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

II. Effects of arbuscular mycorrhizal fungi on the growth of species distributed in different early successional stages

Abstract The effects of arbuscular mycorrhizal fungi on the growth of seven plant species established during the first stages of colonization in different areas of a tropical sand dune system on the Gulf of Mexico were investigated by comparing several growth parameters in 21- and 63-day-old mycorrhizal and non-mycorrhizal plants. There were no significant differences between mycorrhizal and non-mycorrhizal plants in root, stem and leaf biomass after 21 days, but after 63 days, mycorrhizal responsiveness was evident. *Ipomoea pes-caprae*, *Sporobolus virginicus* and *Canavalia rosea,* stoloniferous pioneer species of the beach, embryo dunes and foredunes, were less responsive to the mycorrhizal treatment, following the trend predicted for early seral species. However, large increases in total dry weight, leaf area and relative growth rate of *Chamaecrista chamaecristoides*, *Palafoxia lindenii* and *Trachypogon gouinii* (plants from the beach, embryo dunes and foredunes as well as mobile dunes) suggest that mycorrhizal infection is also crucial for the growth of early successional species. Most species allocated the same or more biomass to shoots than to roots. With the exception of *T. gouinii*, this pattern of biomass allocation was not altered by the mycorrhizal treatment. *C. rosea* and *S. virginicus* showed a higher allocation to the roots in the non-mycorrhizal plants. The possible relationship between mycorrhizae and succession in this tropical sand dune ecosystem is discussed.

Key words Growth analysis · Mycorrhizal responsiveness · Sand dune species · Succession

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Introduction

Although Webley et al. (1952) proposed that: "There can be little doubt that the activity of the soil microorganisms contributes to the maturation of the (sand dune) habitat, and therefore constitutes a biotic factor adding its influence to the other more familiar factors causing changes in the plant communities", research on the role of mycorrhizae in succession in different ecosystems has yielded contrasting results. The classical view that early successional habitats are colonized by non-mycotrophic or facultatively mycotrophic species (Stahl 1900; Dominik 1951; Janos 1980) has been supported by many studies (Nicolson 1960; Reeves et al. 1979; Miller 1979, 1987). While other investigations conclude that disturbed habitats can be colonized by either mycorrhizal or non-mycorrhizal species (Pendleton and Smith 1983; Allen et al. 1984; Schmidt and Scow 1986; Allen 1987, 1988), studies conducted in sand dune ecosystems suggest that arbuscular mycorrhizal fungi (AMF) are essential even in the earliest seral stages of succession (Gemma and Koske 1992). All models agree that plants are necessarily mycorrhizal in late seral stages (Janos 1980; Allen and Allen 1990; Gemma and Koske 1992).

Coastal sand dunes are ideal for investigating the roles of mycorrhizae in succession, as it is possible to examine vegetation through all seral stages from the pioneer to the stabilized zones in a relatively small area. Most research on mycorrhizae of sand dunes has detailed the mycorrhizal status of the colonizing plants and the identification, distribution and abundance of AMF spores (see references in Corkidi and Rincón 1997). It has also been demonstrated that the external mycelium of AMF plays a significant role in the process of dune stabilization, as sand grains are bound together mechanically by their hyphae (Koske et al. 1975; Sutton and Sheppard 1976; Clough and Sutton 1978; Forster 1979; Forster and Nicolson 1981a,b). Although it has been suggested that mycorrhizae are of great ecological

significance for nutrient uptake by plants in sand dunes (Koske et al. 1975; Koske and Polson 1984; Read 1989), where the scarcity of phosphorus, nitrogen and potassium can be extreme (Willis and Yem 1961; Moreno-Casasola 1982; Kellman and Roulet 1990; Maun 1994), this has not been experimentally verified and few studies have reported the influence of AMF on the growth of sand dune species (Nicolson and Johnston 1979; Sylvia and Burks 1988; Gemma and Koske 1989; Koske and Gemma 1995; Little and Maun 1996).

On the Gulf of Mexico, in La Mancha, Veracruz, the very complex topography of the tropical sand dune system has led to a patchy distribution of highly diverse plant species (Moreno-Casasola 1982, 1986; Martínez et al. 1993). While some species have a very restricted distribution, even in specific microenvironments of the first stages of colonization, others persist up to the stabilized areas of the late succession stages (Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988). In contrast to temperate sand dunes, where the main stabilizing plants are members of the Gramineae (Read 1989), the tropical sand dunes of La Mancha have different growth forms of Leguminosae species as well as members of the Compositae, Gramineae and Convolvulaceae (Moreno-Casasola and Espejel 1986; Moreno-Casasola 1988). All species were found to harbor AMF in a previous study (Corkidi and Rincón 1997). The main objective of the present study was to test the hypothesis that plant growth response to AM colonization increases along the successional transition from pioneer habitats to stabilized areas by analyzing the effects of mycorrhizal association on the growth of pioneer plants of the beach and mobile dunes and some which colonize the semi-stabilized areas of this tropical sand dune ecosystem.

