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Changes in arbuscular mycorrhizal associations and fine root traits in sites under different plant successional phases in southern Brazil

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Abstract Fine root morphological traits and distribution, arbuscular mycorrhizal (AM) fungi, soil fertility, and nutrient concentration in fine root tissue were compared in sites under different successional phases: grass plants, secondary forest, and mature forest in Londrina county, Paraná state, southern Brazil. Soil cores were collected randomly at the 0–10- and 10–20-cm depths in three quadrants (50 m^2) in each site. Plants from the different successional stages displayed high differences in fine root distribution, fine root traits, and mycorrhizal root colonization. There were increases in the concentration of nutrients both in soil and fine roots and decrease of bulk soil density along the succession. The fine root biomass and diameter increased with the succession progress. The total fine root length, specific root length, root hair length, and root hair incidence decreased with the succession advance. Similarly, the mycorrhizal root colonization and the density of AM fungi spores in the soil decreased along the succession. Mycorrhizal root colonization and spore density were positively correlated with fine root length, specific root length, root hair length, root hair incidence, and bulk density and negatively correlated with fine root diameter and concentration of some nutrients both in soil and root tissues. Nutrient concentration in root tissue and in soil was positively correlated with fine root diameter and negatively correlated with specific root length, root hair length, and root hair incidence. These results suggest different adaptation strategies of plant roots for soil exploration and mineral acquisition among the different successional stages. Early successional stages displayed plants with fine root morphology and AM fungi colonization to improve the root functional efficiencies for uptake of nutrients and faster soil resource exploration. Late successional stages displayed plants with fine root morphology and mycorrhizal symbiosis for both a lower rate of soil proliferation and soil exploration capacity to acquire nutrients.

Keywords Mineral acquisition · Root distribution · Root hairs · Soil fertility · Specific root length · Tropical forest

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Introduction

Natural plant succession is a continuous process which begins when seedlings of pioneer plants colonize the area and progresses to later stages in which plant competitiveness and tolerance to the environment control species replacement throughout time (Guariguata and Ostertag 2001). Growth rates differ greatly among plant species: as compared to slow-growing species, fast-growing species display more intensive metabolism, higher nutritional requirements (Lusk et al. 2008), and fine roots with higher growth and faster soil exploration and uptake capacity (Comas and Eissenstat 2004). This allows for a more efficient soil exploration due to the higher specific root

length (Wright and Westoby 1999; Raghothama and Karthikeyan 2005). Fine roots of fast-growing species, characterized by low diameter and low tissue density (Comas et al. 2002), have more and longer root hairs (Zangaro et al. 2005) and are generally highly colonized by arbuscular mycorrhizal (AM) fungi, in comparison to slow-growing species (Zangaro et al. 2003; Matsumoto et al. 2005). Fine roots are influenced by soil nutrient availability (Eissenstat et al. 2000; Powers et al. 2005) and their major functions are uptake of water and nutrients from soil (Jackson et al. 1997). Plants grown in low-fertility soils generally present high biomass allocation to the fine roots, use the allocated carbon more effectively, and display alterations in root morphology (Tilman 1994; Comas and Eissenstat 2004). Morphological and physiological changes in fine roots generally show high plasticity in soils with different fertility levels (Hodge 2004). In woody species, the plasticity of fine roots is generally greater in fast-growing species than in slow-growing species (Comas et al. 2002; Zangaro et al. 2007).

Many plant species in natural ecosystems rely on AM fungi for water and nutrient uptake (Read and Perez-Moreno 2003; Smith and Read 1997; Hinsinger et al. 2005; Lynch and Ho 2005). In addition, the mycorrhizal symbioses may reduce biological stresses on the host plant (Newsham et al. 1995), increase plant tolerance to drought, and improve root longevity (Eissenstat et al. 2000). AM fungi are predominant in tropical soils, where they make symbiosis with a wide variety of plant species (Smith and Read 1997). In low-fertility soils, plants usually maintain high levels of AM root colonization (Treseder 2004; Powers et al. 2005). Zangaro et al. (2005, 2007) observed that fast-growing species of native woody species in southern Brazil present higher levels of AM root colonization as compared to slow-growing species and suggested that this could be due to morphological root traits in fast-growing species that favor contact with fungal propagules in the soil. In addition, a more intensive plant metabolism demanding higher amounts of nutrients to support higher growth rates may require an extensive symbiosis to supply nutritional needs.

