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Occurrence of arbuscular mycorrhizal fungi in soils of early stages of a secondary succession of Atlantic Forest in South Brazil

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RESUMO – (Ocorrência de fungos micorrízicos arbusculares em solos de estádios iniciais de uma sucessão secundária da Floresta Atlântica no Sul do Brasil). A diversidade de fungos micorrízicos arbusculares (FMAs) e o potencial de inóculo micorrízico foram determinados em estádios de sucessão secundária da Floresta Atlântica. Dentro de cada estádio - pioneiro, capoeirinha e capoeirão - quatro transectos foram estabelecidos e três amostras de solo foram obtidas por transecto. A comunidade vegetal foi dominada por *Pteridium aquilinium* no estádio pioneiro e *Dodonaea viscosa* e *P. aquilinium* foram co-dominantes na capoeirinha. No capoeirão, *Miconia cinnamomifolia* foi dominante seguida por *Euterpe edulis*. O número total de esporos foi significativamente maior na capoeirinha do que nos outros estádios, embora o número de esporos viáveis permaneceu constante entre os estádios sucessionais. Acaulosporaceae e Glomeraceae foram as famílias predominantes e perfizeram 83% do total de esporos recuperados. Dos 18 morfotipos de esporos recuperados, 10 foram alocados para espécies conhecidas, com uma espécie de *Acaulospora* sp. e uma de *Glomus* sp. sendo os esporuladores predominantes e presentes em todas as amostras. O indíce de diversidade de Simpson e a eqüitabilidade para as espécies de FMAs não diferiram significativamente entre os estádios sucessionais e a riqueza específica de FMAs foi negativamente correlacionada com a riqueza específica vegetal. O solo da Capoeirinha apresentou o maior potencial de inóculo (37%). A dominância da comunidade micorrízica por poucos esporuladores e a relação entre diversidade fúngica e vegetal são discutidos.

Palavras-chave: Glomerales, fungos micorrízicos arbusculares, Floresta Atlântica, sucessão vegetal secundária, diversidade de espécies

ABSTRACT – (Occurrence of arbuscular mycorrhizal fungi in soils of early stages of a secondary succession of Atlantic Forest in South Brazil). Arbuscular mycorrhizal fungi (AMF) species diversity and mycorrhizal inoculum potential were assessed in areas representative of stages of secondary succession in the Brazilian Atlantic Rain Forest. Within each stage - pioneer, 'capoeirinha' and 'capoeirão'- four transects were established and three soil samples were taken along each transect. The plant community was dominated by *Pteridium aquilinium* in the pioneer stage, while *Dodonaea viscosa* and *P. aquilinium* were co-dominants in the 'capoeirinha' stage. In capoeirão, *Miconia cinnamomifolia* was dominant followed by *Euterpe edulis*. Total spore number per 100 g soil was significantly larger in the 'capoeirinha' stage than in the other stages, although the number of viable spores was similar among stages. Acaulosporaceae and Glomeraceae were the predominant families accounting for 83% of the total spores recovered. Of the 18 spore morphotypes, 10 were allocated to known species, with *Acaulospora* sp. and *Glomus* sp. being the dominants recovered in all samples. Simpson's index of diversity and evenness for AMF species were not significantly different among the successional stages and AMF species richness was negatively correlated with plant species richness. Soil from 'Capoeirinha" showed the highest inoculum potential (37%). Dominance of the mycorrhizal community by few sporulators and the relationship between plant and fungal diversity are discussed.

Key words: Glomerales, arbuscular mycorrhizal fungi, Atlantic Rain Forest, secondary plant succession, species diversity

Introduction

Tropical rain forests are one of the most complex, endangered and unknown ecosystems on Earth (De Miranda & Mattos 1992). Approximately one third of these forests are located in Brazil and include the Amazon and the Atlantic forests, the latter spanning the Atlantic coast from the states of Rio Grande do Sul (30°S) to Rio Grande do Norte (6°S) and originally covering around 450,000 km^2. After five centuries of exploitation, expansion of crops, subsistence agriculture, and land speculation, this forest is presently reduced to 15,000 km^2 of primary areas, found in small patches clustered in the Southeastern and Southern regions (Joly *et al.* 1991; De Miranda & Mattos 1992). The high occurrence of endemic species in this forest subject to a high rate of deforestation turns it into a hot spot for biodiversity studies as well as one of the three

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areas ideal for the development of conservation programs (Wilson 1989; Joly *et al.* 1991; De Miranda & Mattos 1992; Terborgh 1992).

