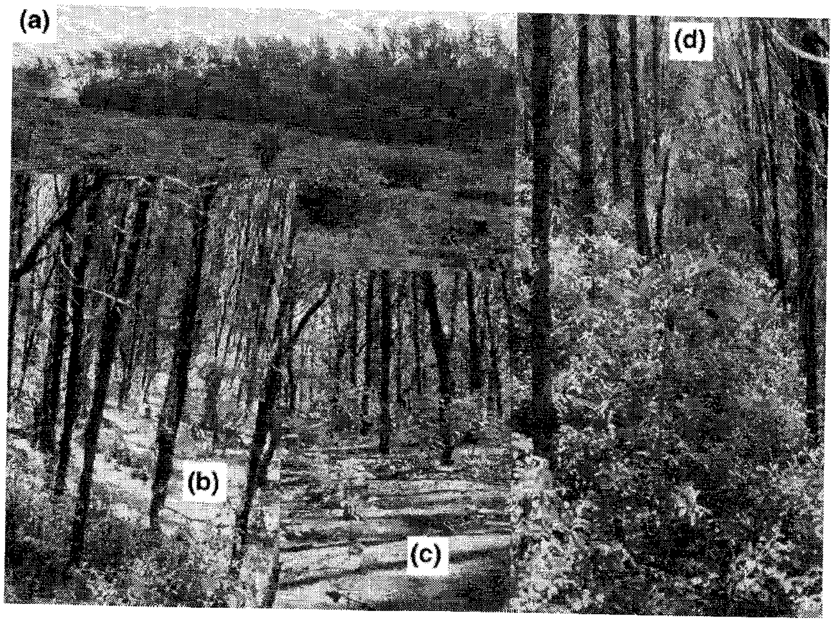

Fig. 14.5 The vegetation in the understory of a planted *Casuarina* forest has changed over time. **a** Panoramic view of the forest growing on previously mobile dunes. **b** Understory species growing beneath *Casuarina* stands. Many species are from nearby tropical rain forest. **c** Understory plants growing beneath *Casuarina* and **d** increasing vegetation cover, height, and diversity

14.4.2 Dispersal Syndrome

The analysis of the dispersal syndrome of the fruits from all the species that we found in the sampled plots shows differences among the five stands. Species whose seeds are dispersed by physical vectors (wind, water, explosion or gravity) were predominant in the *Casuarina* plots located on the foredunes (75 %) (Fig. 14.4b). In the old plots and tropical dry forest, the percentage of species with seeds dispersed by abiotic vectors decreased to 24 and 23 % respectively. Zoochorous species increased in all four *Casuarina* stands in comparison to the *Casuarina* forest on foredunes. In particular, ornithochorous species were most abundant in the oldest stands, as well as in the tropical dry forest (38 and 41 % respectively). It is evident that the most frequent species have an ornithochorous or zoochorous dispersal syndrome, with the exception of *C. equisetifolia*.

The species that we observed in more than ten quadrats, except for *Casuarina*, are commonly found in tropical dry forest and in old secondary forests. Most of them are trees or shrubs, except *G. barbatus* and *P. serratifolia*, two woody lianas that were also found in the tropical dry forest. Most of these species are dispersed by animals (Fig. 14.6; Table 14.1). Woody species were predominantly

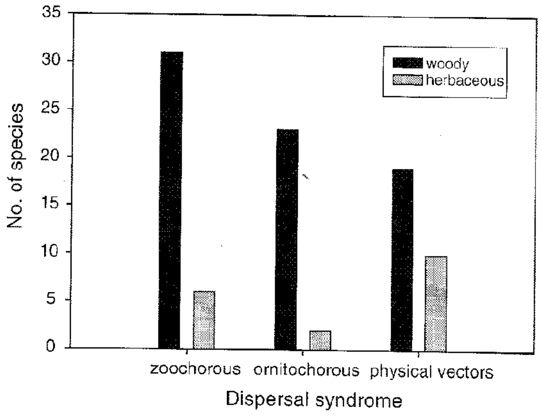

Fig. 14.6 Relationship between seed dispersal syndromes and species growth forms (woody and herbaceous)

