

## Diversity of arbuscular mycorrhizal fungi along a sand dune stabilization gradient: A case study at Praia da Joaquina, Ilha de Santa Catarina, South Brazil\*

Analia S. Cordoba<sup>1)</sup>, Margarida M. de Mendonça<sup>1)\*\*</sup>, Sidney L. Stürmer<sup>2)</sup> and Paul T. Rygielwicz<sup>3)</sup>

<sup>1)</sup> Departamento de Microbiologia e Parasitologia, Universidade Federal de Santa Catarina, Cx. P. 476, Florianópolis, SC 88040–900, Brazil

<sup>2)</sup> Departamento de Ciências Naturais, Universidade Regional de Blumenau, Cx. P. 1507, Blumenau, SC 89010–971, Brazil

<sup>3)</sup> U.S. Environmental Protection Agency, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Corvallis, OR 97333, U.S.A.

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**Species diversity of arbuscular mycorrhizal fungi (AMF) was assessed along a dune stabilization gradient (embryonic dune, foredune and fixed dune) at Praia da Joaquina, Ilha de Santa Catarina. The dunes were chosen as a case study to assess whether diversity and mycorrhizal inoculum potential (MIP) increase along the gradient. Ten soil samples were collected from each stage and pooled, and then six 100-g soil sub-samples were taken to identify and enumerate spores. Twelve AMF species were detected, and all three families in Glomales were represented. Gigasporaceae species dominated the embryonic dune, while Glomaceae species dominated the fixed dune. Total spore numbers and richness increased as the dunes became more stabilized. However, indices of Margalef, Simpson and Shannon reached maximal values at different stages, suggesting that species abundance was different among stages. In both embryonic and fixed dunes, species abundance data fit the broken stick model, while in the foredune the log series model best described the data. The MIP followed spore numbers and increased along the gradient, suggesting that spores are important in initiating root colonization in this system. Relationships between edaphic factors and functional roles of Glomales families as determinants of AMF distribution are discussed.**

**Key Words**—arbuscular mycorrhizal fungi; Glomales; occurrence; sand dunes stabilization; taxonomic diversity.

Stabilizing coastal dunes is a concern in many countries. Introducing plants into destabilized dunes is the most common practice used in stabilization programs (Ranwell, 1972), while restoring microbial communities, such as arbuscular mycorrhizal fungi (AMF), is largely ignored (Koske and Polson, 1984). The AMF are obligate biotrophic microorganisms, widespread in soils, that establish a mutualistic symbiosis with most plants and have multiple roles in ecosystems (Newsham et al., 1995; Smith and Read, 1997).

Some consider AMF as keystone microorganisms, being highly influential in ecosystems, particularly in harsh ecosystems where climatic and edaphic conditions can become stressful to most soil biota (Allen, 1991; Koske and Gemma, 1997). The AMF contribute to

establishing pioneer plants (Allen and Allen, 1988) and regulating plant species composition (Van der Heijden et al., 1998). Hence, some describe AMF as physical engineers (sensu Jones et al., 1997) as they directly or indirectly control resource availability to plants by changing the biotic or abiotic environments. Their role as ecological engineers was implied by Koske (1975), Sutton and Sheppard (1976) and Koske and Polson (1984), who suggested that AMF contribute directly to stabilizing dunes by forming aggregates of sand grains, which have increased resistance to movement by wind. Besides physically transforming dunes, e.g., by extramatrical hyphae aggregating particles, AMF can initiate transformations via chemical processes. They can produce glomalin, a hydrophobic glycoprotein, which contributes to particle aggregation (Wright and Upadhyaya, 1998). Glomalin increases hydrophobicity of soil, allowing greater air penetration and water drainage, thereby favoring aggregation, improving structure, and enhancing gas exchange and moisture conditions, processes essential for optimal plant establishment and growth (Oades, 1993).

Plant community composition changes along the gradient created from coastal to inland dunes are deter-

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\*\* Corresponding author. E-mail: margarid@iaccess.com.br

mined by successional processes. Along the gradient, salt spray, salinity and sand movements are important factors affecting plant community composition (Henriques and Hay, 1988). The classical view that early successional habitats are dominated by non-mycotrophic or facultatively-mycotrophic species is supported by several studies (Nicolson, 1960; Reeves et al., 1979; Miller, 1987; Allen and Allen, 1990; Titus and Moral, 1998). However, studies on sand dunes indicate that AMF are present in the earliest to the latest seral stages (Nicolson and Johnston, 1979; Corkidi and Rincón, 1997; Koske and Gemma, 1997).