In tropical regions, numbers of soil organisms, particularly fungi, are quite high, and include poorly studied groups, especially those fungi associated with vascular plants, which are not adequately known (Solbrig 1991; Hawksworth 1992). The mycorrhizal symbiosis (associations of fungi with plant roots) is common in natural ecosystems such as the Neotropical forests where the association formed by arbuscular mycorrhizal fungi (AMF) (Division Glomeromycota) is prevalent compared to ectomycorrhizal fungi (Janos 1980a). Mycorrhizal fungi play an important role as agents of plant nutrition by improving nutrient uptake to the host, thereby enhancing not only growth rates but also survival of seedlings of many tropical forest species (Janos 1980b). They also act as soil nutrition agents because they are involved in transporting C compounds to the soils and link the plant and the soil systems (Bethlenfalvay & Linderman 1992).

Studies on the occurrence of AMF in tropical forest soils are relatively scarce. As an overall pattern, *Glomus* and *Acaulospora* were the two dominant genera associated with four plant species in Singapore (Louis & Lim 1987), with epiphytic and terrestrial Piperaceae plants in a Costa Rica tropical forest (Maffia *et al.* 1993) and within different habitats in a tropical forest in Mexico (Guadarrama & Álvarez-Sanchez 1999). Johnson & Wedin (1997), surveying a dry tropical forest-grassland transition, detected 28 AMF morphotypes along the gradient where *Glomus aggregatum* and two undescribed *Glomus* were the predominant fungi. In Brazil, Trufem & Viriato (1990) found *Acaulospora foveata* and *Scutellospora heterogama* as the most frequent AMF species recovered from the rhizosphere of several plants of the Atlantic Forest. Gomes & Trufem (1998) recovered 17 taxa from a secondary remnant of the Atlantic Forest and found *Acaulospora foveata*, *Glomus macrocarpum*, *Scutellospora erythropa* and *Acaulospora* sp. as the most frequent species recovered through the sampling period of one year. Despite this research, to our knowledge no studies on the occurrence of AMF in different stages of plant secondary succession in tropical forests in Brazil have been developed.

The Brazilian program of sustainable development of the Atlantic Forest includes as priorities the recovery of disturbed areas and the preservation of primary remnants and secondary vegetation areas (CIMA 1991). For recovery of degraded areas, plant succession plays an important role, and rate and direction of the succession are largely influenced by below-ground processes (Reeves & Redente 1991). Approaches are being developed in Santa Catarina state for management and preservation of forestry plants used for food, timber and medicine. Santa Catarina is outstanding among the Brazilian states as about 30% of the forests have been maintained in large or small patches (Brown & Brown 1990). In order to establish baselines for studies on the role of mycorrhizae in growth and survival of native plants, a synecological approach was adopted to study the abundance and qualitative composition of the AMF communities in early stages of plant succession after deforestation of an area of Atlantic Forest.

Material and methods

Study site – The community of AMF was studied in three distinct sites located in the cities of Santo Amaro da Imperatriz and São Pedro de Alcantâra, located in the State of Santa Catarina, South Brazil. These areas represent different secondary plant communities and are referred to as 'pioneer stage', 'capoeirinha' and 'capoeirão' (Klein 1980), which were used for agriculture (cassava, corn, sugarcane) for a short period of time and then abandoned. Site 1 was representative of the pioneer stage and was dominated by the bracken fern *Pteridium aquilinum* (Dennstaedtiaceae). This area had a fire history approximately seven years ago, was abandoned and then *P. aquilinum* took over forming a pure stand. Site 2 was representative of the 'capoeirinha' stage and was a 12 year-old abandoned pasture dominated by *Dodonaea viscosa* (Sapindaceae). Site 3 was the "capoeirão" stage dominated by *Miconia cinnamomifolia* (Melastomataceae) and had been abandoned for about 40 years.

Climate in both areas is humid temperate with warm summers (Cfa, Koeppen), with annual rainfall ranging from 1,400 mm to 1,600 mm uniformly distributed throughout the year. Average annual temperature is 20 °C and relative humidity is high ranging from 80% to 85%.

