Mycorrhiza (1997) 7:9–15

ORIGINAL PAPER

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Arbuscular mycorrhizae in a tropical sand dune ecosystem on the Gulf of Mexico

I. Mycorrhizal status and inoculum potential along a successional gradient

Accepted: 17 July 1996

Abstract Root samples of 37 species distributed on the beach and along a successional gradient (from mobile to stabilized areas) in a tropical sand dune system on the Gulf of Mexico showed that 97% of the species were mycorrhizal. The mycorrhizal inoculum potential of the sand from several dune areas was compared using two different bioassays. Firstly, the field rate of colonization by arbuscular mycorrhizal fungi of *Chamaecrista chamaecristoides* seedlings transplanted to random plots in the foredunes and in the mobile area was measured. The seedlings were harvested at intervals during 3 weeks to record mycorrhizal structures. In the mobile area, no mycorrhizal colonization was observed during the experiment. In the foredunes, hyphae and external mycelium were present in 40% of the seedlings as early as 8 days after transplanting. After 15 days, arbuscules and vesicles were observed in 60 and 20% of the seedlings, respectively, and after 21 days, 100, 46 and 20% of the seedlings showed hyphae, arbuscules and vesicles, respectively. Secondly, maize seedlings were transplanted to pots previously filled with sand from the foredunes, mobile dunes, grassland and a *Dyphisa robinoides* shrub area. After 1 month, the lowest mycorrhizal inoculum potential was recorded for the mobile dunes and the highest for the shrub area. As expected, mycorrhizal inoculum potential increased with dune stabilization.

Key words Tropical sand dunes · Arbuscular mycorrhizae · Mycorrhizal inoculum potential · Field colonization rate

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Introduction

In coastal sand dune ecosystems, pioneer plants are subjected to deficiency in major nutrients (N, P, K) and organic matter, wide fluctuation in soil moisture and temperature, injury from sand blasting and salt spray, as well as excessive erosion or accretion (Chapman 1976; Moreno-Casasola 1982; Barbour et al. 1985; Maun 1994). It is widely accepted that arbuscular mycorrhizae are important for the establishment, growth and survival of seedlings, particularly in marginal habitats, where the symbiosis improves stress tolerance (Daft et al. 1975; Rozema et al. 1986; Allen 1991; Barea and Jeffries 1995; Koske and Gemma 1995).

Previous studies on mycorrhizae in sand dune ecosystems showed that most colonizing plants are heavily infected by arbuscular mycorrhizal fungi (AMF) (e.g. Giovannetti and Nicolson 1983; Peterson et al. 1985; Puppi and Riess 1987; Koske 1988; Dalpé 1989; Koske and Halvorson 1989; Koske and Gemma 1990; Louis 1990), including species of Aizoaceae, Cyperaceae, Convolvulaceae and Commelinaceae (Koske 1988; Logan et al. 1989), families considered mainly to be non-mycotrophic (Gerdemann 1968; Trappe 1987). Examination of root samples from coastal dunes in Scotland indicated that the degree of AMF colonization varies with the plant succession, increasing from foredunes to fixed dunes (Nicolson 1960). Further studies also concluded that the infection percentage of roots and AMF spore abundance varies with position and season in such ecosystems (Nicolson and Johnston 1979; Jehne and Thompson 1981; Ernst et al. 1984; Giovannetti 1985; Puppi et al. 1986; Sylvia 1986; Gemma and Koske 1988; Koske and Halvorson 1989; Abe et al. 1994; Stürmer and Bellei 1994; Abe and Katsuya 1995). However, almost all we know about mycorrhizae in sand dunes comes from temperate environments (e.g. Nicolson 1960; Bergen and Koske 1984; Ernst et al. 1984; Sylvia 1986; Koske 1987; Koske and Tews 1987; Gemma and Koske 1988, 1989; Gemma et al. 1989; Koske and Halvorson 1989; Blaszkowski 1994).