Materials and methods

The species were mostly perennial and included: (1) three stoloniferous species from the beach, embryo dunes and foredunes, *Canavalia rosea*, *Ipomoea pes-caprae* and *Sporobolus virginicus*, (2) two endemic species of this sand dune ecosystem, *Palafoxia lindenii*, a low shrub which is found in the embryo dunes, foredunes, and mobile areas, and *Trachypogon gouinii*, a rhizomatous Gramineae distributed in the foredunes, mobile dunes and in semi-stabilized areas, (3) *Chamaecrista chamaecristoides*, a sand dune endemic low shrub mainly distributed in the mobile areas, (4) *Panicum purpurascens*, a clumped grass which is the only annual species included and which occurs in the mobile areas but also in more stabilized areas.

The growth experiment was conducted in a greenhouse at the biological station of the Centro de Investigaciones Costeras de la Mancha (CICOLMA), situated in the state of Veracruz on the Gulf of Mexico (19°36' N, 96°22'40"W). Detailed information about the vegetation and physical factors of the sand dunes of La Mancha can be found in Moreno-Casasola (1982, 1988), Moreno-Casasola et al. (1982), Moreno-Casasola and Espejel (1986), and Dubroeucq et al. (1992). Seeds of all species were collected from at least 10 individuals of each species at the time of fruit ripening and 50 seeds of each were chosen at random to determine their average weight (Table 1).

Table 1 Species, family and mean seed weight (n = 50) of plants distributed in a tropical sand dune system on the Gulf of Mexico. Nomenclature according to Moreno-Casasola et al. (1982)

Species	Family	Mean seed weight (g)
Canavalia rosea	Leguminosae	0.65
Ipomoea pes-caprae	Convolvulaceae	0.15
Chamaecrista chamaecristoides	Leguminosae	0.016
Trachypogon gouinii	Gramineae	0.0017
Palafoxia lindenii	Compositae	0.0019
Panicum purpurascens	Gramineae	0.00064
Sporobolus virginicus	Gramineae	0.000193

The sand used for the growth experiment was collected from the foredunes and was dry-sterilized at 100°C for 48 h. Black plastic bags were filled with 3 l of this sand and stored for 4 weeks to avoid phytotoxic effects of heating (Rovira and Bowen 1966). Chemical analysis after sterilization showed 16.2 ppm total phosphorus, 78.1 ppm total nitrogen and 92.5 ppm potassium, pH = 7.9, and 0.49% organic matter (Salas 1994). No nutrient solution was added during the experiment.

Seeds were germinated in the temperature and photoperiod regimes required for each species (Martínez et al. 1992). *C. rosea*, *I. pes-caprae* and *C. chamaecristoides* were mechanically scarified prior to planting to obtain similar emergence times. Five days after germination, 10 seedlings per species were harvested and leaf area, root, stem and leaf dry weight were recorded (initial harvest). A further 40 seedlings per species were transplanted to the plastic bags (one per bag). At the time of transplanting, half of the bags were inoculated with an homogeneous mixture of sand and root fragments collected from the rhizosphere of *P. lindenii* distributed in the embryo dunes and foredunes (mycorrhizal treatment, +M). The other half was not inoculated (non-mycorrhizal treatment, –M). Spore washings were added to both treatments following the methodology of Koide and Li (1989) to reincorporate non-mycorrhizal soil microorganisms. The AMF spore species are currently being identified. The plants were placed at random in the greenhouse and were watered every 2 days.

Three weeks after transplanting, individuals of each species were harvested at random and their roots stained with trypan blue by the procedure of Koske and Gemma (1989) to verify AMF colonization. At the same time, seven mycorrhizal and non-mycorrhizal plants of *C. chamaecristoides*, *C. rosea*, *P. lindenii* and *P. purpurascens* were harvested to measure the effects of AMF. Leaf area and the number of leaves were recorded, and roots, stems and leaves were oven dried at 80°C for 48 h to quantify dry weight. Sixty-three days after germination, all species were harvested and processed as above (final harvest). For *C. rosea*, *I. pes-caprae*, *C. chamaecristoides*, and *P. lindenii* stem length was also measured. For most of the species, 7 plants per treatment of each species were used (6 species × 7 replicates × 2 treatments). However, since many of the non-mycorrhizal plants of *T. purpurea* were severely parasitized, only 4 non-parasitized replicates of this species were included (1 species × 4 replicates × 2 treatments).