Soil samples – Within each site, circular study plots were established and four transects were oriented toward the cardinal points from a center point. On each transect, 3 sampling points were established and soil samples of 2 1 each were taken resulting in 12 samples

per site. The circular area varied in size for each site: 14 m^2 in the 'pioneer stage', 56 m^2 in the 'capoeirinha' and 127 m^2 in the 'capoeirão'. The selection of different areas in each site was based upon area/density curves used for plant ecology studies. Soil chemical analyses were performed by a state government laboratory, CIDASC - Companhia Integrada de Desenvolvimento Agricola de Santa Catarina (Tab. 1).

Plant community analyses – In each site, the percentage of plant cover was calculated using the point-quadrat method (Goodall 1952). At each sample point along the transects, a 1 m^2 quadrat was established and a metal pin of 1 m tall was randomly plotted 25 times inside the quadrat. The plant species touching the pin were recorded and plant cover corresponding to each site was expressed as percentage of pins touched by a particular species. In 'capoeirinha' and 'capoeirão' sites, the cover of trees and shrubs taller than 2 m was estimated by vertical projection of the pin. The number of plant species detected in each quadrat was used to calculate average species richness for each stage.

AMF community – Spores of AMF were extracted, counted and identified from soil samples obtained from each sample point. After homogenizing the soil sample, an aliquot of 100 g soil was used to extract spores by wet-sieving (Gerdemann & Nicolson 1963) followed by centrifugation in a 20% and 60% sucrose gradient. Spores were separated into morphotypes under a dissecting microscope (60x) and mounted on permanent slides with PVLG and PVLG mixed with Melzer's reagent. Spores were identified at 400× with a light microscope, based on spore wall structure, comparisons with original descriptions (Schenck & Perez 1989), "vouchers" preserved on slides and reference isolates described at the International Culture Collection of Arbuscular and Vesicular-Arbuscular Mycorrhizal Fungi (INVAM, West Virginia, USA, http://invam.caf.wvu.edu). The following population indices were assessed: 1) total and viable number of spores, expressed as number of spores per 100 g dry soil, 2) relative abundance expressed as the number of spores of different AMF species as percentage of the total number of spores, and 3) frequency of occurrence as expressed as the percentage of samples including a particular species. Spores were considered viable if they had clear content under the light microscope with intact spore wall and non-viable if they were either empty or showing evidence of parasitism on the spore wall. The number of AMF species recovered from each sample point was used to calculate average AMF species richness for each site. Fungal diversity was estimated with Simpson's index (D) and evenness (E) (Magurran 1988).

Mycorrhizal inoculum potential – The inoculum potential of the mycorrhizal community was estimated through a corn bioassay as described by Moorman & Reeves (1979). Field soil from each successional stage was placed into a 500 g plastic pot (5 pots per stage) and seeded with *Zea mays* L. (corn). One corn plant was left per pot after seedling emergence and plants were grown under greenhouse conditions (day/night photoperiod of 14/10 h, day/night temperatures of 24/21°C, and light intensity from 14 to 17 klux). After 4 weeks, roots were carefully washed away from soil particles under tap water and stained according to Koske & Gemma (1989). Roots were cut in 1-cm segments and inoculum potential was estimated by calculating the percentage of 120 root segments bearing arbuscules, internal hyphae or vesicles, according to the method proposed by Biermann & Linderman (1981).

Statistical analyses – Data on spore counts, inoculum potential, plant and fungal species richness and soil parameters were screened for homogeneity of variance by Levene's test. Spore data were ln(x+1) transformed and mycorrhizal colonization of corn was arcsine square-root transformed. Spearman rank correlation was used to relate spore counts and inoculum potential results to edaphic factors, as well as to establish the relationship between AMF and plant species richness. One-way ANOVA was used to assess the variance accounted for by the successional stages on the soil, fungal and plant parameters evaluated. Multiple

Table 1. Chemical and physical characteristics of soils collected at three successional stages of Atlantic Forest in South Brazil.

Edaphic factors	Pioneer stage	"Capoeirinha"	"Capoeirão"
pH [a]	4.4	4.8	4.8
P (mg Kg^{-1}) [b]	4.0	2.2	2.8
K (mg Kg^{-1}) [b]	82	124	73
Ca + Mg (cmolc kg^{-1}) [b]	4.9	5.46	11.24
Al (cmolc kg^{-1}) [b]	2.67	1.28	1.04
O.M. (%) [c]	9.8	6.9	5.7
Clay (%)	19	24	25

[a] pH in water (1:1); [b] P and K extracted with HCl and H_2SO_4; Al^{3+}, Ca^{2+} and Mg^{2+} extracted with 1 N KCl; [c] O.M. = organic matter, extracted according to Walkley and Black, as described by Nelson & Sommer (1982).

comparisons of means were performed using *t* tests. Analysis was performed using JMP® (SAS Inst. Inc. 1995).