Studies of AMF along dune stabilization gradients have been done mostly in temperate regions. In England, Nicolson and Johnston (1979) found increasing AMF spore densities and species richness along successional stages of the gradient. Studying a secondary successional dune system in the USA, Koske and Gemma (1997) found that AMF species richness and spore population, mycorrhizal colonization of *Ammophila breviligulata* Fern. and mycorrhizal inoculum potential (MIP) increased with successional stage. They also found apparent successional patterns for AMF species from early-established (1–2 years) to late-invader plant species. In a tropical system along the Gulf of Mexico, Corkidi and Rincón (1997) found 97% of plant species were mycorrhizal along a gradient from mobile to stabilized areas. The MIP also increased with dune stabilization, and the responsiveness of plant species to AMF colonization was not correlated with seral status. However, the community structure of AMF was not determined.

Sand dunes in the state of Santa Catarina cover approximately 250 km<sup>2</sup>, approximately 0.3% of the state. Management plans to stabilize dunes include planting unstable areas with specific plant species colonized by AMF populations. It is hoped that the strategy will promote plant successional processes leading to stabilized dunes as demonstrated by Koske and Gemma (1997). Initial studies on AMF diversity and community structure in dune areas of differing stability are considered essential prior to formalizing recovery programs. Such studies allow for widely distributed AMF species to be identified and evaluated for use in culturing, seedling inoculation and planting phases of recovery programs.

Our objective was to sample a typical sand dune system in South Brazil as a case study to assess changes in the community structure of AMF along a stabilization gradient where plant composition and soil properties differ. As a corollary to work of Corkidi and Rincón (1997), we assessed whether AMF species diversity and MIP increase over the gradient. The gradient spanned 650 m and consisted of three successional stages at Praia da Joaquina, Ilha de Santa Catarina. Species diversity and AMF community structure were assessed based on counting and identifying spores recovered from field samples. We also assessed MIP using a corn bioassay.

## Materials and Methods

**Study site** We worked in natural sand dunes at Praia da

Joaquina, Ilha de Santa Catarina (27° 50' S, 48° 34' W), Santa Catarina state, southern Brazil. The climate is Köppen type Cfa (i.e., mesothermic with no dry season and a warm summer) where rainfall is evenly distributed throughout the year (average annual accumulation: 1,521 mm) and the mean annual temperature is 20°C. Relative humidity is high (annual mean: 82%). Prevailing winds (18 to 80 m/s) are northeasterly and southerly (Santos et al., 1997).

A plot (30 × 25 m) was established in each of three stages of stabilization [embryonic dune, foredune and fixed dune, as described by Moreno-Casasola and Espejel (1986)] along a transect from the beach towards inland. Plots were located at 10, 40 and 650 m from the beach line.

Physical conditions and plant communities in the three stages have been described by Reitz (1961) and Bresolin (1979). The embryonic dune constitutes a narrow ridge of sand periodically subjected to flooding. The substrate is wavy with irregular elevations that allow sand grains to be carried by the wind. Soil and plants are constantly influenced by salt spray. The plant community is dominated by pioneer vegetation characterized by halophytes, rhizomatous and stoloniferous perennial plants such as *Blutaparon portulacoides* (St. Hil.) Mears, *Paspalum vaginatum* Sw., *Senecio crassiflorus* (Lam.) DC and *Ipomoea pes-caprae* (L.) Sweet. In the foredune, salt spray is decreased and temperatures at the soil surface can reach 60°C. Soil lacks organic matter (OM) and plants experience periodic droughts. The plant community includes rhizomatous species and those producing very deep root systems reaching the water table. The dominant plant is the grass *Spartina ciliata* Brongn., followed by the less prevalent *I. pes-caprae*, *Remirea maritima* Aubl., *Hydrocotyle bonariensis* Lam., *Scaevola plumieri* Vahl, *Panicum racemosum* Spreng. and *Polygala cyparissias* St. Hill. In the fixed dune, the soil is more compacted, having higher OM and clay contents than soils in the previous stages. The substrate is stabilized and not subject to wind movement, allowing denser clumps of vegetation to form consisting mainly of shrubs and small trees. Plants in this stage include *Vitex megapotamica* (Spreng.) Moldenke, *Eugenia catharinae* Berg., *Campomanesia littoralis* Legrand, *Gaylussacia brasiliensis* Meissn., *Polypodium lepidopteris* Sodiro, *Myrcia* spp., and *Dodonaea viscosa* Jacq.

