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C. Alarcón · G. Cuenca

Arbuscular mycorrhizas in coastal sand dunes of the Paraguaná Peninsula, Venezuela

Abstract Arbuscular mycorrhizal colonization was measured in the most abundant plant species of the Paraguaná Peninsula, northwestern Venezuela. These plant species included: *Acacia tortuosa*, *Argusia gnaphalodes*, *Croton punctatus*, *Croton rhamnifolius*, *Egletes prostrata*, *Melochia tomentosa*, *Panicum vaginatum*, *Scaevola plumieri*, *Sporobolus virginicus*, *Suriana maritima*, *Leptothrium rigidum*, and *Fimbristylis cymosa*. Mycorrhizal colonization was assessed using the Trouvelot et al. (1986) method that allows for simultaneous evaluation of frequency of colonization (%F), intensity of colonization (%M), and the proportion of arbuscules (%A) and vesicles (%V) present in the roots. Average frequency of colonization was 69%. The highest frequency of colonization was around 92% in *C. rhamnifolius* and *A. tortuosa*; in the other species, it varied from 49 to 86%. *L. rigidum* and *F. cymosa* were considered nonmycorrhizal because its colonization was very scarce and at all times appeared without arbuscules. Average intensity of colonization was 7%. The highest intensity of colonization was 18% in *C. rhamnifolius*. In the other species, it varied from 3 to 15%. *Paspalum vaginatum*, *A. gnaphalodes*, *M. tomentosa*, and *S. maritima* had their fungal structures tightly packed in modified little ovoid roots. In general, frequency of AM colonization was high and similar to those reported for other tropical ecosystems, whereas the intensity of AM colonization was low and similar to values obtained in analogous studies in disturbed ecosystems.

C. Alarcón · G. Cuenca
Instituto Venezolano de Investigaciones Científicas (IVIC),
Centro de Ecología,
P.O. Box 21827 Caracas, 1020-A, Venezuela

C. Alarcón (✉)
Centro de Investigaciones en Ecología y Zonas Áridas
(CIEZA), Universidad Nacional Experimental
Francisco de Miranda (UNEFM),
Coro, Falcón, Venezuela
e-mail: micoduna@yahoo.es
Tel.: +58-212-5041449
Fax: +58-212-5041088

Introduction

Coastal sand dunes are extreme environments, whose complex dynamics mainly depends on wind exposure, sand deposition, sand texture, slope, and fluctuations in soil moisture (Moreno-Casasola et al. 1982; Carter and Wilson 1988). These characteristics influence plant colonization in accordance with microenvironmental conditions (high irradiance and high temperature), where the plants that are established may exhibit adaptations to survive in these extreme environments (Moreno-Casasola et al. 1982; Moreno-Casasola 1988; Rose 1988). Previous studies on mycorrhizas have shown that plants of coastal sand dunes are abundantly colonized by arbuscular mycorrhizal fungi (AMF) (Giovannetti and Nicolson 1983; Puppi et al. 1986), including species belonging to families considered mainly to be nonmycorrhizal (Trappe 1987; Corkidi and Rincón 1997a).

In coastal sand dunes, vegetation and soil microorganisms play a fundamental role in sand stabilization. In particular, arbuscular mycorrhizas (AMs) are ubiquitous symbioses between fungi and plants that act in important processes in the soil–plant interface, such as improving plant nutrition by increased nutrient and water uptake (Harley and Smith 1983); enhancing establishment, growth, and survival of seedlings due to improved stress tolerance (Allen 1991; Barea et al. 1991; Koske and Gemma 1995, 1996); binding of sand grains into large aggregates (Tisdall and Oades 1982); and improving soil structure that can influence plant succession (Nicolson 1960; Koske et al. 1975).

AMs in sand dune ecosystems have been extensively studied in temperate regions, but in the tropical and subtropical zones, ecological studies are scarce. A few studies have been conducted in Australia (Koske 1975; Logan et al. 1989), Hawaii (Koske 1988; Koske and Gemma

1990, 1996), Brazil (Stürmer and Bellei 1994), and the Gulf of Mexico (Corkidi and Rincón 1997a,b). In Venezuela, not even surveys have been carried out in these environments.