Table 14.1 List of the most frequent species and their seed dispersal syndrome

Zoochorous	Ornithochorous	Physical vectors
Acacia cornigera (L.) Willd.	*Bursera simaruba* (L.) Sarg.	*Casuarina equisetifolia* L.
Chiococca coriacea M. Martens & Galeotti	*Casearia corymbosa* Kunth	*Gonolobus barbatus* Kunth
Hamelia patens Jacq.	*Cestrum dumetorum* Schltdl.	*Matayba clavelligera* Radlk.
Lycianthes lenta (Cav.) Bitter	*Citharexylum ellipticum* D. Don	
Malvaviscus arboreus Cav.	*Coccoloba barbadensis* Jacq.	
Passiflora serratifolia L.	*Jacquinia macrocarpa* Cav.	
Piper amalago L.	*Rhacoma uragoga* (Jacq.) Baill.	
Solanum diphyllum L.	*Rivina humilis* L.	
Xylosma panamensis Turcz.	*Sideroxylon celastrinum* (Kunth) T.D. Penn.	
	Stemmadenia donnell-smithii (Rose) Woodson	

zoochorous and ornithochorous, while herbaceous species were mostly dispersed by physical vectors and a few were zoochorous (Fig. 14.6).

The PCA analyses of the 49 plots located in the five study sites explained 85.20 % of the accumulated variance (Axis 1 and 2, Fig. 14.2). Axis 1 shows a gradient from samples that combine *Casuarina* with other species (in the old *Casuarina* stands) and tropical dry forest (located on the left and in the center of the ordination space). In this case, the occurrence and dominance of *Casuarina* in the old stands separates them from those located in the tropical dry forest. In turn, plots from young and mature *Casuarina* stands with very few species were located in the center of the ordination space along Axis 1, and clearly separated from the

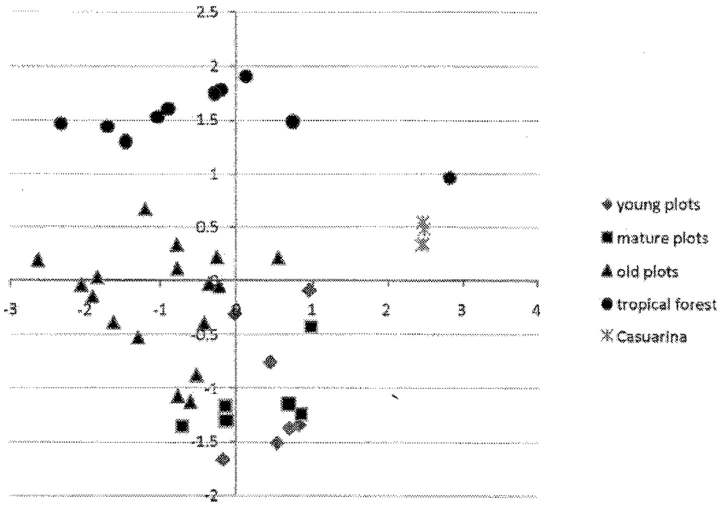

Fig. 14.7 Principle component analysis (PCA) variance–covariance explaining 85.20 % of the accumulated variance. *Axis 1* shows a gradient from samples of tropical dry forest and *Casuarina* plots with other species (old, mature, young) and plots from *Casuarina* stand with hardly any accompanying species. *Axis 2* shows a gradient of species richness, from tropical dry forest plots, rich in species, to species-poor young and mature plots

old stands and the tropical dry forest. *Casuarina* stands in nearby foredunes showed very few accompanying species and were located at the extreme positive end of Axis 1. That is, foredune plots with almost a monospecific *Casuarina* stand were different from the rest of the quadrats that we sampled (Fig. 14.7). Axis 2 shows a gradient from tropical dry forest plots (at the top), rich in species and with no *Casuarina* trees, old plots (also rich in species, along the center) and mature and young plots (species poor) at the negative end of Axis 2.

14.4.3 Soil Analysis

Dune soils where *Casuarina* stands were planted are considered Endogleyic Arenosols, in which horizons are formed mainly by fine, loose sand, representing 75 % of the mineral fraction. A thin homogeneous layer of fresh organic remains, from the litter of *Casuarina* trees, was found to be in direct contact with the mineral sandy soil. In the young *Casuarina* stand, we observed an AC horizon (0–8 cm) in the soil, with a very dark brown color (10YR2/2) dominant in 80 % of the horizon and a more pale brown color (10YR6/3) in 20 % of the soil. We observed very few fine roots (<1.0 mm). The color of horizon Cg (8–56 cm) was a dominant dark brownish grey (10YR4/2) mixed with yellowish brown diffuse mottles (10YR5/8), which is evidence of a slight hydromorphism.