In the Gulf of Mexico, there is a tropical sand dune system (La Mancha) with a very complex topography related to a high diversity of plant species, which includes all stages of stabilization from mobile to fixed dunes (Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986). In view of the low nutrient content of the sand dune substrates of this tropical ecosystem (Moreno Casasola et al. 1982; Valverde 1992), it was expected that a high percentage of species would be associated with AMF and that mycorrhizal inoculum potential would increase with dune stabilization. This paper reports the occurrence of AMF in species from different successional stages of this ecosystem, and compares the mycorrhizal inoculum potential of sand from four different areas. Since, in addition to spores, infected roots and mycelia can function as mycorrhizal propagules (Read et al. 1976), inoculum potential was measured by bioassays of extracted soils and intact substrates in field observations of infection rate.

Materials and methods

Study site

The study was conducted in the biological station "Centro de Investigaciones Costeras de La Mancha" (CICOLMA) situated in the central part of the state of Veracruz, on the Gulf of Mexico (19°36'N, 96°22'40"W) (Fig. 1). Details of the climate, which is Koëppen type Aw_2 (tropical forest, warm with seasonal rain in summer, although about 10% of precipitation falls in winter), and the climatic periods are reported by Moreno-Casasola (1982) and Castillo and Carabias (1982), respectively.

The prevailing winds are from the North (not from the ocean), so that the sand dunes of CICOLMA are of the parabolic type and are oriented N-S (Moreno-Casasola 1982). Moreno-Casasola and Espejel (1986) defined six zones considering sand movement, salinity and depth of the water table: the beach, embryonic dunes and foredunes, blowouts and active dunes, humid and wet slacks, a sheltered zone behind the foredunes and fixed dunes. Because of the temperature and precipitation regimes, this area is surrounded by tropical, semi-deciduous forest. A detailed description of the vegetation and physical factors of La Mancha sand dunes is given by Moreno-Casasola (1982, 1986, 1988), Moreno-Casasola et al. (1982), Moreno Casasola and Espejel (1986), and Dubroeucq et al. (1992).

Root sampling and mycorrhizal colonization

Root samples of 37 species were cut directly from plants collected at the beach, embryo dunes and foredunes, mobile and semi-mobile area, grassland, wet slacks and fixed dunes in July 1991, October 1991, April 1994 and/or August 1994 (mainly during the rainy season).

To analyze the successional and seasonal patterns of colonization by AMF, roots from three endemic species, distributed in different areas of the dunes were sampled in May and September 1994 (dry and rainy seasons, respectively). Attempts were made to sample in the windy season (November–February) but fine fresh roots were very hard to find. The species sampled were: *Trachypogon gouinii* Fourn. ex Hemsl. (Gramineae), which was collected in the foredunes, mobile areas and a stabilized area, *Palafoxia lindenii* Gray (Compositae), which was found in the foredunes, embryo dunes and mobile areas, and *Chamaecrista chamaecristoides* (Collad.) I. and B. (Leguminosae), which was sampled in the mobile dunes. The temperatures and precipitation in the years of root collection are given in Figure 2.

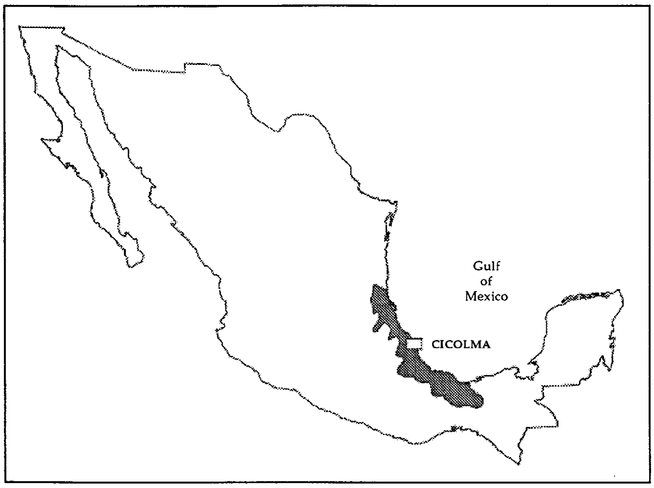

Fig. 1 Tropical sand dunes at the Centro de Investigaciones Costeras de La Mancha in Veracruz, Mexico