The sand dunes on the Paraguaná Peninsula, Venezuela, are located in a tropical semiarid area with precipitation erratic in time and space and with high evaporation rates that generate a constant water deficit in the soil (Medina 1985). They represent vulnerable barriers against very complex patterns of wind dynamics. The NE Trade Winds directly affect sand movement and the dune stabilization process and make this system more dynamic than other sand dune systems, thus, causing different stages ranging from highly mobile to fixed dunes (Goddard and Picard 1976). In view of the stress conditions in the mobile dunes, it is expected that a high percentage of plant species would be associated with AM fungi and that this would vary with the position in the dune.

This paper reports the floristic inventory of the mobile sand dunes of Paraguaná Peninsula and evaluates the presence of mycorrhizal colonization in the different topographic units of these dunes.

Materials and methods

Study site

The study was conducted on a coastal sand dune area at Paraguaná Peninsula, located in northwestern Venezuela (11°48′N, 69°47′W) (Fig. 1a). The littoral area of the eastern coast of the Paraguaná Peninsula is covered by sandy soil, usually deep and mobile with some denuded patches. The climate is typical of tropical semiarid areas; mean temperature is 28.3°C and rainfall is erratically distributed with a tendency to accumulate at the end of the year. Annual precipitation averages 382 mm (Fig. 1b). The coastal sand dunes are an extensive strip with variable width between 100 and 300 m, and 15 km long. These areas receive the influence of tides and surf spray. In addition, the NE Trade Winds continually blow over the coast.

The study site included a littoral zone with an incipient band of embryonic dunes of 1- to 1.5-m height with scarce plant cover and a following zone, constituted by dunes with 2.5-m height with patchy plant cover. These were situated to seaward of semiestablished and stable dunes. Five topographic units in the sand dune were selected in this study: plain, hollow, slope, crest, and consolidated dune or *médano*. Selected sites had the following characteristics: *plain*, at the beach, close to the high-tide mark with 25 to 35 m or 40 m wide; *hollow*, depression among the dunes, occurring throughout the study site; *slope*, dune arms, located between plain and crest topographic units; *crest*, the exposed area located on the top of dune; and *médano*, the following zone of contiguous dunes, covered with only woody plants. The *médano* area is less exposed to wind than the other topographic units.

Fig. 1 a Study site in the Paraguaná Peninsula (rectangle) and **b** the climate diagram of Adícora in northwestern Venezuela
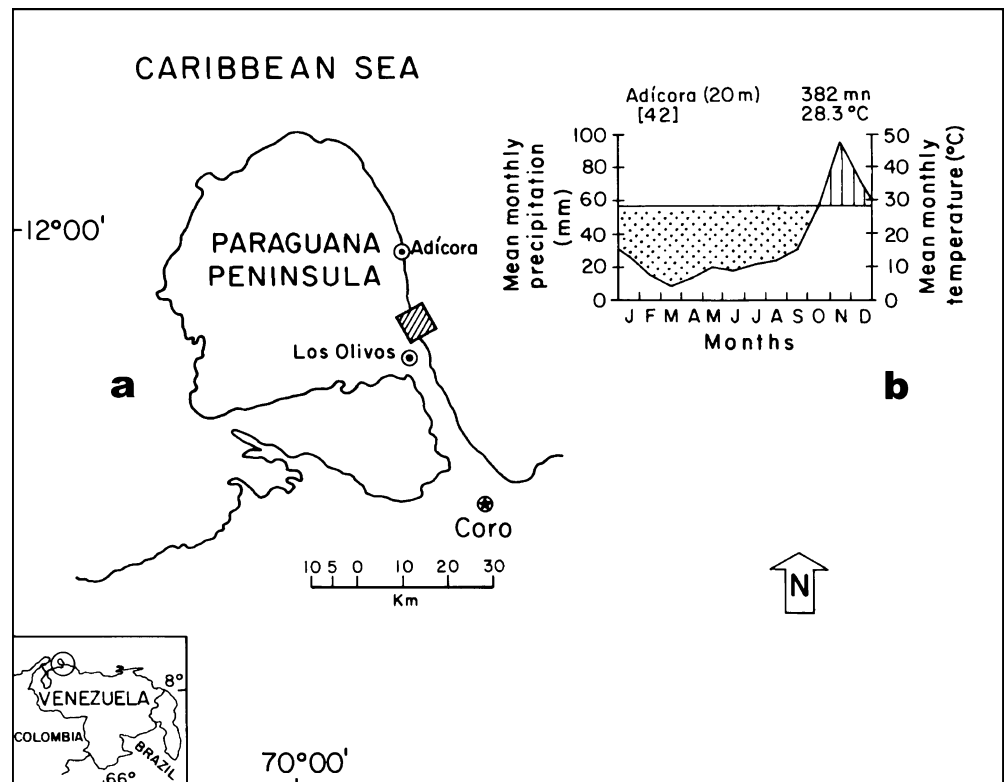
Vegetation description