Results and discussion

Plant community composition – In the 'pioneer stage', *Pteridium aquilinum* (Dennstaedtiaceae) formed a pure stand with 100% coverage (Tab. 2). In the 'capoeirinha' stage, 30 plant species were detected, and *Dodonaea viscosa* (Sapindaceae) predominated with 88% coverage. *P. aquilinum* was still present although at lower frequency than in the previous stage (Tab. 2). Although detected with low frequencies of coverage, members of Poaceae and Asteraceae were commonly represented in this stage. The highest number of plant species (56) was detected in the 'capoeirão' stage where none of the plants from early stages were present. The canopy was dominated by *Miconia cinnamomifolia* (Melastomataceae) with 100% coverage followed by *Euterpe edulis* (Arecaceae) with 50% (Tab. 2). Other common plants in this stage were members of Rubiaceae, Myrtaceae, Piperaceae, and Melastomataceae as well several ferns.

AMF community composition and abundance – The total number of AMF spores was significantly higher in the 'capoeirinha' stage (850 spores/100g dry soil) than in the pioneer stage and 'capoeirão', although only 21% were viable (Fig. 1A-B). Spore counts were not significantly different between the pioneer stage (250 spores) and 'capoeirão' (225 spores). The number of viable spores was not significantly different among stages and ranged from 170 to 188 spores per 100 g dry soil (Fig. 1B). No significant correlation was detected between spore counts and edaphic factors.

Overall, Acaulosporaceae and Glomeraceae were the predominant families, with 61% and 22% frequency, respectively. They were followed by Gigasporaceae (11%) and Archaeosporaceae (6%). Members of the family Paraglomeraceae and Pacisporaceae were not detected at any stage. At the genus level, *Acaulospora* was the predominant genus (55%) followed by *Glomus* (21%). This pattern of predominance of Glomerales families and genera was also observed within each successional stage.

Eighteen (18) spore morphotypes were recovered from all successional stages, 10 of which could be attributed to known species. The most frequent species

Table 2. Dominant plant species with coverage > 5% in three successional stages of the Atlantic Forest in South Brazil.

Plant species	Family	Cover (%)
Pioneer stage		
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	100
"Capoeirinha"		
Dodonaea viscosa (L.) Jacq.	Sapindaceae	88
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	54
Vernonia chamissonis Less.	Asteraceae	22
Tibouchina urvilleana (DC.) Cogn.	Melastomataceae	17
Scleria sp.	Cyperaceae	9
"Capoeirão"		
Miconia cinnamomifolia (DC.) Naud.	Melastomataceae	100
Euterpe edulis Mart.	Arecaceae	50
Piper sp. 1	Piperaceae	28
Piper sp. 2	Piperaceae	15
Anemia sp.	Schizaeaceae	14