**Soil sampling** In summer (February) 1997, 10 plant individuals were randomly selected at each stage and 1.5 L of soil surrounding the root system of each plant was removed. The 10 soil samples per stage were pooled and homogenized. Pooled samples were used for: 1) soil physical and chemical analyses (methods are mentioned briefly in footnotes of Tab. 1); 2) AMF spore recovery, identification and enumeration; and 3) measuring MIP. All samples were stored (4°C) in sealed plastic bags for up to one month until processed.

**AMF spore recovery and identification** Spores were identified from six sub-samples (100 g each) taken from each pooled sample. Spores were extracted using the wet-sieving procedure (Gerdemann and Nicolson, 1963)

followed by sucrose gradient (20% and 60%) centrifugation. Spores were transferred to Petri plates and only spores appearing viable (color, shape, surface conditions and cell content) under the dissecting microscope were categorized into morphotypes, counted and subsequently mounted permanently in PVLG and Melzer's reagent. Spores were identified by comparing specimens with original species descriptions, voucher specimens and reference isolates described by the International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM, West Virginia, USA, <http://invam.caf.wvu.edu>).

**Mycorrhizal inoculum potential** The MIP was assessed using the corn bioassay technique (Moorman and Reeves, 1979). Corn (*Zea mays* L.) seeds were surface sterilized with sodium hypochlorite (20%) for 60 min, repeatedly rinsed with sterile water, and germinated in sterilized sand. Soil from each stage was mixed with sterilized sand (1 : 1, v/v) and placed in 500 mL plastic pots (15 pots per stage). One corn seedling was transplanted to each pot. Plants were grown under greenhouse conditions (day/night, 14/10 h; day/night temperatures, 24/21°C; light, 14 to 17 klux) and watered daily. For each stage, plants from 5 randomly selected pots were harvested at 20, 30 and 40 d after planting. Roots were carefully washed from the soil, stained according to Koske and Gemma (1989), and scored for mycorrhizal colonization using the grid-line intersection method (Giovannetti and Mosse, 1980). Values are expressed as percentage of mycorrhizal colonization.

**Indices, abundance models and statistical analyses** Species abundance is expressed as numbers of spores of each species recovered per 100 g of soil. Relative family abundances (%) in the Glomales were calculated using total numbers of spores recovered in the families divided by the total number of spores recovered. Numbers of species and spore counts per species were used to determine Margalef's diversity index ( $D_{Mg}$ ); the heterogeneity indices of Simpson's dominance (D) and Shannon's diversity (H); and evenness using Shannon's diversity index (E) (Magurran, 1988). Numbers of spores for each species were plotted as rank-log abundance graphs to obtain curves depicting community structures. Goodness-of-fit analyses were then performed against theoretical curves of the geometric series, log series and broken stick models (Magurran, 1988).

## Results

**Soil chemical and physical properties** Soil pH was similar among the three stabilization stages (Tab. 1). Concentrations of P, K, Na, and Mg tended to increase as dune stabilization increased. Calcium and Al were not detectable. Organic matter (OM) increased from 0.4% in the embryonic dune to 0.8 and 1.1 % in the foredune and fixed dune, respectively. Soil texture was sandy with the highest levels of silt and clay found in the fixed dune (Table 1).

**AMF species** Fungi of all three families of Glomales were detected along the gradient, and relative presence

Table 1. Chemical and physical characteristics of soils collected at the embryonic dune, foredune and fixed dune at Praia da Joaquina, Ilha de Santa Catarina, Brazil.