Plant distribution in the coastal sand dunes was determined by the point method (Barbour et al. 1987). Percentage cover and cover density were assessed by 20 points in an imaginary strip located in each topographic unit using an 8-mm iron rod. A total of 40 strips of 20 m length × 2 m wide were analyzed, ten for each topographic unit. Percentage cover of each species was calculated according the following equation:

$$\text{Percent cover} = \text{Number of "pins" which coincided with species A at least once} \times 100 / \text{Total number of "pins"}$$

The cover density (expressed in percentage) weights each species by its canopy thickness, or cover repetition, at each point:

$$\text{Percentage of cover density} = \text{Number of contacts with species A} \times 100 / \text{Total number of contacts}$$

This type of sampling is particularly sensitive to changes in herbaceous shrubby vegetation type, which prevails in coastal dunes (Goldsmith and Harrison 1976). In addition, a floristic inventory of plant species was performed for each topographic unit.

The matrix of floristic similarity between different topographic units was obtained using the Sørensen coefficient I_s (Sørensen 1948):

$$I_s = 2w / (a + b)$$

where a is the total number of species in topographic unit a; b the total number of species in topographic unit b; and w the total number of species in both topographic units. The similarity matrix was subjected to weighted pair-group method and the dendrogram was drawn. This methodology could have two limitations: it is possible that the floristic list for a topographic unit might not be complete, and some species could be included in an erroneous position, especially ecotone species. However, it does give a general idea about floristic affinity between topographic units.

Soil chemical analysis

Soils from the five topographic units were sampled once during the 2-year field period. The analyses were performed on the 0- to 15-cm top fraction. Three composite soil samples were homogenized, air-dried and sieved (<2 mm), and the pH was measured in water (1:5) and in 1 M KCl (1:5). Soil texture was evaluated by the hydrometer method (Bouyoucos 1992). Organic matter was assessed using the Walkey–Black method (Jackson 1976) and total N was measured using a micro-Kjeldahl. Extractable P was assessed by the method of Murphy and Riley (1962) after the extraction with $NaHCO_3$ according to Olsen et al. (1954). Exchangeable Ca^{2+}, K^+, and Mg^{2+} were measured by atomic absorption spectrophotometry. Data presented are the mean values of the composite samples.

Arbuscular mycorrhizal colonization

Fine roots (1–3 g) of five individuals from each of the most abundant plant species were extracted to evaluate AM colonization. Only roots smaller than 3-mm diameter were stained (Phillips and Hayman 1970). Mycorrhizal colonization was assessed using the Trouvelot et al. (1986) method. Each root sample constituted of 30 fragments of 1-cm length, mounted in a mixture of glycerol and lactic acid (v/v). This method allows for the simultaneous evaluation of frequency of colonization (%F), intensity of colonization (%M), and the proportion of arbuscules (%A) and vesicles (%V) present in the roots. Frequency of colonization (%F) was calculated by the following equation:

$$F\% = 100(N - no) / N$$

where N is the number of root fragment observed and no is the number of root fragments without AM colonization. The intensity of AM colonization (%M) in each root segment was scored based in the whole presence of the fungus in the entire fragment using values from 0 to 5. Numbers indicate the proportion of root cortex colonized by the fungus, i.e., 0, without colonization; 1, colonization trace; 2, less than 10%; 3, from 11 to 50%; 4, from 51 to 90%; and 5, more than 90% of the volume of root segment occupied by the fungus. Then, the intensity of colonization (%M) as estimated by the following equation:

$$M\% = (95n5 + 70n4 + 30n3 + 5n2 + n1) / N$$

where $n5$, $n4$, $n3$, $n2$, and $n1$ are the numbers of fragment in the respective categories 5, 4, 3, 2, and 1.

A similar system was used to calculate frequency of arbuscules (%A) and vesicles (%V), but in this case, the categories were 1 (without arbuscules or vesicles), 2 (less than 10%), 3 (from 11 to 50%), and 4 (more than 50% of the volume of the root fragment occupied by structures of these types) (Trouvelot et al. 1986). Also, this method was

used to quantify the presence of coils or peletons (%*C*) and hyphae (%*H*) formed by AM fungi. For the assessment of mycorrhizal colonization, only fungi with aseptate irregular walls were taken into account (Barea et al. 1991).