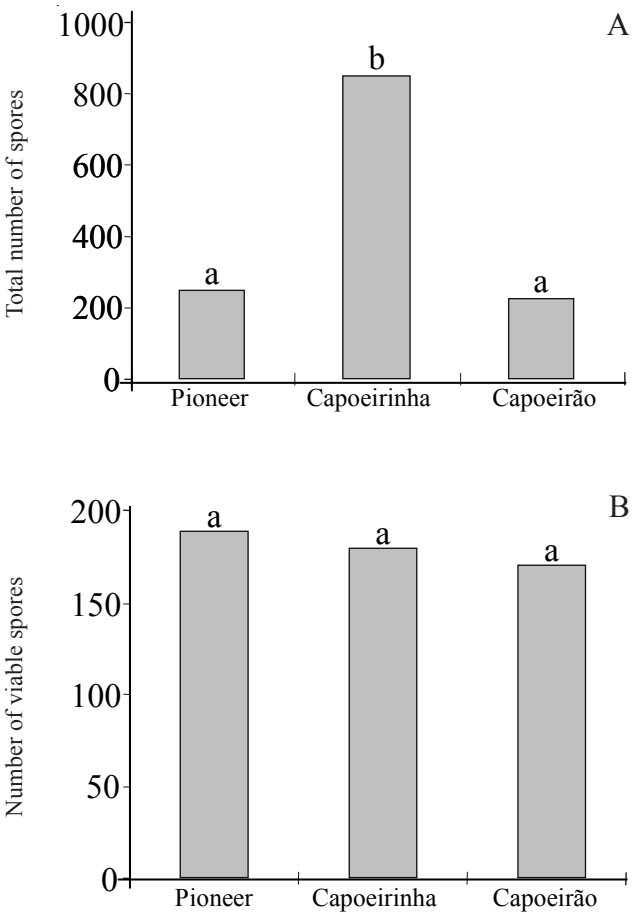

Figure 1. Means of total number of spores (A) and number of viable spores (B) per 100 g of soil recovered within each successional stage. Bars with the same letter are not significantly different ($P < 0.05$).

recovered were *Acaulospora* sp.1 and *Glomus* sp. 4, both with 100% frequency, followed by *Entrophospora colombiana* and *A. scrobiculata* (Tab. 3). All remaining species were found in less than 50% of the samples. *Acaulospora* sp.1 and *Glomus* sp. 4 accounted for 43% and 39% of the spores recovered, respectively. The majority of AMF species occurred in low spore densities as their relative abundance was < 1% (Tab. 3).

Diversity indices – The highest number of spore morphotypes was found in the pioneer stage (15) followed by 'capoeirão' (14) and 'capoeirinha' (9). Average fungal species richness followed the same trend, and average plant species richness increased along the successional gradient (Fig. 2A-B). Simpson's diversity (D) and Evenness (E), calculated for the fungal community, were not influenced by successional stage (Fig. 2C-D). Across all stages, the number of fungal species was negatively correlated with the number of plant species (Fig. 3; $P < 0.0001$, $r^2 = 0.36$).

Table 3. Frequency of occurrence and relative abundance of AMF species recovered in three successional stages of the Atlantic Forest in South Brazil.

Family/AMF Species	Frequency (%)	Relative abundance (%)
ACAULOSPORACEAE		
Acaulospora sp. 1 (similar to *A. delicata*)	100	43
A. scrobiculata Trappe	50	4
A. mellea-like	44	< 1
A. bireticulata Rothwell & Trappe	36	< 1
Acaulospora sp. 2 (similar to *A. lacunosa*)	33	< 1
A. rehmii Sieverding & Toro	30	< 1
Acaulospora sp. 3 ("small-creamish")	28	< 1
A. foveata Janos & Trappe	25	< 1
A. tuberculata Janos & Trappe	16	< 1
A. morrowiae-like	14	< 1
Entrophospora colombiana Spain & Schenck	66	2
GLOMERACEAE		
Glomus sp. 4 (similar to *G. glomerulatum*)	100	39
Glomus pansihalos Berch & Koske	14	< 1
Glomus sinuosum Gerdemann & Bakshi	8	< 1
Glomus sp. 5 (similar to *G. etunicatum*)	5	< 1
ARCHAEOSPORACEAE		
Archaeospora leptoticha (Schenck & Smith) Morton & Redecker	17	< 1
GIGASPORACEAE		
Gigaspora sp. 6 (similar to *G. decipiens*)	47	< 1
Scutellospora pellucida Koske & Walker	5	< 1

Mycorrhizal inoculum potential – The highest inoculum potential was detected in the 'capoeirinha' stage where 37% of corn root segments were colonized by arbuscular mycorrhizal fungal structures, followed by the pioneer stage (25%) and 'capoeirão' (10%). Inoculum potential values were significantly different ($P < 0.05$) between different successional stages.

This study on the diversity of glomeralean fungi is the first survey of these soil microorganisms associated with plant communities in distinct stages of secondary succession in Atlantic Forest in Southern of Brazil. In the Southeastern region, Aidar *et al.* (2004) found 29 taxa of AMF in a chronosequence of Atlantic Forest successional stages; however, they discussed differences in fungal species richness regarding wet and dry season and comparison with other studies rather than wiht plant successional stages. Our results may contribute to the knowledge of fungus species distribution in tropical regions, where fungi associated with vascular plants are scantly studied and poorly known (Hawksworth 1991). Moreover, AMF have not been adequately registered from tropical forests, although their role in plant species survival and growth is well established (Janos 1980b). We recognize that our conclusions concerning AMF species diversity and distribution are based solely on field recovered spores which may not represent the entire AMF community, and therefore our results should be interpreted cautiously.