Characteristics	Embryonic	Foredune	Fixed
pH <sup>a)</sup>	6.1	6.0	5.9
P (mg/Kg) <sup>b)</sup>	3.4	5.4	7.5
K (mg/Kg) <sup>b)</sup>	2.7	9.5	13.6
Na (mg/Kg)	1.4	2.7	6.1
Ca (mg/Kg) <sup>b)</sup>	0	0	0
Mg (mg/Kg) <sup>b)</sup>	0	8.2	32.7
Al (mg/Kg) <sup>b)</sup>	0	0	0
CEC (c mol <sub>c</sub> /kg) <sup>c)</sup>	0.52	0.69	0.82
Base saturation (%)	1	15	37
O.M. (%) <sup>d)</sup>	0.4	0.8	1.1
Clay (%)	2.0	1.0	3.0
Silt (%)	4.0	2.0	6.0
Sand (coarse) (%)	89.0	91.0	72.0
Sand (fine) (%)	5.0	6.0	19.0

a) pH in water (1 : 2.5).

b) P and K extracted with HCl and H<sub>2</sub>SO<sub>4</sub>; Al<sup>3+</sup>, Ca<sup>2+</sup> and Mg<sup>2+</sup> extracted with 1 N KCl.

c) CEC = cation exchange capacity.

d) O.M. = organic matter, extracted according to Walkley and Black, as described by Nelson and Sommers (1982).

of spores in each family changed markedly among the three stages (Fig. 1). Members of Gigasporaceae dominated in the embryonic stage, accounting for 78% of all spores recovered in this stage, and decreased to 6% in the fixed dune (Fig. 1). In contrast, Glomaceae spores were not detected in the embryonic dune, accounted for only 8% of recovered spores in the foredune and dominated the fixed dune (84%). Over 50% of recovered spores in the foredune belonged to Acaulosporaceae,

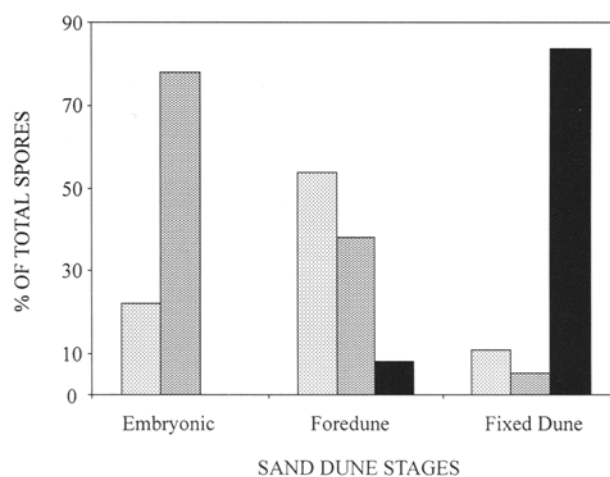


Fig. 1. Relative spore abundances of AMF families in Glomales, Acaulosporaceae (▨), Gigasporaceae (■) and Glomaceae (■) over a sand dune stabilization gradient at Praia da Joaquina, Ilha de Santa Catarina, Brazil. Values are the mean of six sub-samples taken from the pooled soil samples obtained in each type of sand dune along the gradient.

Table 2. Spore abundance (per 100 g soil) of AMF species, species richness and Margalef's diversity index in the embryonic dune, foredune and fixed dune at Praia da Joaquina, Ilha de Santa Catarina, Brazil.

AMF Species	Spore abundance <sup>a)</sup>		
	Embryonic	Foredune	Fixed
<b>Gigasporaceae</b>			
<i>Gigaspora albida</i> Schenck & Smith	6.3	50.7	10.5
<i>Scutellospora weresubiae</i> Koske & Walker	3.5		
<i>S. coralloidea</i> (Trappe, Gerd. & Ho) Walker & Sanders	2.8	4.7	
<i>S. pellucida</i> (Nicol. & Schenck) Walker & Sanders	3.3	8.5	1.8
<b>Acaulosporaceae</b>			
<i>Acaulospora scrobiculata</i> Trappe		81.2	
<i>A. gerdemannii</i> Schenck, Spain & Sieverding	3	8.2	6.8
<i>Acaulospora</i> sp. 1 <sup>b)</sup>	1.5	2.2	16.3
<b>Glomaceae</b>			
<i>Glomus constrictum</i> Trappe		14.2	10.2
<i>Glomus occultum</i> Walker & Koske			14.5
<i>Glomus</i> sp. 1 <sup>c)</sup>			49.0
<i>Glomus</i> sp. 2 <sup>c)</sup>			97.5
<i>Glomus</i> sp. 3 <sup>c)</sup>			8.5
Average spore number (N)	20.4	169.7	215.1
Species richness (S)	6	7	9
Margalef's index (D <sub>Mg</sub> )	1.64	1.16	1.48

<sup>a)</sup> Values represent the mean of six sub-samples taken from the pooled soil samples obtained at each stage of dune stabilization.