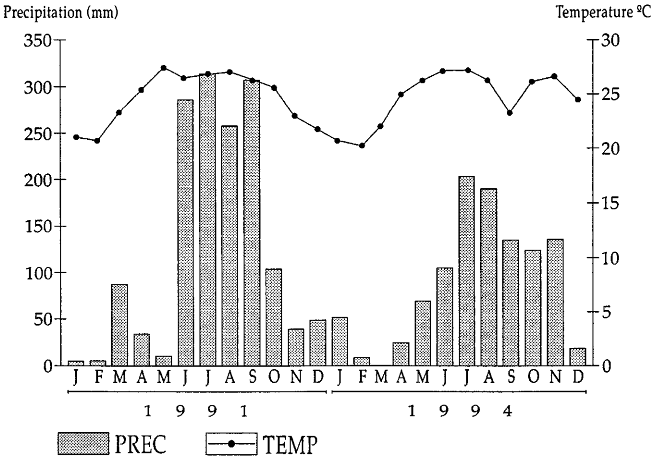

Fig. 2 The temperature (*Temp*) and precipitation (*Prec*) regimes of the root collection periods

At the moment of sampling, the roots were stored in 50% alcohol and subsequently cleared and stained with trypan blue for AMF colonization assessment (Koske and Gemma 1989). The root segments were subsampled, cut into 1-cm segments and mounted on microscope slides in acid glycerol to be examined by Nomarski differential interference contrast optics (× 40–100). AMF colonization percentage was measured using the line intersection method (Giovannetti and Mosse 1980). Mycorrhizal structures (hyphae, hyphal coils, vesicles or arbuscules) were only scored when they crossed the grid-line, and the results were expressed as percentage segments containing internal structures. Mycorrhizal colonization was measured in 100 root segments taken at random from a compound sample of at least 3 individuals per species. To compare the colonization percentages of *T. gouinii*, *P. lindenii* and *C. chamaecristoides* in the different seasons and dune areas, 50 root segments from 5 individuals per species and zone were examined.

The non-parametric analysis of variance (Kruskal-Wallis test) was used to test for significant differences in AMF colonization percentages of *T. gouinii* in the three different areas and between the dry and rainy seasons. For *P. lindenii* and *C. chamaecristoides,* the Mann-Whitney test was used for the same purpose (Zar 1974).

Mycorrhizal inoculum potential from different successional areas

To determine the mycorrhizal inoculum potential of the beach and different successional areas of the tropical dune system, two different experiments were undertaken:

Experiment 1:pot bioassay

Unsifted sand containing root fragments was collected at the end of the 1991 rainy season (October) directly from the rhizosphere of plants distributed in the foredunes, mobile dunes, grassland and a *Dyphisa robinoides* (Leguminosae) shrub area. Reports on the nutrient content of sand from each area by Moreno-Casasola et al. (1982), Kellman and Roulet (1990), and Valverde (1992) show that, although organic matter content increased from the mobile to the stabilized area, the value at the beach was not different from that of the stabilized area. Very low PO_4 values were also reported around the dune system, (0.46, 0.81 and 1.49 ppm for the beach, and a mobile and a stabilized area, respectively).

Twenty black plastic bags were filled with 3 l of sand from each area and one 3-day-old maize seedling was transplanted into each. All of the pots were distributed at random outside the greenhouse of CICOLMA, i.e. they were subjected to the natural temperature regimes of the sand dune system (Fig. 2). Three plants were randomly chosen to be harvested 1 week and 1 month after transplanting (3 plants × 4 areas × 2 harvests). Roots were separated and processed as above, with 100 random root segments per replicate to assess AMF colonization percentage. In addition to the frequency of infection (F% = number of segments containing AMF structures out of every 100 intersections examined), the density of root colonization (proportion of the root cortex occupied by AMF, M%) was determined following the procedure suggested by Trouvelot et al. (1986). The non-parametric analysis of variance (Kruskal-Wallis test) was used to test for significant differences among areas in each harvest (Zar 1974).