In the plots with mature *Casuarina* trees, horizon A1 (0–5 cm), showed a dark brown color (10YR2/2), with organic remains slightly decomposed and numerous very fine roots, less than 1 mm in diameter. The lower horizon, Cg (5–60 cm) is predominantly pale brown (60 %–10YR6/3) and brown (40 %; 10YR4/3), indicating a slight hydromorphism. This last horizon had very few roots.

In the old *Casuarina* plots, some of the trees have already fallen down and the wood is dry. In this area, the phreatic level is only 30 cm deep. Horizon A1 (0–9 cm) in this site is very dark brown (10YR2/2) and medium-sized roots (with mean diameter ranging from 2 to 5 mm) are common. The next horizon, Cg (9–35 cm) was dark brownish grey (10YR4/2) with dark yellowish brown veins (10YR4/6) that follow the root distribution. This soil shows a greater hydromorphism than that found at the other two sites.

The chemical characteristics of the soil showed differences between the *Casuarina* stands. In general, pH values varied strongly from alkaline to extremely alkaline in the old *Casuarina* plots. The carbon concentration, in the first horizon, increased in the old plots. In this site organic matter is incorporated into the soil, thus more root activity was observed. The concentrations of exchangeable cations (Ca, Mg, K, Na) were, in all sites, higher in the upper horizons than in the lower, emphasizing the high to very high calcium and sodium values. The calcium carbonate concentration showed no significant variation between sites. The chemical composition of the saturation extract showed significant differences among sites (Table 14.2). For example, the ion concentration measured with electrical conductivity shows that there was a tendency to decrease from the young *Casuarina* stands to the old ones, a situation that can be attributable to the increment in organic matter content (FAO 1998). In this case, the electrical conductivity values indicate that soils are saline to moderately saline (Hillel 2000), so it is likely that the established plant communities are semi-tolerant to salinity. Soluble salts in the saturation extract are virtually restricted to sodium and calcium among the cations, and chloride and sulfate between the anions. This is consistent with the marine influence on the dune soils. The relative dominance of sodium is associated with the high levels of chlorine, while the abundance of calcium is related to high levels of sulfate (Richards 1954). Bicarbonate concentration tends to increase from the young plots to the old plots, a situation explained by the greater root and microbial activity in the older stands with a high CO_2 production, which generates bicarbonate.

14.5 Discussion

As expected, *Casuarina* was the dominant tree in all our study plots (except for the tropical dry forest, of course), creating an almost uniform canopy cover. Nevertheless, we found that natural regeneration is occurring in the hydromorphic soils, especially in the old *Casuarina* stands. Here, diversity and species composition were similar to the tropical dry forest growing on coastal dunes (tropical dry forest

Table 14.2 Chemical composition of the sand from *Casuarina* stands of different ages in two soil horizons (AC and Cg)

Site	pH	C (%)	N	$CaCO_3$	Ca^{2+} ($cmol_c\ kg^{-1}$)	Mg^{2+}	K^+	Na^+	EC (mS/cm)	Cl^- (meq/L)	HCO_3	SO_4	$Ca2^+$	Mg^{2+}	K^+	Na^+
					Exchangeable cations					Soluble anions and cations						
Young *Casuarina*																
AC (0–8 cm)	8.3	1.8	0.10	10.5	11.3	2.5	0.2	2.5	5.4	42.2	9.3	5.9	18.1	10.6	2.3	69.1
Cg (8–56 cm)	9.7	1.2	0.02	12.4	4.9	0.9	0.1	0.4	1.0	6.4	3.2	0.96	3.8	2.3	0.2	8.3
Mature *Casuarina*																
A1 (0–5 cm)	7.6	2.8	0.18	9.0	20.4	3.1	0.2	1.0	4.2	25.7	13.8	2.7	36.8	14.5	0.9	17.4
Cg (5–60 cm)	8.6	0.12	0.02	12.9	5.1	0.8	0.1	0.4	2.4	19.3	2.7	1.5	16.6	6.8	0.4	12.8
Old *Casuarina*																
A1 (0–5 cm)	9.6	7.1	0.37	10.3	12.4	2.6	0.3	5.4	3.7	20.3	25.7	4.3	9.5	20.6	0.9	51.7
Cg (9–35 cm)	9.1	0.18	0.03	12.8	5.3	1.4	0.1	0.5	1.2	8.8	4.6	1.1	4.8	3.2	0.2	10.0

stand): many of the tropical dry forest species were found in the old stands as well as tropical dry forests from close-by dunes (Castillo-Campos and Medina-Abreo 2005; Castillo-Campos and Travieso-Bello 2006). However, *Casuarina* stands on foredunes were species-poor, although the sizes of these trees were similar to the mature and old *Casuarina* stands on hydromorphic soils. Foredunes were between 2.5 and 3.5 m tall and soils were not hydromorphic.