<sup>b)</sup> Putative new species.

<sup>c)</sup> Non-identified species.

which was the second most abundant family in the embryonic dune; their numbers were relatively low in the fixed dune.

Spores of four genera from Glomales families were recovered in the three stages (Table 2). *Glomus* was represented by five species recovered mainly from the fixed dune, followed by *Scutellospora* and *Acaulospora* (three species each, Table 2). *Gigaspora* was represented by *G. albida*, and *Entrophospora* was not detected.

Twelve AMF species were detected along the gradient; four could not be placed into described taxa (Table 2). Only four AMF species were detected in all three stages, *A. gerdemannii*, *Acaulospora* sp. 1, *G. albida* and *S. pellucida*. Some species were recovered only from one stage: *S. weresubiae*, only in the embryonic dune; *A. scrobiculata*, only in the foredune; and *Glomus occultum*, *Glomus* sp. 1, *Glomus* sp. 2 and *Glomus* sp. 3, only in the fixed dune. We attempted trap cultures with field soil to detect non-sporulating AMF species but we found only a few spores of four additional species (data not shown).

There was a trend of greater total spore abundance and species richness as dune stability increased (Table 2). Only approximately 20 spores/100 g soil were recovered in the embryonic dune. Comparable values for the foredune and fixed dune were approximately 170 and 215, respectively. Six AMF species were recovered in the embryonic dune, 7 in the foredune, and 9 in the fixed dune. Margalef's diversity index did not follow the

pattern of increasing richness as dune stability increased; 1.64, 1.16 and 1.48 in the embryonic dune, foredune and fixed dune, respectively.

**Diversity indices and abundance models** The embryonic and fixed dunes had lower Simpson's dominance (D), 0.20 and 0.27, respectively, compared with the foredune (0.33). Evenness (E) values and Shannon's diversity (H) were 0.95 and 1.71 in the embryonic dune (Table 3). Respective values in the fixed dune were 0.75 and 1.64, and in the foredune, 0.70 and 1.37. Patterns for heterogeneity and evenness values among the stages were reflected in the spore abundance curves (Fig. 2) and the results of fitting the distribution models to abundance data. Abundance curves varied according to stabilization stage (Fig. 2). The broken stick model fit the spore abundance data of the embryonic dune at  $0.95 < p < 0.98$ , and of the fixed dune at  $0.50 < p < 0.70$ . The log series model fit the data of the foredune at  $0.80 < p <$

Table 3. Heterogeneity indices and evenness values for AMF communities in three stages of sand dunes along the stabilization gradient at Praia da Joaquina, Ilha de Santa Catarina, Brazil.

Indices	Embryonic dune	Foredune	Fixed dune
Simpson's dominance (D)	0.20	0.33	0.27
Shannon's diversity (H)	1.71	1.37	1.64
Shannon's evenness (E)	0.95	0.70	0.75

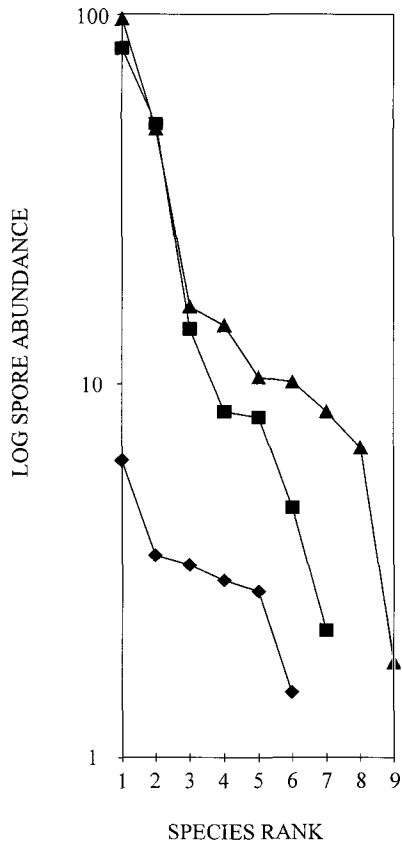


Fig. 2. Species rank-log abundance curves for AMF communities recovered from an embryonic dune (◆), foredune (■) and fixed dune (▲) at Praia da Joaquina, Ilha de Santa Catarina, Brazil.