Attempts were made to quantify viable and non-viable spores (empty or dead spores) and the latter were commonly recovered from all sites (Fig. 1). Herrera & Ferrer (1980) stressed that a high proportion of empty or dead spores in relation to living spores was a common feature of glomeralean fungal spores in tropical soils. Lipid-rich spores and fungal hyphae are subject to predation and parasitism as they serve as a food source for a wide range of soil animals (Rabatin & Stinner 1988). In this study, most of the dead spore walls presented transverse striations and papilla as shown by Boyetchko & Tewari (1991) in *Glomus dimorphicum* spores. These signs of parasitism were present predominantly in a globose to rod-like shaped, small (60-80 μm) brown *Glomus* spore, which accounted for most of the dead spores. This *Glomus* is a common inhabitant of soils in Santa Catarina as high quantities of parasitized spores have also been detected in apple, pear and peach orchards around the state (S.L. Stürmer & M.M. Mendonça, personal

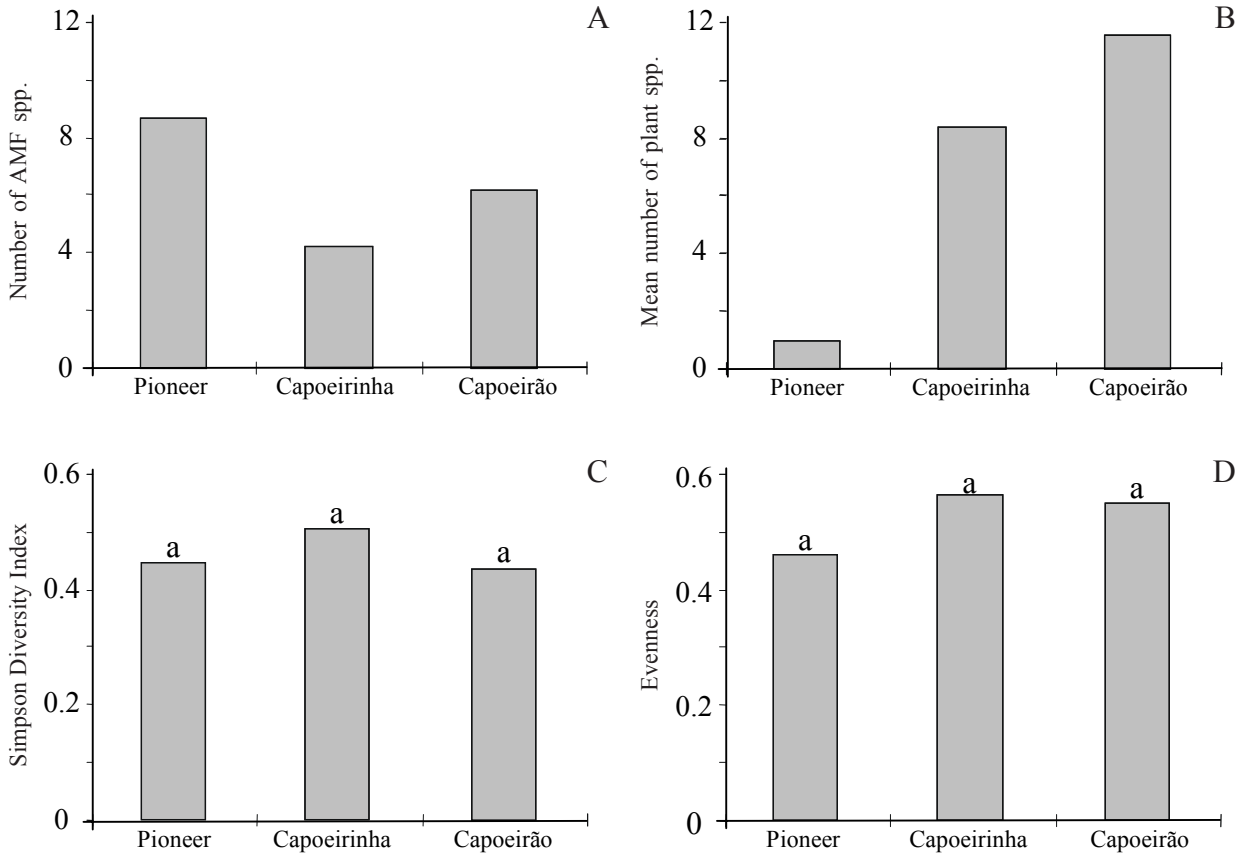

Figure 2. Comparisons of the stages (pioneer, capoeirinha, capoeirão) of plant secondary succession according to (A) mean number of AMF species, (B) mean number of plant species, (C) Simpson index of diversity of the AMF spore community, and (D) evenness for fungal spore community. Within graphs, bars with the same letter indicates that values are not significantly different ($P < 0.05$).

observation). Interesting is that spores of other glomeralean genera were rarely parasitized with striations and papilla and they were rather usually empty or with contents turned black.