The data were analyzed by classical growth analysis (Hunt 1982). The data from the initial and the final harvests were used to calculate the specific leaf area (SLA, leaf area per unit leaf weight), leaf area ratio (LAR, leaf area as a fraction of the total dry weight), root/shoot ratio (R/S), root (RWR), stem (STWR), leaf (LWR) and shoot (SWR) weight ratios as fractions of the total dry weight, relative growth rate (RGR, increase in dry weight per unit total dry weight with time) and net assimilation rate (NAR, the rate of dry weight production per unit leaf area) (Evans 1972; Causton and Venus 1981; Hunt 1982). The NAR is only reported for the species in which measurement of initial leaf

area was possible. For members of the Gramineae, the dry weight of leaves and stems were measured together as shoot weight, and neither SLA, STWR nor LWR were calculated.

The mycorrhizal dependency (RFMD) of 63-day-old plants was calculated from (dry weight mycorrhizal plant minus dry weight non-mycorrhizal plant)/dry weight mycorrhizal plant (Plenchette et al. 1983). The results from mycorrhizal and non-mycorrhizal treatments were compared using Student 's t–test (Zar 1974).

Results

The effects of AMF on growth and biomass allocation of species from different early successional stages of the sand dunes are shown in Table 2. There were no significant differences between mycorrhizal and non-mycorrhizal treatments for any of the species after 21 days (data not shown); however, striking differences emerged at 63 days. Mycorrhizal plants of *C. chamaecristoides*, *P. lindenii*, *T. gouinii* and *P. purpurascens* had significantly higher root, stem and leaf dry weights than non-mycorrhizal plants. The root dry weights of mycorrhizal and non-mycorrhizal *C. rosea* plants did not differ significantly, there was a slight increment in leaf dry weight and the total dry weight increased by 50%. Most notably, mycorrhizal plants of this species produced considerably longer stems (23–90 cm longer than the longest non-mycorrhizal stem) with considerably higher dry weights than the non-mycorrhizal plants. No change in dry weight due to mycorrhizae was evident in *I. pes-caprae* or *S. virginicus*.

All species with a higher final dry weight after inoculation with AMF also showed significantly higher relative growth rates, ranging from *C. rosea*, (an increase of 0.005 g g^{-1}day^{-1}), *P. purpurascens* (0.012 g g^{-1}day^{-1}), *T. gouinii* (0.015 g g^{-1}day^{-1}), *P. lindenii* (0.019 g g^{-1}day^{-1}) to *C. chamaecristoides* (0.026 g g^{-1}day^{-1}) (Table 2).

In terms of biomass allocation, in *I. pes-caprae*, *C. chamaecristoides* and *P. lindenii*, the contributions of root and shoot to the final dry weight (R/S, RWR, SWR) in mycorrhizal and non-mycorrhizal plants were not significantly different. However, for *I. pes-caprae*, biomass allocation to the stem (STWR) was lower in plants inoculated with mycorrhizal fungi. Compared with the other species, *P. lindenii*, *C. rosea* and *S. virginicus* showed a higher allocation to the shoots than to the roots in both treatments (R/S<1), and *C. rosea* (a less responsive species) and *S. virginicus* (a non-responsive species) showed a further allocation to shoots when mycorrhizal, as demonstrated by significantly lower values of R/S and RWR for +M. Although it seems that non-mycorrhizal plants of *P. purpurascens* invested proportionally more biomass in the root than mycorrhizal plants, this could be due to the severe reduction in aerial parts. *T. gouinii* was the only species to allocate more biomass to roots than to shoots when mycorrhizal (Table 2).

Table 2 Root (R), stem (ST), leaf (L) and shoot (S) dry biomass (g), stem length (STL) (cm), root/shoot dry weight ratio (R/S), root weight ratio (RWR), stem weight ratio (STWR), leaf weight ratio (LWR), shoot weight ratio (SWR) and relative growth rate (RGR) (g g^{-1} day^{-1}) of mycorrhizal (+M) and non-mycorrhizal (−M) plants of different species distributed in a tropical sand dune ecosystem on the Gulf of Mexico. The data represent the means ± standard error of 7 replicate plants grown for 63 days. Different letters between treatments indicate significant differences according to the Student's t-test ($P<0.05$)