0.90. All other attempts to fit these two models, and to fit the geometric series model generally yielded probability values less than 0.30.

**Mycorrhizal inoculum potential** Mycorrhizal colonization of corn, the bioassay host, tended to increase from

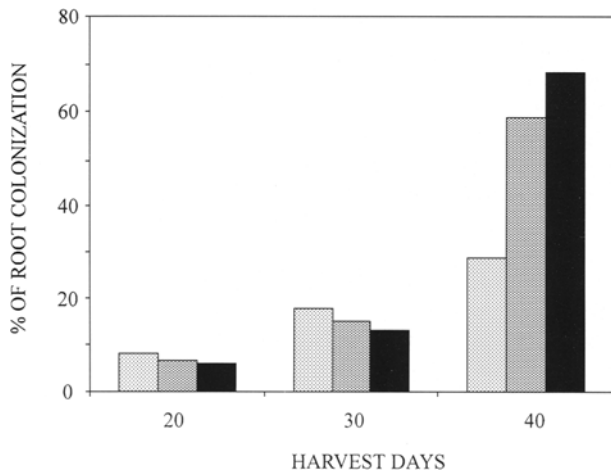


Fig. 3. Arbuscular mycorrhizal colonization of corn plants, harvested 20, 30 and 40 d after initiating the bioassay, for soils from the embryonic dune (□), foredune (▤) and fixed dune (■) at Praia da Joaquina, Ilha de Santa Catarina, Brazil.

the 20<sup>th</sup> to the 40<sup>th</sup> day of plant growth for all stages (Fig. 3). Colonization ranged from approximately 5 to 8% after 20 d for the three stages. After 30 d, colonization tended to be greater in the embryonic dune than in the fixed dune soil. After 40 d, colonization in the foredune and fixed dune soils appeared similar, at 58.8% and 68.5%, respectively, and tended to be greater than the value found for the embryonic dune soil.

**Discussion**

Our case study highlights possible marked changes in AMF community structure over the successional/stabilization gradient that occurs at Joaquina Beach. These changes, when considered with the role of AMF in plant establishment and subsequent survival and growth, indicate that further study is needed to understand the mechanisms contributing to the structure of both the plant and fungal communities inhabiting dune systems. We observed changes at the familial, generic and species levels of AMF taxonomy. The MIP also changed over the gradient, increasing with increasing dune stabilization. We appreciate that most of the conclusions drawn from this case study are based on spore numbers in field soils, and may not represent the entire AMF community. Therefore, we interpret our results cautiously. Our results suggest patterns of community structure related to dune succession and can aid in developing hypotheses related to species and genera in Glomales.

There was a striking difference in the relative distribution of AMF families along the gradient; as sporulation by Gigasporaceae taxa decreased, sporulation by species of Glomaceae increased, and members of Acaulosporaceae slightly dominated in the foredune (Fig. 1). Three hypotheses may explain the dominance of Gigasporaceae in the embryonic dune. The first hypothesis concerns spore characteristics. Fungi in Gigasporaceae include large-spored species that produce one to several germination tubes (especially *Gigaspora*). Large spores with high lipid contents contain large amounts of carbon (C), which may be reserves and important for spore survival during initial growth of multiple germination tubes (Koske, 1981) in soils without susceptible roots, a frequent condition in the embryonic dune. These attributes may be important for rapid and efficient colonization of new roots produced in the embryonic dune.

The second hypothesis involves functional roles of the families in Glomales. Gigasporaceae species may benefit plant communities by increasing soil aggregation, while Glomaceae species may assist plants by altering mineral nutrient relations (Miller and Jastrow, 1992). In prairies undergoing restoration, increased numbers of soil macroaggregates were associated with increased biovolumes of *Gigaspora gigantea* spores and decreased biovolumes of *Glomus constrictum* and *G. etunicatum* spores (Miller and Jastrow, 1992). Similarly, percentages of water-stable aggregates tended to be higher in soils containing *Gigaspora rosea* than in soils containing either *Glomus mosseae* or *G. etunicatum* (Schreiner and

Bethlenfalvay, 1995). Thus, the extramatrical hyphae of Gigasporaceae, enmeshing and entrapping soil particles into larger aggregates, may stabilize the plant community in the embryonic dune where plant cover is sparse and the soil is subject to dislocation.