Experiment 2:rate of colonization by AMF in the foredunes, mobile dune and grassland

To compare how long it takes for a seedling to become colonized by AMF in the different natural areas of the dune system, three 2 × 2-m plots were distributed at random at the beach, in an area covered by *Sporobolus virginicus*, *Canavalia rosea* and *Ipomoea pes-caprae*, in the mobile dune and in a *T. gouinii* grassland zone. Each square was divided into 20-cm grids and one 5-day-old seedling of*C. chamaecristoides* was transplanted at the center of each square in October 1994. This was at the end of the rainy season, which is one of the natural periods of germination and establishment for *C. chamaecristoides* (Martínez and Moreno-Casasola 1993). To ensure seedling survival, the plants were artificially watered every 2 days and shading was avoided by previously removing the aerial parts of the foredunes and grassland zone vegetation. Since this was done without disturbing the ground, the natural inoculum potential of hyphal network and/or spores was preserved in each square. The sites distributed in the mobile dune were devoid of vegetation and plant removal was not necessary.

Five seedlings for each square (15 per area) were randomly chosen to be harvested at intervals for 3 weeks. Their roots were carefully separated, fixed and stained by the methods described above and the presence of arbuscular mycorrhizal structures scored. Because of the small size of the roots, no attempts were made to record colonization percentage**.** Results from the grassland zone are not reported because insufficient seedling replicates survived in this area, probably as the result of herbivory.

Results

Mycorrhizal status

The mycorrhizal structures and colonization values of the species distributed along the different successional stages of the CICOLMA sand dunes are shown in Table 1. Ninety-seven percent of the species sampled were associated with AMF, including members of the reportedly non-mycorrhizal families Aizoaceae, Commelinaceae, Convolvulaceae and Cyperaceae (Gerdemann 1968; Trappe 1987), although no arbuscules were recorded in members of these families. At the beach, embryo dunes and foredunes, all species formed mycorrhizae except *I. stolonifera*, which contained only hyphae in a low percentage of roots. All of the species collected in the mobile dune and stabilized areas were colonized by AMF structures.

The AMF colonization percentages of *T. gouinii*, *P. lindenii* and *C. chamaecristoides*, which were collected in different successional areas of the sand dune system in the rainy and dry seasons, are shown in Table 2. For *T. gouinii*, there were no statistically significant differences in colonization between the foredunes, mobile and grassland areas or between the two seasons. In contrast, the colonization percentage for *C. chamaecristoides* in May was significantly lower than that recorded in September.

Mycorrhizal inoculum potential

Experiment 1:pot bioassay

The percentage AMF colonization and the densities of maize root cortex colonized by AMF recorded 8 and 30 days after seedling transplantation to sand from four different areas (foredunes, mobile dune, grassland and shrub area) are shown in Table 3. In the first harvest, a mean of 10% root infection was found in all areas, and the density of root colonization ranged from 0.3% in the foredunes to 2% in the grassland, but no statistically significant differences in AMF colonization in the four different substrates were found. At the second harvest, the lowest inoculum potential was observed in the mobile area and the highest in the shrub area of *D. robinoides* ($P < 0.05$). Similarly, the density of root colonization was lowest in the mobile dune and highest in the shrub area ($P < 0.05$) (Table 3).

Experiment 2:field bioassay

In the foredunes, external mycelium and internal hyphae were present after 1 week in 40% of the seedlings. Nine out of 15 seedlings (60%) had arbuscules 15 days after transplanting. Three weeks after transplanting, hyphae, arbuscules and vesicles were registered in 100,

Table 1 Collection sites and dates, colonization percentages by arbuscular-mycorrhizal fungi (AMF) and mycorrhizal structures found in plants distributed in different successional stages of a tropical sand dune ecosystem on the Gulf of Mexico. Nomenclature is in accordance with Moreno-Casasola et al. (1982) (*B* beach, *ED* embryo dune, *MD* mobile dune, *SA* stabilized area, *WS* wet slack)