Species	Treatment	R	ST	L	S	STL	R/S	RWR	STWR	LWR	SWR	RGR
Canavalia rosea	+M	0.93[a] ±0.16	0.77[a] ±0.17	1.32[a] ±0.18	2.08[a] ±0.19	65.5[a] ±20	0.45[a] ±0.06	0.31[a] ±0.03	0.25[a] ±0.03	0.44[a] ±0.04		0.035[a] ±0.001
	−M	0.77[a] ±0.15	0.46[b] ±0.05	0.94[b] ±0.16	1.41[b] ±0.2	18.3[b] ±2	0.54[b] ±0.05	0.35[b] ±0.05	0.21[a] ±0.03	0.43[a] ±0.04		0.030[b] ±0.001
Ipomoea pes-caprae	+M	0.95[a] ±0.34	0.40[a] ±0.09	0.39[a] ±0.10	0.79[a] ±0.19	15.0[a] ±1.4	1.20[a] ±0.21	0.53[a] ±0.05	0.23[a] ±0.04	0.22[a] ±0.02		0.021[a] ±0.001
	−M	0.85[a] ±0.07	0.56[a] ±0.10	0.36[a] ±0.06	0.92[a] ±0.15	10.8[a] ±1.2	0.95[a] ±0.09	0.48[a] ±0.03	0.31[b] ±0.03	0.20[a] ±0.02		0.022[a] ±0.000
Chamaecrista chamaecristoides	+M	0.18[a] ±0.06	0.086[a] ±0.02	0.12[a] ±0.030	0.19[a] ±0.05	25.5[a] ± 3	0.93[a] ±0.3	0.46[a] ±0.10	0.22[a] ±0.04	0.31[a] ±0.08		0.083[a] ±0.002
	−M	0.04[b] ±0.01	0.022[b] ±0.003	0.03[b] ±0.006	0.05[b] ±0.008	15.0[b] ± 1.3	0.78[a] ±0.2	0.43[a] ±0.06	0.26[a] ±0.07	0.30[a] ±0.03		0.057[b] ±0.003
Palafoxia lindenii	+M	0.04[a] ±0.009	0.045[a] ±0.006	0.046[a] ±0.006	0.09[a] ±0.01	16[a] ± 1.1	0.41[a] ±0.17	0.28[a] ±0.08	0.35[a] ±0.05	0.36[a] ±0.07		0.075[a] ±0.001
	−M	0.02[b] ±0.006	0.012[b] ±0.004	0.015[b] ±0.004	0.03[b] ±0.008	10[b] ± 1.83	0.70[a] ±0.35	0.39[a] ±0.12	0.27[b] ±0.05	0.33[a] ±0.09		0.056[b] ±0.004
Sporobolus virginicus	+M	0.05[a] ±0.02			0.13[a] ±0.029		0.35[a] ±0.06	0.26[a] ±0.034			0.74[a] ±0.03	0.074[a] ±0.003
	−M	0.05[a] ±0.02			0.09[a] ±0.029		0.55[b] ±0.2	0.35[b] ±0.066			0.65[b] ±0.07	0.071[a] ±0.003
Trachypogon gouinii	+M	0.62[a] ±0.27			0.27[a] ±0.06		2.14[a] ±0.5	0.67[a] ±0.07			0.33[a] ±0.05	0.047[a] ±0.001
	−M	0.05[b] ±0.026			0.06[b] ±0.057		1.15[b] ±0.5	0.5[b] ±0.12			0.50[b] ±0.11	0.032[b] ±0.0007
Panicum purpurascens	+M	0.03[a] ±0.01			0.13[a] ±0.005		0.26[a] ±0.15	0.19[a] ±0.08			0.80[a] ±0.08	0.032[a] ±0.007
	−M	0.007[b] ±0.002			0.006[b] ±0.001		1.19[b] ±0.5	0.52[b] ±0.10			0.47[b] ±0.10	0.022[b] ±0.002

Inoculation with AMF significantly increased both leaf area and number of leaves of *C. rosea*, *C. chamaecristoides*, *P. lindenii*, *T. gouinii* and *P. purpurascens* but only leaf area of *S. virginicus*. Leaf area ratio and specific leaf area also increased significantly in *C. rosea*, *C. chamaecristoides* and *P. lindenii* after inoculation. The net assmilation rate did not differ between mycorrhizal and non-mycorrhizal plants for any of the species (Table 3).

The RFMD values for the different species at day 63 increased in the order *I. pes-caprae* < *S. virginicus* < *C. roseae* < *P. lindenii* = *P. purpurascens* < *C. chamaecristoides* < *T. gouinii* (Table 4).

Discussion

Even though in nature "...mycorrhizae have evolved as the norm of terrestrial plant nutrition, not the exception"... (Trappe 1977), species show a wide range of responses to AMF symbiosis (Plenchette et al. 1983; Habte and Manjunath 1991).

Early successional species are typically non-mycorrhizal or facultatively mycorrhizal (Janos 1980; Allen and Allen 1990), but the growth responses to AM colonization of all the sand dune species presented in this study did not correspond exactly to their seral status; contrasting mycorrhizal responsiveness was demonstrated by the different pioneer species.