The abundance of root hairs was quantified using a relative scale from 0 to 3 (0, absent; 1, few; 2, common; 3, abundant). Root hair width was also measured using a calibrated ocular micrometer (n=20/each species). In addition, to detect fine endophytes (Brundrett et al. 1994), the diameters of ten stained hyphae selected at random were measured.

Statistical analyses

The nonparametric Mann–Whitney test was used to test significant differences in ranges of AM colonization between topographic units. Also, multiple range analysis based in analysis of variance (ANOVA) was used to identify homogeneous groups between plant species and mycorrhizal structures. Finally, the correlation matrix of studied variables was calculated (Sokal and Rohlf 1972).

Results

Vegetation description

Vegetation from Paraguaná Peninsula coastal sand dunes is floristically poor, with only about 15 species of plants belonging to 11 families. Seventy three percent of the species are herbaceous and the remaining are shrubby. The five dominant species were *Sporobolus virginicus* (L.) Kunth., *Paspalum vaginatum* Sw., *Argusia gnaphalodes* (L.) Heine, *Suriana maritima* L., and *Egletes prostrata* (Sw.) Kuntze. The three first species alone are responsible for 53% of the total cover. Twelve species contributed to 15% cover and the remainder was bare soil
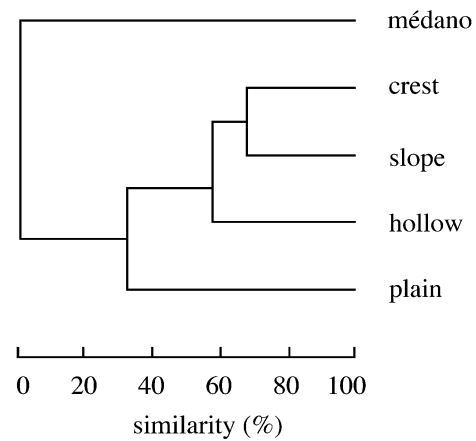
Fig. 2 A dendrogram with the indices of similarity of Sørensen of topographic positions in coastal sand dunes

(32%). The plants formed dense patches, according to the cover density values obtained (Table 1).

The vegetation survey in the sand dunes allowed the distinguishing of four groups of species according to their distribution in the dune. *S. virginicus*, *P. vaginatum*, *Croton punctatus* Jacq., and *A. gnaphalodes* occurred in almost all studied units; *Chamaesyce dioica* (H.B.K.) Millsp., *Sesuvium portulacastrum* L., *Ipomoea pes-caprae* (L.) Sweet. and *Scaevola plumieri* (L.) Vahl. grew in the plains. *Leptothrium rigidum* Kunt, *Fimbristylis cymosa* R. Br., *E. prostrata*, and *M. tomentosa* L. grew mainly in hollows. Finally, *S. maritima*, *C. rhamnifolius* H.B.K., and the shrubby form of *Acacia tortuosa* (L.) Willd. occurred on crests. The last species shows two very distinct morphologies: one as a prostrate shrub that is found only on crests, and the other form is the well developed erect tree that appeared only on the *médano* position. Of course, some of these species grew in the ecotonal unit (slope). A similarity dendrogram shows that crest, slope, and hollow form a similar group (60%). The plain unit only shares

Table 1 Species, family, and topographical positions where the plant species of coastal sand dunes of the Paraguaná Peninsula grew