Our results clearly demonstrated that the family Acaulosporaceae and the genus *Acaulospora* predominated in the mycorrhizal fungal community associated with plants along the successional gradient. These results are contradictory to other findings in tropical forests where the family Glomeraceae and the genus *Glomus* were dominant (Herrera & Ferrer 1980; Louis & Lim 1987; Guadarrama & Álvarez-Sánchez 1999). In Brazil, Trufem (1990) found 12 species of *Acaulospora* and 11 species of *Glomus* associated with native plants in a primary tropical forest at Ilha do Cardoso and Trufem & Viriato (1990) detected five and six species of *Acaulospora* and *Glomus*, respectively, from plants occurring at the Alto da Serra de Paranapiacaba Biological Reserve. These results indicate either a dominance of *Glomus* species or a co-dominance of both genera in tropical forest regions. Our study along a successional gradient corroborates those of Aidar *et al.* (2004) who detected 13 species of *Acaulospora* and 11 species of *Glomus* in a chronosequence within an area of Atlantic Rain Forest. We speculate that predominance of the Acaulosporaceae in our study could be the result of either contemporary ecological (*e.g.*, soil chemical characteristics, plant species) or historical factors (*e.g.*, dispersal, local extinction). Soil factors have been implicated as determinants of AMF distribution and members of Acaulosporaceae could be favored by the low pH found in soils of all three stages as has been reported in the literature for distinct ecosystems (Porter *et al.* 1987; Siqueira *et al.* 1989). Conversely, considering that our study encompasses areas in secondary succession up to 40 years after land abandonment, we could hypothesize that members of Acaulosporaceae are dominant in early to intermediate stages while Glomeraceae predominates in more advanced stages of the succession process or in undisturbed areas of tropical forests. Indeed,

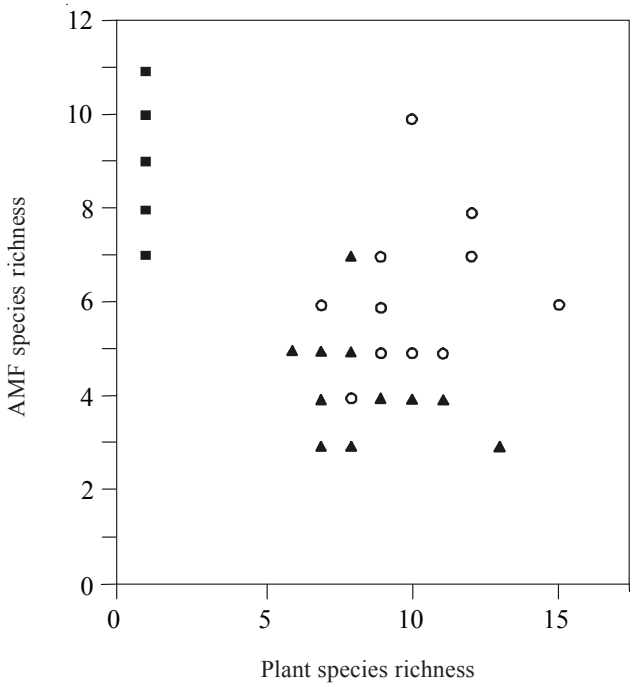

Figure 3. Relationship between plant and AMF species richness recorded in each sample within the pioneer, capoeirinha and capoeirão stages of plant secondary succession. ■ = Pioneer; ▲ = 'Capoeirinha'; ○ = 'Capoeirão'.

predominance of Glomeraceae in tropical forest is the finding of investigations in mature primary forest (Louis & Lim 1987; Guadarrama & Álvarez-Sánchez 1999). Further studies on AMF diversity considering several successional stages and secondary and primary forest areas are necessary to test this hypothesis.