The third hypothesis links soil chemical properties to distribution of AMF. Specifically, the relatively higher presence of Gigasporaceae species was associated with lower levels of P, K and OM in the embryonic dune (Table 1). Porter et al. (1987) reported that AMF species distributions were related to soil properties. Specifically, *Gigaspora* spp. were found in samples with the least OM. Johnson et al. (1991) found the presence of *Scutellospora* species was negatively correlated with levels of soil C among old field successional stages. Gigasporaceae fungi are dominant in areas of sand dunes adjacent to water (Koske and Halvorson, 1981; Sylvia, 1986; Koske, 1987; Stürmer and Bellei, 1994), where OM does not accumulate, although this family can co-dominate with Glomaceae under some circumstances (Abe et al., 1994).

Glomaceae species were the predominant sporulators in the fixed dune, where OM tended to accumulate and soil fertility was higher than in the embryonic dune. In the fixed dune, soil is stabilized and its movement is reduced or eliminated unless catastrophic conditions occur. We suspect that mycorrhizas benefit plants via enhanced mineral nutrition and protection against root pathogens. Glomaceae, then, might be expected since they are more efficient in absorbing nutrients than are species from other families (Jakobsen et al., 1992; Pearson and Jakobsen, 1993). We speculate that OM also affects the occurrence and abundance of Glomaceae, although the literature on this effect is scant (e.g., Hepper and Warner, 1983; St. John et al., 1983). Quintero-Ramos et al. (1993) reported a positive correlation between mycorrhizal colonization by three *Glomus* spp. and soil OM content, but other Glomales genera were not evaluated. The correlation coefficient between soil OM and spore numbers appeared higher for *Glomus* spp. than for *Acaulospora laevis*, but the difference between the coefficients for the two genera was not significant (Porter et al., 1987). Although these studies suggest that OM regulates AMF establishment and distribution, more studies are needed. Alternatively, sporulation by *Glomus* spp. might be favored in more fertile soils (i.e., fixed dune), where P and K levels were at least two-fold higher than in the embryonic dune. Johnson and Pflieger (1992), working in field plots amended with a complete fertilizer, found relative abundance of *Glomus intraradices* was significantly increased and abundance of *Gigaspora* spp. and *Scutellospora calospora* were reduced compared with non-amended plots.

Acaulosporaceae tended to dominate in the fore-dune, and was followed by Gigasporaceae, although the proportion of each family was more evenly distributed compared with values in the other two stages (Fig. 1). The pattern can be explained by the dominance of *Acaulospora scrobiculata*; it was the most abundant (51%) in an adjacent fore-dune (Stürmer and Bellei,

1994), and appears associated with pioneer plant species in three geographically distinct dune systems on Ilha de Santa Catarina (Mendonça, Milde, Stürmer and Rygiel-wicz, unpublished results).

In the embryonic and fixed dunes, AMF data best fit the broken stick model while the best fit in the intermediate fore-dune was with the log series model (Fig. 2). Some researchers have used abundance models to describe resource partitioning where abundance is approximately equivalent to niche space occupied (Magurran, 1988). These models were developed primarily by studying animals and plants where individuals can be easily counted (Magurran, 1988). Thomas and Shattock (1986) described abundance patterns of filamentous fungi in the phylloplane of *Lolium perenne* L. using the geometric and log series models. We used spore numbers, which are one measure of abundance (cf. biomass). Abundance curves also may indicate C allocation (one example of resource partitioning) for sporulation, and spores growth and survival (Stürmer and Bellei, 1994; Morton et al., 1995). We do not have corroborating data on physiological processes when interpreting the fit of these models. We hope that our case study will encourage other studies to test hypotheses concerning processes contributing to AMF community structure.

The broken stick model, applied in the embryonic and fixed dunes, is thought to describe communities that are partitioning one resource (Magurran, 1988). It is considered the biological expression of a uniform distribution (high evenness), implying that an important ecological factor is being shared more or less evenly. The embryonic dune has the lowest dominance value (caused by relatively uniform abundance of Gigasporaceae) and the highest Shannon diversity value (Table 3). These values are coupled with the greatest evenness value calculated among the stages (Fig. 1). In the embryonic dune, Gigasporaceae species may become evenly distributed and prevalent by allocating C to a smaller number of large multiple-germinating spores (Table 2), each spore capable of encountering a multitude of roots compared with the colonization potential of the other AMF present. This strategy is consistent with the putative role of Gigasporaceae to promote soil aggregation. Also, as the embryonic dune is a more restrictive environment with a lower leaf area index (personal observation), C allocated to mycobionts may be reduced, precluding the production of many large spores.