Ipomoea pes-caprae, *C. rosea* and *S. virginicus* are all stoloniferous species which creep over the sand surface and their distribution is restricted to the beach, embryo dunes and foredunes (Moreno-Casasola et al. 1982; Moreno-Casasola and Espejel 1986). Although these species are reported as mycorrhizal in the natural conditions of sand dunes (Logan et al. 1989; Koske and Gemma 1990; Corkidi and Rincón 1997), their growth responses to AMF are very clearly those of model pion-

Table 3 Leaf area (LA) (cm^2), leaf number (LN), specific leaf area (SLA) ($cm^2\,g^{-1}$), leaf area ratio (LAR) ($cm^2\,g^{-1}$) and net assimilation rate (NAR) ($g\,cm^2\,day^{-1}$) of 63-day-old mycorrhizal (+M) and non-mycorrhizal (−M) plants of species distributed in a tropical sand dune ecosystem on the Gulf of Mexico. Data represent the mean ± standard error of 7 replicates. Different letters indicate statistically significant difference between the mycorrhizal and non-mycorrhizal treatments according to Student's *t*-test ($P < 0.05$)

Species		LA	LN	SLA	LAR	NAR
Canavalia rosea	+M	313.2[a] ±36.4	6[a] ±0.8	240.5[a] ±22.6	105.6[a] ± 12.4	0.0006[a] ±0.0001
	−M	181.8[b] ±35.2	4[b] ±0.8	190.8[b] ±10.8	82.5[a] ± 8.5	0.0007[a] ±0.0005
Ipomoea pes-caprae	+M	48.5[a] ±11.9	7[a] ±1	124.9[a] ±10.5	28.8[a] ± 4.8	0.0006[a] ±0.0001
	−M	45.7[a] ± 7.6	8[a] ±2	125.4[a] ± 8.9	25.6[a] ± 2.9	0.0006[a] ±0.0008
Chamaecrista, chamaecristoides	+M	38.8[a] ± 8.7	19[a] ±4	330.3[a] ±34.2	101.8[a] ± 17.1	0.0007[a] ±0.0006
	−M	6.5[b] ± 1.6	7[b] ±2	250.4[b] ±34.2	75.5[b] ± 11.1	0.0006[a] ±0.0001
Palafoxia lindenii	+M	15.7[a] ± 1.9	10[a] ±1	343.5[a] ±16.3	123.9[a] ± 18.6	0.0006[a] ±0.0009
	−M	3.7[b] ± 1.3	5[b] ±1	241.1[b] ±18.9	79.2[b] ± 16.6	0.0006[a] ±0.0001
Sporobolus virginicus	+M	22.3[a] ± 5	12[a] ±2		72.4[a] ± 18.2	
	−M	15.3[b] ± 3.8	10[a] ±3		65.4[a] ± 14.9	
Trachypogon gouinii	+M	27.7[a] ± 5.3	10[a] ±1		36.2[a] ± 11.9	
	−M	4[b] ± 1.8	4[b] ±1		58[a] ± 39.3	
Panicum purpurascens	+M	22.4[a] ±14.8	8[a] ±0.5		306.7[a] ±106	
	−M	2.2[b] ± 0.6	4[b] ±0.5		166[a] ± 34.6	

Table 4 Distribution and mycorrhizal dependency (RFMD) of species from different successional stages of a tropical sand dune system on the Gulf of Mexico

Species	Mycorrhizal dependency	Beach	Embryo dunes and foredunes	Mobile dune	Semi-stabilized area
Ipomoea pes-caprae	−10	————————————————			
Sporobolus virginicus	− 6	————————————————			
Canavalia rosea	27	————————————————			
Palafoxia lindenii	64		————————————————		
Panicum purpurascens	64			————————————————	
Chamaecrista chamaecristoides	77			———————————	
Trachypogon gouinii	84				————————————————

eer species, i.e. they are non-responsive or less responsive than late seral species. Similar results for the genus *Ipomoea* were found in studies with *I. pes-caprae* from the sand dune system of La Mancha (Salas 1994; Pérez-Maqueo 1995), *I. wolcottiana* from a tropical deciduous forest in Mexico (Huante et al. 1993), and *I. brasiliensis* from Hawaiian sand dunes (Koske and Gemma 1995). The longer stems of mycorrhizal *C. rosea* could be ecologically significant for a stoloniferous species, even though the overall response to AMF was not very high. Stem length is an important characteristic of postrate, creeping growth forms (Bell 1984; Slade and Hutchings 1987), particularly when subjected to burial by sand accretion (Moreno-Casasola et al. 1982; Moreno-Casasola 1988).

Palafoxia lindenii and *T. gouinni*, are found in the foredunes but, like *C. chamaecristoides*, they are very important pioneer species of the mobile areas (Moreno-Casasola 1986; Martínez et al. 1993). The high mycorrhizal response of these two species suggests that mycorrhizal infection is crucial for the growth and development of such early seral plants.

Plants with very different mycorrhizal responsiveness interact at the beach, embryo dunes and foredunes. It is interesting that *I. pes-caprae*, the least responsive species, is the species most tolerant to inundation (Pérez-Maqueo 1995) and is found close to the drift line, an area of high disturbance and high nutrient concentrations (Read 1989; Allen and Allen 1990; Pérez-Maqueo 1995). Moreover, it has been demonstrated that inoculation with AMF can cause an increase in mortality of the beach – foredune species *P. lindenii* and *C. rosea* when they are subjected to flooding conditions (Pérez-Maqueo 1995).