This study showed a trend of species diversity of AMF being negatively correlated with plant species diversity along the successional gradient. Data from a temperate region showed that AMF diversity tended to increase with successional rank in an old field succession (Johnson *et al.* 1991), while fungal diversity was relatively uniform in a desert ecosystem despite the diversity in the plant community (Bethlenfalvay *et al.* 1984). Increase in AMF species richness was accompanied by an increase in plant diversity and ecosystem productivity in simulated macrocosms of temperate ecosystems (van der Heijden *et al.* 1998). In tropical conditions, this relationship has never been appropriately addressed and is poorly understood. Janos (1980a) suggested that populations of AMF in the tropics may be buffered by residual spore pools against changes, making mycorrhizal fungal communities resistant to changes in plant community composition. He also emphasizes that if disturbance is not severe, fungal populations can reach equilibrium 5-10 years after abandonment of shifting cultivation. Our results support Janos's hypothesis on the buffering capacity of the mycorrhizal community. The successional stages studied herein had a past history of cultivation with cassava, corn, and sugarcane, which are mycotrophic species that probably contributed to the spore pool available to the plant species that initiated the secondary succession process. Indeed, recent results of Picone (2000) demonstrated that spore density and fungal community of AMF were relatively similar between pasture and primary rain forest, and therefore, mycorrhizal fungi should not limit plant secondary succession. Conversely, results of van der Heijden *et al.* (1998) on the relation between AMF and plant diversity were not observed in this study. However, we recognize that our measurement of AMF diversity probably does not represent the entire fungal community as it does not account for cryptic non-sporulating species colonizing plant roots (Stutz & Morton 1996).

The mycorrhizal community in all successional stages, analyzed through fungal sporulation, was dominated by two species, namely *Acaulospora delicata*-like and *Glomus glomerulatum*-like, which together accounted for 82% of the spores recovered. Dominance by these species and low relative abundance of the remainder is reflected by the low evenness measure (Fig. 2D). The evenness value in this study is comparable with that found by Cuenca & Lovera (1992) for a revegetated area, where two fungal species dominated the mycorrhizal community. As a general pattern, studies reporting spore counts from the field in tropical forest areas indicated that few fungal species are the dominant sporulators. Louis & Lim (1987) found many different spore types in a lowland rain forest in Singapore, but one species was always dominant at each site. In a dry tropical forest surveyed by Johnson & Wedin (1997), *Paraglomus occultum*-like spores accounted for 2,938 spores out of the 3,441 total spores counted. In each of the tropical rain forests in Nicaragua and Costa Rica sampled by Picone (2000), two *Glomus* species were also the most prolific sporulators, accounting for more than 90% of the total spores produced by the entire mycorrhizal community. We speculate that dominance by few AMF sporulators is related to either entanglement of roots of different species that mycorrhizal fungi could bridge through their external mycelium or absence of seasonality in tropical environments, where stable microclimate at the soil

surface can be found and no marked dry and wet season detected. As a result, most AMF species would not be influenced by seasonal variations that could trigger sporulation and therefore they can allocate carbon mostly for vegetative growth in the soil or in the highly available plant root systems.

We found that changes in plant species diversity are not followed by changes in AMF species diversity along stages of plant succession of a tropical rain forest. In our study, this relationship was impaired mainly because of the pioneer stage, where only one plant species (*Pteridium aquilinium*) was present but had the highest mean number of AMF species per sample (Fig. 2A). The relationship between plant versus AMF species diversity is not completely clear and understood for most natural ecosystems. This relation is probably nonexistent considering the ubiquitous presence of these fungi in plant communities and absence of host specificity by the fungi. Van der Heijden *et al.* (1998) inoculated different numbers of AMF species in a macrocosm simulating old-field ecosystems from North America. They observed that the lowest value of plant diversity was found in non-inoculated treatments while the highest value was detected when 8-14 species of AMF were present in the macrocosms. For tropical conditions, this relationship has never been studied whether under natural condition or under controlled conditions.

Results of this study contribute to knowledge of the geographical distribution of AMF species resident in tropical soils. Further studies should assess AMF diversity covering additional stages along the successional gradient and the study of mycorrhizal dependency and responsiveness of plants from different successional groups. This approach would lead to a better understanding of interactions between arbuscular mycorrhizal fungi and tropical forest plants which can be used for management and recuperation of this threatened ecosystem, the Brazilian Atlantic Rain Forest.

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