Cover (%) and cover density (%) of these species according to the point method

Species	Family	Topographical positions	Cover (%)	Cover density (%)
Sporobolus virginicus (L.) Kunth.	Poaceae	Plain–slope–crest–hollow	34.2	43.2
Paspalum vaginatum Sw.	Poaceae	Plain–crest–hollow	13.3	15.7
Argusia gnaphalodes (L.) Heine.	Borraginaceae	Plain–slope–crest–hollow	5.4	4.8
Suriana maritima L.	Simaroubaceae	Crest	3.2	4.2
Egletes prostrata (Sw.) Kuntze.	Asteraceae	Hollow	3.0	4.0
Croton punctatus Jacq.	Euphorbiaceae	Slope–crest–hollow	2.5	3.3
Melochia tomentosa L.	Sterculiaceae	Hollow	1.6	1.1
Scaevola plumieri (L.) Vahl.	Dipsacaceae	Plain	1.1	1.8
Fimbristylis cymosa R. Br.	Cyperaceae	Hollow	1.0	2.3
Leptothrium rigidum Kunt.	Poaceae	Hollow	0.9	1.3
Chamaesyce dioica (H.B.K.)	Euphorbiaceae	Plain	0.6	0.5
Acacia tortuosa (L.) Willd.	Mimosaceae	Crest–médano	0.5	0.6
Ipomoea pes-caprae (L.) Sweet.	Convolvulaceae	Plain	0.3	0.1
Croton rhamnifolius H.B.K.	Euphorbiaceae	Crest	0.2	0.1
Sesuvium portulacastrum L.	Aizoaceae	Plain	0.1	0.1

Table 2 Sandy soil chemical analyses from topographic positions on the study site (0- to 15-cm depth)

Site	pH (H$_2$O)	pH (KCl)	N total (mg N/g PS)	P available (cg P/g)	Organic matter (%)	Na (cmol$_c$/kg)	K (cmol$_c$/kg)	Mg (cmol$_c$/kg)	Ca (cmol$_c$/kg)	Bulk density (g/ml)
Plain	8.7	9.0	0.18	19.80	0.70	2.79	0.13	2.86	20.78	1.36
Hollow	8.7	8.9	0.18	21.54	0.80	2.60	0.15	2.89	19.94	1.33
Slope	8.8	8.9	0.21	21.11	0.70	2.91	0.14	2.91	15.68	1.41
Crest	8.7	8.7	0.21	21.92	0.70	3.03	0.14	2.99	19.78	1.36
Médano	8.8	9.0	0.28	18.30	0.80	3.68	0.27	3.63	15.80	1.40
Mean	8.7	8.9	0.21	20.53	0.74	3.00	0.17	3.06	18.40	1.37
SE	0.0	0.1	0.02	0.66	0.02	0.18	0.03	0.15	1.10	0.01

SE Standard error

33.3% of plant species with the previous group. The consolidated dune position (*médano*) constitutes a different entity, where only *A. tortuosa* grows as its tree form (Fig. 2).

Soil chemical analysis

Soil characteristics of the five topographic units were similar. All soils were sandy and strongly alkaline. Soil N, Mg^{2+}, and K$^+$ were low. In contrast, P, Ca^{2+} and Na$^+$ had intermediate values (Table 2).

Arbuscular mycorrhizal colonization

The plant species studied had structures belonging to AMF in their fine roots. The average frequency of colonization was 68.8%. *A. tortuosa* (L.) Willd. and *C. rhamnifolius* had the highest AMF frequencies. *F. cymosa* and *L. rigidum* had the lowest AM frequencies (Table 3). The ranges of frequency (%F) of AM colonization in different topographic positions of the coastal sand dunes on Paraguaná Peninsula were compared with the nonparametric Mann–Whitney *U* test. There were no statistically significant differences (Table 4).

The average intensity of colonization was 7.2%. *C. rhamnifolius* had the highest AM intensity (17.7%) and *L. rigidum* had the lowest (0.5%). Again, *F. cymosa* and *L. rigidum* had the lowest AM intensity (Table 3). The ranges in intensity (%M) of arbuscular mycorrhizal colonization did not show statistically significant differences (Table 4).

The frequencies of arbuscules, vesicles, and coils in plant species measured using the method of Trouvelot et al. (1986) are shown in Table 3. Ten plant species of the total (83%) had arbuscules. Average arbuscule frequency was close to 3%. *S. plumieri* had the highest arbuscule frequency. *L. rigidum* and *F. cymosa* did not have arbuscules. Mean vesicle frequency was close to 1.5%. *P. vaginatum* had the highest vesicle frequency. Only *L. rigidum* did not have vesicles. Average coil frequency was close to 1.4%. *C. rhamnifolius* presents the highest coil frequency. Again, *L. rigidum* and *F. cymosa* did not have coils.

For the ANOVA, the values of frequencies of AM colonization and each AM structure (arbuscules, coils and vesicles) of plant species were transformed by log(1+x). Between species, differences were significant for all frequencies (*p*<0.05). A posteriori analysis of multiple ranges revealed the presence of three groups with different frequency of coils: *F. cymosa* and *L. rigidum* formed the first group without coils; *C. rhamnifolius* and *S. plumieri* constituted the second one with the highest frequency of coils; and the remaining plant species formed a third group with similar frequency of coils.