In spite of the lower mycorrhizal inoculum potential of the mobile dunes, the mycorrhizal species are frequent (Corkidi and Rincón 1997). The fact that *C. chamaecristoides* develops mycorrhizal infection in mobile dunes, and has a high mycorrhizal responsiveness could be of considerable ecological significance. This species is an endemic low shrub of the sand dunes of Mexico and is highly tolerant of sand accretion, erosion, very poor nutrient levels and drought (Moreno-Casasola 1986; Martínez and Rincón 1993; Martínez et al. 1994). It is the first colonizing plant and the most important stabilizing element in areas of intense sand movement on the windward and the leeward slopes and arms and crests of mobile dunes (Moreno-Casasola and Espejel 1986). Once *C. chamaecristoides* is established, species such as *Schizachyrium sp.*, *T. gouinii*, *P. purpurascens* and *P. lindenii* appear. Interestingly, the latter three species are at least as responsive to AMF as *C. chamaecristoides*. Allen and Allen (1980) reported that, although mycorrhizal colonization is severely reduced after disturbance, in an early successional habitat both infection spore number increase when mycotrophic plants are present.

Trachypogon gouinii and *P. purpurascens*, species which persist up to the stabilized areas, are among the most AMF responsive species found in this study. *P. purpurascens* mycorrhizal plants observed for 120 days after transplanting had spikes, while the non-mycorrhizal plants were dying (L. Corkidi, unpublished results).

Similar high responses to AMF association were also found for other late seral species from this tropical sand dune system. *Macroptilium atropurpureum*, *Crotalaria incana* and *Tecoma stans* showed marked increases in growth parameters, and *Pectis saturejoides* produced flowers when mycorrhizal but did not survive when non-mycorrhizal (L. Corkidi, unpublished results).

In coastal sand dune systems, pioneer plants are subjected to considerable stress due to scarcity of nitrogen, phosphorus, potassium, organic matter, and water (Moreno-Casasola 1982; Maun 1994). Therefore, it might be expected that plants in these ecosystems would grow relatively slowly and allocate a larger fraction of biomass to their roots (Chapin 1980, 1988; Lambers and Poorter 1992). The low growth rates measured for the mycorrhizal and non-mycorrhizal sand dune species in this study coincide with the growth rates obtained for *C. chamaecristoides*, *C. rosea*, *I. pes-caprae*, *T. gouinii*, *P. lindenii* and *Schizachyrium scoparium* under high nutrient conditions (Martínez and Rincón 1993; Valverde et al. 1996) without water stress (Martínez et al. 1994).

No differences were found between mycorrhizal and non-mycorrhizal treatments in the net assimilation rate for any species in this study, suggesting that the mycorrhizal association did not influence plant growth through higher biomass gain per unit leaf area. However, since the relative growth rate is linearly related to leaf area ratio ($RGR = NAR \times LAR$) (Lambers and Poorter 1992), increases that occurred in other parameters related to leaf area i.e. leaf area, leaf number, leaf area ratio and specific leaf area (even in some of the less-responsive species) may be of more ecological importance.

Regarding biomass allocation, the very different growth forms (stoloniferous, rhizomatous, short shrubs) of the plants in this experiment preclude extrapolation of the high root/shoot ratios expected at other sites poor in nutrients to this sand dune ecosystem. Most species allocated the same or more biomass to aerial than to below-ground organs and, with the exception of some members of the Gramineae, mycorrhizal treatment did not change the general pattern of allocation (R/S).

The higher allocation of biomass to aerial parts in *C. rosea* is supported by other studies with this species under competition (Salas 1994), flooding with freshwater and saltwater (Pérez-Maqueo 1995) and nutrient-rich regimes (Valverde et al. 1996). This was also the general pattern of allocation found for other clonal species (Slade and Hutchings 1987).

The high mycorrhizal status of all coastal sand dunes species surveyed throughout the world (see references in Corkidi and Rincón 1997), the stabilization of these

ecosystems by AMF through binding sand grains into aggregates (Koske et al. 1975; Sutton and Sheppard 1976; Clough and Sutton 1978; Forster 1979; Forster and Nicolson 1981a, b), and studies on the dispersion of AMF in Hawaii (Koske and Gemma 1990), all support the statement by Webley et al. (1952) quoted at the beginning of this paper. The differences in the mycorrhizal responsiveness of different pioneer species reported here are also important evidence.