The other end of the gradient (i.e., fixed dune) may not be as restrictive as the embryonic dune. Plant size, leaf area index and stocking densities are much higher here than in the embryonic dune and fore-dune (personal observation), perhaps resulting in C allocation to mycobionts modified by direct competition for light interception among competing plants. Here, C allocation may not be as reduced as in the embryonic dune (note, the higher OM content in the fixed dune, Table 1). Simpson's dominance, Shannon's diversity and evenness values are intermediate in the fixed dune (Table 3). *Glomus* spp. spores dominate, and they may be obtaining C to promote both hyphal growth and sporulation. Indeed,

the MIP of the fixed dune soil was the highest among the three stages (Fig. 3). Also, the abundance of smaller, single-germinating, *Glomus* spp. spores was over 12 times greater in the fixed dune compared with the value in the embryonic dune (Table 2).

The log series model, used to fit the foredune data, can apply where species are thought to arrive in an unsaturated habitat at random intervals of time and occupy the remaining niche hyperspace (Magurran, 1988). A small number of abundant species and a large proportion of rare species is characteristic. This model is most applicable where a few factors might dominate. In the foredune, while species richness is not greatly different from that in the embryonic dune (Table 2), two species (*Acaulospora scrobiculata* and *Glomus constrictum*) appear, *Scutellospora weresubiae* disappears compared with the more restrictive embryonic dune (Table 2). Thus the single unit change in richness masks the total change in species composition.

Abundance of *Gigaspora albida* increased in the foredune compared with the embryonic dune (Table 2). Evenness and Shannon's diversity were reduced (Table 3), and dominance was high in the foredune. Unlike in the fixed and embryonic dunes, the shoulder in the foredune abundance curve was less pronounced (Fig. 2). Both *A. scrobiculata* and *Gigaspora albida* appear to meet the model criterion of a small number of abundant species, while the remaining five species are less prevalent. In the foredune, the three most abundant species have spores that are either large with multiple germination tubes, or small with single germination tubes (Table 2). It appears that the resource availability in the foredune may not be like that at either end of the gradient (Table 1). There may be multiple controlling factors affecting resource allocation in the foredune, which are intermediate to those at either end of the gradient, as indicated by the multiple growth strategies of the AMF. This suggests that the species may be occupying complementary niche space.

The MIP tended to differ after 30 and 40 d of growth of corn (Fig. 3). In general, MIP increased from the embryonic to the fixed dune, which agrees with findings that MIP increases with dune stabilization (Corkidi and Rincón, 1997). Although high within-site spatial variability can exist in the bioassay, its extent is dependent on the host (Brundrett and Abbott, 1995). The predominant family found in each stage and the type of infective propagules produced provides insight to our results. After 30 d, high MIP was found for the embryonic dune soil (Fig. 3), where Gigasporaceae dominated and whose spores seem to be the only propagules initiating colonization (Biermann and Linderman, 1983; Pearson and Schweiger, 1994). Despite low spore numbers at this stage, Gigasporaceae species may have strategies (e.g., multiple germination) to colonize roots rapidly when present, and so could be considered c-colonizers (sensu Grime, 1979). However, after 40 d, MIP was higher in the foredune and fixed dune, where Acaulosporaceae and Glomaceae dominated. Species from these families have multiple propagules

(e.g., spores, hyphal fragments and mycelia within roots) that can initiate colonization (Jasper et al., 1989). Our results also suggest that, after initially penetrating the root cortex, Acaulosporaceae and Glomaceae species grow faster and colonize roots more aggressively than Gigasporaceae species.

We found interesting apparent changes in the AMF communities along the dune gradient at Praia da Joaquina. Factors affecting these changes are not fully understood, but our evaluation indicates they entail edaphic and biological characteristics including different functional roles among the Glomales families. Gigasporaceae spp., possibly serving as physical engineers in the embryonic dune or where improvement in soil structure may be beneficial, are especially noteworthy. Soil characteristics frequently are thought to determine AMF community structure, but little specific understanding has emerged from this generalization. We offer these specific observations as starting points from which further study can be initiated to test hypotheses.

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