Table 3 Frequency (F) and intensity (M) of arbuscular mycorrhizal colonization, with frequencies of arbuscules (A), vesicles (V), coils (C), and hyphae (H) according to the Trouvelot et al. (1986) method in plant species from the coastal dunes of the Paraguaná Peninsula, Venezuela

Species	%F	%M	%A	%V	%C	%H
Acacia tortuosa	92.2	9.0	4.4	2.2	0.6	1.0
Croton rhamnifolius	92.0	17.7	7.6	3.7	4.1	7.6
Croton punctatus	85.8	9.3	2.6	0.4	1.9	2.4
Paspalum vaginatum	84.7	10.2	3.5	5.6	1.3	2.7
Sporobolus virginicus	76.7	4.5	0.7	0.6	0.5	1.2
Argusia gnaphalodes	74.0	6.0	1.9	0.8	0.7	1.7
Suriana maritima	68.7	4.6	1.2	1.1	1.4	2.5
Melochia tomentosa	68.0	5.1	1.2	1.0	0.3	1.5
Scaevola plumieri	64.2	15.1	8.7	1.6	3.8	7.7
Egletes postrata	49.3	3.4	0.9	0.5	1.0	1.1
Fimbristylis cymosa	40.7	1.3	0.0	0.2	0.0	0.0
Leptothrium rigidum	28.7	0.5	0.0	0.0	0.0	0.0
Average	68.8	7.2	2.7	1.5	1.4	2.5
Standard error	5.8	1.5	0.8	0.5	0.4	0.7

Table 4 Ranges of frequency (%F) and intensity (%M) of arbuscular mycorrhizal (AM) colonization of plant species in different topographic positions of the coastal sand dunes on Paraguaná Peninsula

Parameter	Topographic positions				Médano
	Plain	Slope	Crest	Hollow	
Plant species	*S. virginicus*, *P. vaginatum*, *A. gnaphalodes*, *S. plumieri*	*S. virginicus, A. gnaphalodes, S. maritima, C. punctatus, E. prostrata, M. tomentosa, F. cymosa, A. tortuosa*	*S. virginicus*, *P. vaginatum*, *A. gnaphalodes*, *S. maritima*, *C. punctatus*, *C. rhamnifolius*, *A. tortuosa*	*S. virginicus*, *P. vaginatum*, *A. gnaphalodes*, *C. punctatus*, *E. prostrata*, *M. tomentosa*, *F. cymosa*, *L. rigidum*	*A. tortuosa*
Average and range frequency arbuscular mycorrhizal colonization (%F)	74.9 (64.2–84.7)[a]	69.4 (40.7–92.2)[a]	82.0 (68.7–92.2)[a]	63.5 (28.7–85.8)[a]	92*
Intensity of arbuscular mycorrhizal colonization (%M)	9.0 (4.5–15.1)[b]	5.4 (1.3–9.3)[b]	8.8 (4.5–17.7)[b]	5.0 (0.5–10.2)[b]	9*

Equal letters indicate nonsignificant differences between the topographic positions ($p<0.05$) according to the Mann–Whitney U test.
*The Mann–Whitney U test was not applied.

The overall appearance of AM fungi in root systems under the microscope can be categorized into three groups. *A. gnaphalodes*, *P. vaginatum*, *S. maritima*, and *M. tomentosa* constitute a group of species characterized by an AM colonization localized mainly inside fine roots with a particular ovoid or ellipsoid form (Fig. 3). *L. rigidum* and *F. cymosa* represent another group, where no arbuscules or coils were observed in their root systems, although their cortical cells contained intraradical spores and hyphae with numerous entry points but without apparent continuity in between. The last group, formed by the remaining species, had roots with no unusual structural features and with %F and %M of colonization homogeneously distributed across roots.

Root hair abundance, range of internal hyphal diameter, and presence of fine endophyte in the studied plant species are shown in Table 5. The abundance of root hairs decreased in the following order: *L. rigidum* (3), *F. cymosa* (2), *A. gnaphalodes* (1), and *S. virginicus* (1). Root hair length varied from 87 to 300 μm. The high variation of

Fig. 3 Intact ellipsoid roots with mycorrhizas in *Paspalum vaginatum*

hyphal diameter found in the plant species studied in this work suggested that there was more than one type of AMF colonizing root systems. Mean hyphal diameter varied between 0.1 and 1.3 μm. The correlation matrix revealed a negative relationship between the presence of root hairs and both the frequency and the intensity of colonization (Table 6).