References

Allen EB, Allen MF (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. J Appl Ecol 17:139–147

Allen EB, Allen MF (1990) The mediation of competition by mycorrhizae in successional and patchy environments. In: Grace JB, Tilman GD (eds) Perspectives on plant competition. Academic, New York, pp 367–389

Allen MF (1987) Re-establishment of mycorrhizas on Mount-St Helens: migration vectors. Trans Br Mycol Soc 88:413–417

Allen MF (1988) Re-establishment of VA mycorrhizae following severe disturbance: comparative patch dynamics of a shrub desert and a subalpine volcano. Proc R Soc Edinb 94:63–71

Allen MF, MacMahon JA, Andersen DC (1984) Re-establishment of Endogonaceae on Mount St. Helens: survival of residuals. Mycologia 76:1031–1038

Bell AD (1984) Dynamic morphology: a contribution to plant population ecology. In: Dirzo R, Sarukhán J (eds) Perspectives on plant population ecology. Sinauer, Sunderland, Mass, pp 48–65

Causton DR, Venus JC (1981) The biometry of plant growth. Arnold, London

Chapin FS (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260

Chapin FS (1988) Ecological aspects of plant mineral nutrition. Adv Min Nutr 3:161–191

Clough KS, Sutton JC (1978) Direct observation of fungal aggregates in sand dune soil. Can J Microbiol 24:333–335

Corkidi L, Rincón E (1997) Arbuscular mycorrhizae in a tropical sand dune ecosystem on the Gulf of Mexico. I. Mycorrhizal status and mycorrhizal inoculum potential along a successional gradient. Mycorrhiza 7:9–15

Dominik T (1951) Studies of mycotropism of plants growing in sand dunes or inland. (in Polish) Acta Soc Bot Pol 21:125–164

Dubroeucq D, Geissert D, Moreno-Casasola P, Millot G (1992) Soil evolution and plant communities in coastal dunes near Veracruz, Mexico. Cah O.R.S.T.O.M. Ser Pedol XXVII:237–250

Evans GC (1972) The quantitative analysis of plant growth. Blackwell, Oxford London

Forster SM (1979) Microbial aggregation of sand in an embryo dune system. Soil Biol Biochem 11:537–543

Forster SM, Nicolson TH (1981a) Microbial aggregation of sand in a maritime sand dune succession. Soil Biol Biochem 13:205–208

Forster SM, Nicolson TH (1981b) Aggregation of sand from a maritime embryo sand dune by microorganisms and higher plants. Soil Biol Biochem 13:199–203

Gemma JN, Koske RE (1989) Field inoculation of American beachgrass (*Ammophila breviligulata*) with V-A mycorrhizal fungi. J Environ Manag 29:173–182

Gemma JN, Koske RE (1992) Are mycorrhizal fungi present in early stages of primary succession. In: Read DJ, Lewis DH, Fitter AH, Alexander IJ (eds) Mycorrhizas in ecosystems. CAB International, Wallingford, UK, pp 183–189

Habte M, Manjunath A (1991) Categories of vesicular-arbuscular mycorrhizal dependency of host species. Mycorrhiza 1:3–12

Huante P, Rincón E, Allen EB (1993) Effect of vesicular-arbuscular mycorrhizae on seedling growth of four tree species from the tropical deciduous forest in Mexico. Mycorrhizae 2:141–145

Hunt R (1982) Plant growth curves: the functional approach to plant growth analysis. Arnold, London

Janos DP (1980) Mycorrhizae influence tropical succession. Biotropica 12:56–64

Kellman M, Roulet N (1990) Nutrient flux and retention in a tropical sand-dune succession. J Ecol 78:664–676

Koide RT, Li M (1989) Appropriate controls for vesicular-arbuscular mycorrhiza research. New Phytol 111:35–44

Koske RE, Gemma JN (1989) A modified procedure for staining roots to detect VA mycorrhizas. Mycol Res 92:486–488

Koske RE, Gemma JN (1990) VA mycorrhizae in strand vegetation of Hawaii: evidence for long distance codispersal of plants and fungi. Am J Bot 77:466–474

Koske RE, Gemma JN (1995) VA mycorrhizal inoculation of Hawaiian plants: a conservation technique for endangered tropical species. Pac Sci 49:181–191

Koske RE, Polson WR (1984) Are VA mycorrhizae required for sand dune stabilization? Bioscience 34:420–424

Koske RE, Sutton JC, Sheppard BR (1975) Ecology of Endogone in Lake Huron sand dunes. Can J Bot 53:87–93

Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. Adv Ecol Res 23:187–261

Little LR, Maun MA (1996) The "*Ammophila* problem" revisited: a role for mycorrhizal fungi. J Ecol 84:1–7

Logan VS, Clarke PJ, Allaway WG (1989) Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. Aust J Plant Physiol 16:141–146

Martínez ML, Rincón E (1993) Growth analysis of *Chamaecrista chamaecristoides* (Leguminosae) under contrasting nutrient conditions. Acta Oecol 14:521–528

Martínez ML, Valverde T, Moreno-Casasola P (1992) Germination response to temperature, salinity, light and depth of sowing of ten tropical dune species. Oecologia 92:343–353