Species	Collection site	Collection date	AMF colonization (%)	Hyphae	Hyphal coils	Vesicles	Arbuscules
Aizoaceae							
Sesuvium portulacastrum	B, ED	Apr/94	19	×	×	×	
Asclepiadaceae							
Asclepiadaceae	WS	Aug/94	41	×		×	
Bignoniaceae							
Tecoma stans[a]	SA	Aug/94		×		×	
Cactaceae							
Opuntia stricta var. dillenii	SA	Jul/91	33	×		×	
Commelinaceae							
Commelina aff. erecta	SA	Oct/91	30	×		×	
Compositae							
Ambrosia artemisifolia	SA	Aug/94	84	×	×	×	
Bidens pilosa	WS	Jul/94	36	×	×	×	×
Florestina tripteris	SA	Jul/94	12	×		×	
Palafoxia lindenii	ED	Aug/94	16	×	×	×	×
Pectis saturejoides	MD	Oct/91	84	×	×	×	×
Pluchea odorata[a]	SA	Aug/94		×		×	
Porophyllum numularium	SA	Jul/91	42	×		×	×
Convolvulaceae							
Ipomoea pes-caprae	B	Jul/91	39	×	×	×	
Ipomoea stolonifera	B	Jul/91	3				
Cyperaceae							
Cyperus articulatus	B	Jul/91	8	×		×	
Euphorbiaceae							
Croton punctatus	B	Oct/91	24	×	×		
Euphorbiaceae	B	Oct/91	31	×			
Gramineae							
Aristida aff. romeriana	SA	Jul/9	62	×	×	×	
Boutelous repens	SA	Jul/91	18	×		×	
Panicum purpurascens	MD	Jul/91	76	×		×	×
Trachypogon gouinii	MD	Jul/91	12	×	×	×	×
Schyzachirium sp.	SA	Jul/91	43	×		×	×
Sporobolus virginicus	B	Jul/91	48	×	×	×	×
Leguminosae							
Canavalia rosea	B	Jul/91	46	×		×	×
Chamaecrista chamaecristoides	MD	Jul/91	86	×		×	
Crotalaria incana	SA	Jul/91	84	×		×	
Diphysa robinoides	SA	Jul/91	31	×		×	
Enterolobium cyclocarpum	SA	Aug/94	58	×		×	
Macroptilium atropurpureum[a]	SA	Jul/91		×		×	
Schrankia quadrivalvis	SA	Jul/91	36	×		×	
Myrtaceae							
Eugenia capuli[a]	SAA	Aug/94		×		×	
Rosaceae							
Chrysobalanus icaco[a]	SA	Aug/94		×		×	
Rubiaceae							
Randia laetevirens[a]	SA	Aug/94		×		×	
Sterculiaceae							
Walteria indica	SA	Jul/91	28	×	×	×	×
Turneraceae							
Turnera ulmifolia	SA	Jul/91	32	×		×	
Umbelliferae							
Hydrocotyle bonariensis	WS	Aug/94	76	×	×	×	×
Verbenaceae							
Lippia nodiflora	WS	Aug/94	48	×	×	×	×

[a] Species collected from seedlings; not enough seedlings were present to assess mycorrhizal colonization

Table 2 Ranges of AMF colonization of *Trachypogon gouinii, Palafoxia lindenii* and *Chamaecrista chamaecristoides* sampled in different areas of the tropical sand dune ecosystem of La Mancha, Veracruz during the dry (May) and rainy (September) seasons. Different letters denote significant differences between seasons, according to the Mann-Whitney test ($P<0.05$). The symbols in the right column indicate significant (**) or nonsignificant (ns) differences at $P<0.001$ between areas, according to the non-parametric Kruskal-Wallis or Mann-Whitney test

Species	Sampling date	Foredunes	Mobile dune	Stabilized area	Level of significance
Trachypogon gouinii	May	a (30–64)	a (30–78)	a (28–72)	ns
	Sept	a (24–68)	a (40–72)	(44–85)	ns
Palafoxia lindenii	May	a (2–40)	a (8–60)		ns
	Sept	a (0–6)	b (10–30)		**
Chamaecrista chamaecristoides	May		a (2–34)		
	Sept		b (30–64)		