Discussion

In these coastal sand dunes, grass and herb species (mainly stoloniferous) grow on the plain close to the beach. Shrub species occur on the crests. Herbaceous and acaulescent shrubs frequently grow in the hollows. Finally, woody plant species grow in semistabilized and stabilized dunes (médano) behind the mobile ones. Bare soil dominates the whole community and plants are distributed in patches. This vegetation pattern is very similar to other tropical and subtropical sand dunes (Moreno-Casasola et al. 1982; Corkidi and Rincón 1997a,b; García 1997).

In these mobile and semimobile dunes, sand movement has been mentioned as a key factor in plant distribution, as distributions change drastically during the dune stabilization process. In fact, Moreno-Casasola (1986) suggested that there is a close interaction between plant species, vegetation cover, sand movement, and dune shape. This would explain why there are species that only occur on specific positions, for example, *S. plumieri* that only grows on plains or *S. maritima* and *C. rhamnifolius* that grow on crests. Also, *A. tortuosa* is the only plant species that occurs in consolidated dune. However, this system can be considered as a continuum because some plant species grow in the adjacent positions, like some just mentioned.

The vegetation type present in these coastal sand dunes, locally called Los Médanos, can be defined as littoral psammophilous meadows sensu Huber and Alarcón (1988).
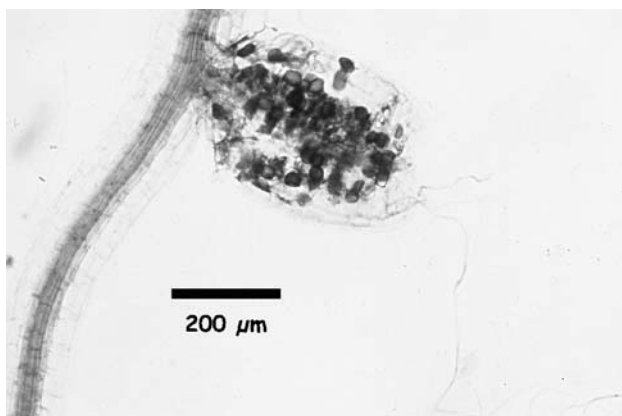
Table 5 Root hair abundance, range of internal hyphal diameter, presence of fine endophyte, and modified roots with mycorrhizas in the species from sand dunes in the study sites at Paraguaná Peninsula

Species	Root hair abundance	Range of hyphal diameter (cm)	Presence of fine endophyte	Presence of ovoid or ellipsoid roots with mycorrhizas
Acacia tortuosa	0	1.3–7.8	+	−
Argusia gnaphalodes	1	1.3–3.9	+	+
Croton rhamnifolius	0	1.3–2.6	+	−
Croton punctatus	0	2.6–7.8	−	−
Egletes prostrata	0	1.3–3.9	+	−
Fimbristylis cymosa	2	1.3–3.9	+	−
Leptothrium rigidum	3	2.6	−	−
Melochia tomentosa	0	1.3–2.6	+	+
Paspalum vaginatum	0	2.6–7.8	−	+
Scaevola plumieri	0	2.6–7.8	−	−
Sporobolus virginicus	1	2.6–7.8	−	−
Suriana maritima	0	<1.3–3.9	+	+

The positive sign (+) indicates presence and the negative sign (−) indicates not observed

Table 6 Correlation matrix of root hair presence, frequency of hyphae, presence of modified roots, hyphal length, frequency, and intensity of mycorrhizal colonization for plants of the study sites

	Species	Root hairs	Hyphal frequency	Presence of modified roots	Frequency of AM	Intensity of AM
Species	1					
Root hairs	0.0127	1				
Hyphal Frequency	0.2074	−0.6029	1			
Presence of modified roots	0.2560	−0.2471	0.0921	1		
Frequency of AM	−0.2428	−0.7343	0.4251	0.1859	1	
Intensity of AM	−0.1709	−0.6257	0.7570	−0.1046	0.6971	1

Although the diversity of species and families seems very low for a tropical ecosystem, it is indeed very similar to the diversity reported for other semiarid tropical zones from northwestern Venezuela (Alarcón 1994, 2001). This is in contrast to temperate sand dunes where the number of plant species is ten times higher than these psammophilous meadows (Logan et al. 1989).