Our results show that only under conditions of high moisture in the soil such as those occurring in the hydromorphic sand of the Port of Veracruz, can native species colonize the understory of *Casuarina* stands. These species are also found in nearby tropical dry forests growing on sand dunes. Thus, under these circumstances, removal of the exotic trees would probably accelerate the natural recovery of native species since they were already growing beneath the trees. It is also important to bear in mind that although recovery of natural vegetation is possible in the circumstances mentioned above, native species should preferably be promoted as the species for plantations because the risk of an aggressive exotic is always latent and potentially very damaging to biodiversity and the natural functioning of ecosystems. Native species can probably only grow beneath *Casuarina* trees under specific circumstances (hydromorphic soils).

Our studies concur with those of Parrotta (1995), who confirmed that in a degraded tropical coastal dune in Puerto Rico, up to 19 native forest species were established beneath a canopy of three exotic species: *C. equisetifolia, Eucalyptus robusta*, and *Leucaena leucocephala*. In our case, however, it was interesting that in the *Casuarina* stands growing on relatively drier foredunes and nonhydromorphic soils, we did not find any tropical dry forest species growing beneath the canopy of *Casuarina*. In fact, we observed significant differences between foredune and hydromorphic stands, both in growth forms and species richness and diversity.

We also found species that are common to coastal wetlands (*Hydrocotyle bonariensis, S. diphyllum, Syngonium podophyllum*). This provides further evidence of a humid substrate owing to the closeness of the water table, which is also shown by the hydromorphism of the soils analyzed. In the older *Casuarina* stands, the improved organic matter conditions of the substrate were enhanced by the hydromorphic attributes of the soil that tend to reduce mineralization rates of the organic residues.

Seed dispersal syndromes also changed in the different stands. In all of them we found species dispersed by wind and animals, although the number of species in each one differed. The relative importance of zoochorous species during colonization by native species in *Casuarina* plantations in degraded coastal dune vegetation was also found by Parrotta (1995) in Costa Rica. Here, and in coincidence with our results, the plantations that were introduced are probably acting as bird perching sites and seeds are constantly being introduced into the plots.

In summary, we observed that tropical dry forest species may colonize the understory beneath *Casuarina* stands under particular circumstances:

(1) There are neighboring tropical dry forests or remnants with abundant seeds to be dispersed into the abandoned stands.
(2) There are important bird populations.
(3) There are perching sites for birds.
(4) Soils are hydromorphic and water is not too limiting.

Certainly, in Mexico there is a great need to restore tropical dry forests growing on dunes, because most of them have disappeared in the region, and because these woody species are useful and people have cut down the trees without planting more to replace them (Moreno-Casasola and Paradowska 2009). Also, the introduction of cattle has resulted in vegetation loss. Frequently, and because the species grows fast and tolerates the extreme coastal dune environment, *Casuarina* trees have been used in reforestation programs in the tropics, ignoring the fact that it is an exotic and invasive species. However, in the humid swales and low-lying areas where litter can be decomposed at a relatively fast rate, restoration actions could be implemented to enhance the growth and establishment of tropical dry forest vegetation already growing in the understory. The gradual removal of the exotic tree would lead to an advanced state of natural regeneration.

It is noteworthy to highlight that the establishment of the tropical dry forest may take a long time. Locally, it is known that *C. equisetifolia* trees live 40–45 years. We observed that some of the trees in the old plots were already dying, which means that the natural regeneration and colonization process in the old stands has been occurring for about 40–45 years and still there were significant differences with the tropical dry forest stands. This implies that restoration by natural regeneration is a long process that lasts more than 4 decades.

Finally, although in high moisture conditions there is a potential for restoration beneath *Casuarina* stands, it is important to bear in mind that native species should preferably be promoted as the species for plantations since the risk of an aggressive exotic is always latent and potentially very damaging to biodiversity and the natural functioning of ecosystems.

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