Table 3 Ranges of AMF colonization (F%) and density of root cortex colonized (M%) in maize plants transplanted to four substrates collected in different successional areas of the tropical sand dune ecosystem of La Mancha, Veracruz. Different letters indicate significant differences between the areas ($P<0.05$), according to the non-parametric analysis of variance (Kruskal-Wallis test)

	8 days F%	8 days M%	31 days F%	31 days M%
Embryo dunes	a (3–18)	a (0.07–0.8)	a (29–59)	a (7–8)
Mobile dune	a (1–8)	a (0.01–1)	b (12–30)	b (2–3)
Grassland	a (0–26)	a (0–6)	a (42–60)	c (4–5)
Dyphysa robinoides shrub area	a (7–13)	a (0.4–1)	c (80–85)	d (13–17)

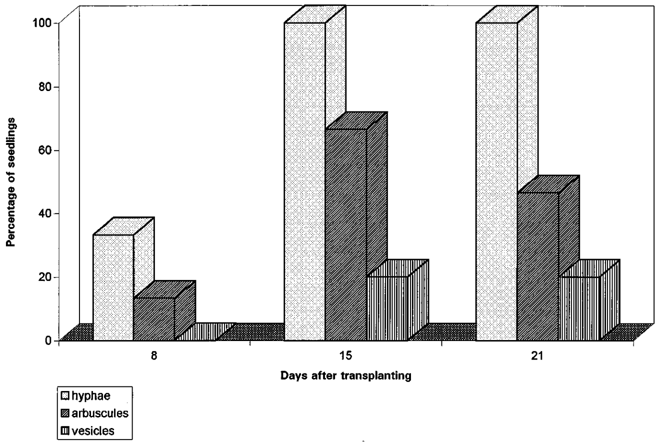

Fig. 3 Percentage of *Chamaecrista chamaecristoides* seedlings with mycorrhizal structures (hyphae, arbuscules and vesicles) 8, 15 and 21 days after being transplanted to the foredunes

46 and 20% of the seedlings, respectively (Fig. 3). In contrast, no mycorrhizal structures were recorded in the mobile area during the 21 days of the experiment.

Discussion

The high percentage of species with AMF found in this tropical sand dune system is consistent with that found in other dunes throughout the world, either temperate or sub-tropical.

At the beach, close to the high-tide mark, the tropical sand dune of La Mancha is mainly colonized by *Sesuvium portulacastrum* (Moreno-Casasola and Espejel 1986). This species is a succulent member of the Aizoaceae family (which is considered to include mainly non-mycorrhizal plants) (Gerdemann 1968). Although this species is reported as non-mycorrhizal in the sand dunes of Hawaii (Koske and Gemma 1990) and Singapore (Louis 1990), AMF hyphae and vesicles were found in some of our samples. Hyphal coils and vesicles have also been reported in individuals of *S. portulacastrum* collected in the coastal sand dunes of New South Wales, Australia (Logan et al. 1989) and in a salt marsh of the Ganges river in India (Sengupta and Chauduri 1990). In Veracruz, Mexico, *S. portulacastrum* occurs in monospecific patches, forming small hummocks in the beach or in association with *I. pes-caprae* (close to the sea) and with *P. lindenii* (towards the embryo dunes) (Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988). AMF in non-mycorrhizal species have also been found growing with infected neighbors (Read 1989).

Other studies on the mycorrhizal status of species distributed at the drift lines yielded contrasting results. While in European sand dunes, these sites were reported to be colonized by members of non-mycorrhizal families (Chenopodiaceae, Cruciferae and Caryophyllaceae) (Stahl 1900; Giovannetti and Nicolson 1983;

Read 1989), in Hawaii most of the seedlings growing in the drift line area were associated with AMF (Koske and Gemma 1990). In La Mancha, the same stolons of *I. pes-caprae* showed lower AMF colonization percentages at the beach towards the drift line than in the embryo dunes and foredunes (Reynaldo García, personal communication).