AMF seems to constitute an important component of these littoral meadows, because 90% of the plant species have values of mycorrhizal colonization greater than 50%. This high percentage of species with AMF found in these tropical sand dunes is consistent with that found in other dunes throughout the world, either temperate or tropical (Koske and Halvorson 1981; Giovannetti and Nicolson 1983; Koske and Gemma 1990; Louis 1990).

The average colonization frequency (68.8%) was higher than the values for the dunes of other latitudes. For example, it was 60% in Canada (Koske et al. 1975), 54% in Scotland (Nicolson and Johnson 1979; Koske and Halvorson 1981), 50% in the Atlantic USA (Koske and Polson 1984), 39% in Australia (Logan et al. 1989), 30% in Greece (Vardavakis 1992), 20% in Italy (Puppi et al. 1986), and 32–40% in the Gulf of Mexico (Corkidi and Rincón 1997a). Our values were similar to the average colonization frequency (67%) reported by Louis (1990) for tropical sand dunes in Singapore. Data previously mentioned were obtained by the method of Giovannetti and Mosse (1980), instead of that of Trouvelot et al. (1986) used by us. In addition to inherent differences due to methods, the variations found between our value and the others cited could be associated with the inoculum present, and its effectiveness and permanence in the area, which, as a whole, allow subsequent colonization.

The presence of tightly packed hyphae, vesicles, and arbuscules of AM in fine roots with ovoid or ellipsoid form was observed in plant species of different families with no apparent evolutionary relationship. These plant species do not share a similar topographic unit, because *A. gnaphalodes* and *P. vaginatum* grow in all the positions, *S. maritima* mostly grows in the crest, and *M. tomentosa*

Table 7 Frequency and intensity of arbuscular mycorrhizal colonization measured according to the Trouvelot et al. (1986) method in several tropical ecosystems

Location	%F	%M	Source
Sand dunes	68.8	7.2	This work
White sand shrublands	93.4	38.0	De Andrade et al. 1994
Natural savanna I	79.8	27.3	De Andrade et al. 1994
Natural savanna II	61.5	11.9	Lovera and Cuenca 1996
Revegetated savanna	48.8	17.1	Lovera and Cuenca 1996
Old disturbed savanna	49.0	7.0	Lovera and Cuenca 1996

is located in the hollows. As far as we are aware, there are no references in the specialized literature dealing with these characteristic structures in shrub or herbaceous species; the only entries deal with woody plant species (Herrera et al. 1988; Duhoux et al. 2001). We speculate that the structures observed are produced by different senescence rates between mycorrhizal and nonmycorrhizal roots, but the functional role is not clear, and their possible implication in the dynamics of the AM in these coastal sand dunes requires further elucidation in the future.

The AM colonization in the coastal sand dunes reveal that the species with the highest density of root hairs possess the lowest presence of mycorrhizas, or no mycorrhizas at all, as in the grass *L. rigidum*. Baylis (1975), Peat and Fitter (1993), St. John (1980), Allen (1991), and Michelsen (1993) have obtained a similar inverse relationship between the presence of AM and the abundance of root hairs.

Although AM hyphae and vesicles were found in *F. cymosa*, the lack of arbuscules suggests some type of saprophytic relationship (Brundrett 1991), and in consequence, not a mycorrhizal one. These species, *L. rigidum* and *Capparis odoratissima* Jacq, an evergreen woody species of the xerophyte forest of Falcón State (Vietez 1990), constitute the nonmycorrhizal species detected up to now for the semiarid lands of Venezuela.

The comparison of average mycorrhizal frequency and intensity of mycorrhizal colonization in roots between diverse tropical ecosystems reveals that these coastal sand dunes possess frequency values similar to others reported for natural ecosystems, particularly in savannas with herbaceous plants (Table 7). However, mycorrhizal intensity (%M) values are very low, comparable to values reported for disturbed savannas in La Gran Sabana in southeastern Venezuela. This last result is not surprising, because dunes are natural ecosystems where the wind produces a constant disturbance.

In conclusion, we suggest that mycorrhizas play an ecologically important role in these coastal sand dunes, due to their presence in the majority of the species and to the presence of the AM fungal structures in special rootlets that suggest some functional convergence in totally different taxonomic families.

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