Martínez ML, Moreno-Casasola P, Castillo S (1993) Biodiversidad costera: playas y dunas. In: Salazar-Vallejo SI, González NE (eds) Biodiversidad marina y costera de México. Com Nal Biodiversidad y CIQRO, Mexico, pp 160–181

Martínez ML, Moreno-Casasola P, Rincón E (1994) Sobrevivencia y crecimiento de plántulas de un arbusto endémico de dunas costeras ante condiciones de sequía. Acta Bot Mex 26:53–62

Maun MA (1994) Adaptations enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio 111:59–70

Miller RM (1979) Some occurrences of vesicular-arbuscular mycorrhizae in natural and disturbed ecosystems of the Red Desert. Can J Bot 57:619–623

Miller RM (1987) Mycorrhizae and succession. In: Jordan III WR, Gilpin ME, Áber JD (eds) Restoration ecology. A synthetic approach to ecological research. Cambridge University Press, Cambridge, UK, pp 205–220

Moreno-Casasola P (1982) Ecología de la vegetación de dunas costeras: factores físicos. Biotica 7:577–602

Moreno-Casasola P (1986) Sand movement as a factor in the distribution of plant communities in a coastal dune system. Vegetatio 65:67–76

Moreno-Casasola P (1988) Patterns of plant species distribution on coastal dunes along the Gulf of Mexico. J Biogeogr 15:787–806

Moreno-Casasola P, Espejel I (1986) Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean sea of Mexico. Vegetatio 66:147–182

Moreno-Casasola P, van der Maarel E, Castillo S, Huesca ML, Pisanty I (1982) Ecología de la vegetación de dunas costeras: Estructura y composición en el Morro de la Mancha, Ver. Biotica 7:491–526

Nicolson TH (1960) Mycorrhizae in the Gramineae. II. Development in different habitats particularly sand dunes. Trans Br Mycol Soc 43:132–145

Nicolson TH, Johnston C (1979) Mycorrhiza in the Gramineae. III. Glomus fasciculatus as the endophyte of pioneer grasses in a maritime sand dune. Trans Br Mycol Soc 72:261–268

Pendleton RL, Smith BN (1983) Vesicular-arbuscular mycorrhizae of weedy and colonizer plant species at disturbed sites in Utah. Oecologia 59:296–301

Pérez-Maqueo 0 (1995) Análisis del efecto de los disturbios en la dinámica de la playa del Morro de la Mancha, Veracruz. MSc thesis, UNAM, Mexico

Plenchette C, Fortin JA, Furlan V (1983) Growth responses of several plant species to mycorrhiza in a soil of moderate P fertility. I. Mycorrhizal dependency under field conditions. Plant Soil 70:191–209

Read DJ (1989) Mycorrhizas and nutrient cycling in sand dune ecosystems. Proc R Soc Edinb 96:89–100

Reeves FB, Wagner DW, Moorman T, Kiel J (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed versus natural environments. Am J Bot 66:1–13

Rovira AD, Bowen GD (1966) The effects of microorganisms upon plant growth. II. Detoxication of heat-sterilized soils by fungi and bacteria. Plant Soil 25:129–141

Salas M (1994) Efecto de las micorrizas vesículo-arbusculares en la competencia por nutrimentos entre dos especies pioneras de dunas costeras del Morro de la Mancha, Veracruz. BSc thesis, UNAM, Mexico

Schmidt SK, Scow KM (1986) Mycorrhizal fungi on the Galapagos Islands. Biotropica 18:236–240

Slade AJ, Hutchings MJ (1987) Clonal integration and plasticity in foraging behaviour in Glechoma hederaceae. J Ecol 75:1023–1036

Stahl E (1900) Der Sinn der Mycorhizenbildung. Eine vergleichend-biologische Studie. Jahrb Wiss Bot 34:539–668

Sutton JC, Sheppard BR (1976) Aggregation of sand dune soil by endomycorrhizal fungi. Can J Bot 54:326–333

Sylvia DM, Burks JN (1988) Selection of a vesicular-arbuscular mycorrhizal fungus for practical inoculation of Uniola paniculata. Mycologia 80:565–568

Trappe JM (1977) Selection of fungi for ectomycorrhizal inoculation in nurseries. Annu Rev Phytopathol 15:203–222

Valverde T, Pisanty I, Rincón E (1996) Growth response of six tropical dune plant species to different nutrient regimes. J Coastal Res 12 (in press)

Webley DM, Eastwood DJ, Gimingham CH (1952) Development of a soil microflora in relation to plant succession on sand-dunes, including the rhizosphere flora associated with colonizing species. J Ecol 40:168–178

Willis AJ, Yem EW (1961) Braunton Burrows: mineral nutrient status of the dune soils. J Ecol 49:377–390

Zar JH (1974) Biostatistical analysis. Prentice Hall, London