Of the species sampled at the beach, embryo dunes and foredunes, only *I. stolonifera* was non-mycorrhizal. All of the other species, *I. pes-caprae*, *C. rosea*, *S. virginicus*, *Croton punctatus* and *P. lindenii* were colonized by AMF. Nicolson (1960) also stressed the surprisingly high levels of AMF colonization of pioneer embryo dunes. *S. virginicus* was also reported as mycorrhizal on Heron Island, Australia (Peterson et al. 1985) and in Hawaiian sand dunes (Koske and Gemma 1990), *C. rosea* in Australia (Logan et al. 1989) and *I. pes-caprae* in Singapore (Louis 1990). The contrasting mycorrhizal status of different species of the same genus *Ipomoea* (*I. pes–caprae* as mycorrhizal, *I. stolonifera* as non-mycorrhizal) was also reported in Australian sand dunes with *I. brasiliensis* and *I. cairica* (Logan et al. 1989). The high percentage of mycorrhizal species in this area is consistent with the high mycorrhizal inoculum potential shown by the bioassay and by the infection rate field experiment at the end of the rainy season.

Considering the mobile and semi-mobile areas of this tropical dune system, it is important to stress that all of the species collected in the mobile dune, *C. chamaecristoides*, *P. lindenii*, *Pectis saturejoides*, *Schizachyrium sp*., *T. gouinii* and *Panicum purpurascens*, were heavily colonized by AMF, despite the low mycorrhizal inoculum potential shown by the bioassay in these areas. These species were mainly collected towards the arms and crests of the mobile dune. It is interesting that the mean AMF colonization of *T. gouinii* in the mobile area was not significantly different from that at the beach or in the grassland zone on either of the two sampling dates. This contrasts with results from other dunes around the world, where AMF colonization of plants at sites with low plant density was lower than in areas with a high plant density (Nicolson 1960; Nicolson and Johnson 1979; Koske and Halvorson 1981; Koske and Polson 1984).

The low incidence of AMF association in the mobile dune, observed in the field experiment on infection rate, may be due to seedling transplantation in the most mobile and unstable part of the dune, where no vegetation was present. One source of inoculum for plants in the mobile dunes could be infected roots and external mycelium of previously established individuals, in this case mainly *C. chamaecristoides*, the first colonizer of the mobile areas (Moreno-Casasola and Espejel 1986). We compared the mycorrhizal infection of *P. purpurascens* seedlings collected close to or far from *C. chamaecristoides* and found that only those closeby became infected (Corkidi 1996). Similarly, AMF colonization of *Festuca rubra* was more extensive when the plant was establishing under *Ammophila arenaria* on British sand dunes (Read 1989). Additional experiments are required to test this hypothesis for the CICOLMA sand dunes.

As expected, the mycorrhizal inoculum potential increased in the successional gradient from the mobile to the stabilized areas of the dune system (grassland and shrub area), and all species sampled at these sites were associated with AMF.

A seasonal pattern of root colonization by AMF, expected from the marked differences between the dry and rainy seasons, was not observed in all the species sampled. Only the values for *C. chamaecristoides* increased in the rainy season, coinciding with its flowering period (Castillo and Carabias 1982). However, fine fresh roots were not available in the dry-windy season and it is likely that AMF colonization is very low in this season, due to the drier conditions with poor root growth. In addition, colonization does not necessarily imply physiological activity, and it would be helpful to quantify the proportions of hyphae, vesicles, arbuscules and hyphal coils, as well as their viability, on each date, to investigate the seasonal patterns of infection of this tropical dune system.

Acknowledgements We wish to thank Patricia Moreno-Casasola and Marisa Martínez for the identification of the sand dune species and helpful discussions. We are grateful to Edith B. Allen and Richard E. Koske for their valuable suggestions, comments and advice. We also thank the CICOLMA staff for their help in the care of the plants at the Biological Station, as well as Irma Acosta, Nérida Pérez, Suraya Borrego, Octavio Pérez Maqueo, Reynaldo García and José Cherbowsky for support during the field and laboratory experiments. Valuable discussions with Pilar Huante and Ma. Esther Sánchez considerably improved this study. We are indebted to two anonymous reviewers for their comments and interest in the improvement of this paper. This investigation was supported by CONACgT and DGAPA-UNAM (IN-207093).

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