The relationship between fine roots and nutrient availability in the soil is related to the control of fine root production and the partition of below-ground carbon and may also predict the consequences of environmental changes for the stock and dynamics of roots (Guo et al. 2004; Powers et al. 2005). Thus, different functional groups of plants that characterize different phases of succession are expected to show differences in root distribution, morphological fine root traits, and degrees of association with AM fungi. Knowledge about such aspects may help to improve understanding on how plant structures involved in nutrient uptake (fine roots and mycorrhiza) are related to plant species composition along the succession. Thus, the aim of this work was to assess the relationships among morphological root traits and mycorrhizal fungi in plants from different stages of tropical succession in southern Brazil, characterized by a scenario of continuum of soil fertility. In this context, three sites were chosen: a grass site, a secondary forest, and a mature forest which can be considered to represent the process of succession advance.

Materials and methods

Study sites

The sites are localized in Londrina county, Paraná state, southern Brazil (23°27′ S, 51°15′ W). The climate is Cfa-mesotermic according to Köppen, characterized by hot summers, no defined dry season, and an average temperature of above 22°C in the warmest month. Monthly rainfall totals over 1,600 mm rainfall per year (Chagas e Silva and Soares-Silva 2000) and the soil is classified as Rhodic Ferralsol, according to FAO (1994).

The grass site of approximately 50,000 m^2 was located at the campus of the State University of Londrina. This area had the A and B soil horizons removed in 1986 when the upper 3 m of soil layer was removed with bulldozer and the subsoil remained exposed to natural native plant establishment. At present, the grasses *Paspalum notatum* and *Cynodon* sp are the dominant vegetation in the area and there is no occurrence of trees or shrubs. The grasses are slow growing and the site presents clearings without vegetation where the soil, with a low fertility level, remains exposed along the year. This area represents an early plant succession stage on a degraded low-fertility soil.

In the secondary forest, the vegetation was regenerated naturally after pasture was abandoned in 1987, following soil degradation after 50 years of inadequate cultural practices. Pioneer and early secondary native species dominate the community of tree species, such as: *Alchornea triplinervia*, *Anadenanthera colubrina*, *Croton floribundus*, *Parapiptadenia rigida*, and *Tabernaemontana australis*. Some young late-successional species such as *Cedrela fissilis* also occur, in addition to some seedlings of climax species such as *Guarea kunthiana* and *Trichilia elegans* in the understory. The herbaceous component is characterized by species typical of shaded environments.

The mature forest site consisted of a tropical, primary, semideciduous forest. This site is located in the State Park "Mata dos Godoy" (Parque Estadual Mata dos Godoy). The forest is rich in species diversity and shows a complex canopy and structure, with trees up to 40 m tall. The most common families are Lauraceae, Myrtaceae, Meliaceae, Leguminosae, Apocynaceae, and Euphorbiaceae. The most common tree species are *Actinostemom concolor*, *Aspidosperma*

polyneuron, *Balfourodendron riedelianum*, *Cedrela fissilis*, *Euterpe edulis*, *Gallesia integrifolia*, *Sorocea bonplandii*, and the genera *Guarea* and *Trichilia*. This site is 2 km apart from the secondary forest and 15 km from the grass site.

Field sampling and soil characteristics

Three 50-m^2 quadrants were marked out in the mature forest, secondary forest, and grass site. Twenty intact soil cores (45 mm in diameter and 100 mm in depth=0.159 dm^3) were collected at two depths (0–10 and 10–20 cm) at random locations in each quadrant delimited in each site during January and February 2005. For each site, 30 soil cores (five on each quadrant and soil depth) were used for extracting roots and the remaining 30 soil cores were used for enumerating AM fungi spores and soil characteristics, totalizing 180 samples. The soil cores were placed in labeled plastic bags and stored at 5°C until use. To obtain only fine roots of the adult trees, the soil cores of the two forests were collected in points avoiding fine roots of the seedlings and herbs. The soil cores used for soil fertility assessments were dried at room temperature. Five soil samples from each depth and site were pooled to form one composite sample prior to chemical analyses. Results of these analyses are shown in Table 1. The carbon was extracted with 2 M $Na_2Cr_2O_7$ + 5M H_2SO_4 and determined by colorimetry. Ca and Mg were extracted with 1 M KCl and determined by titration. P was extracted by Mehlich-1 and determined by colorimetry. K was extracted by Mehlich-1 and determined by flame photometry. Available mineral N (NH_4^+ + NO_3^-) was determined in 2 M KCl extracted by semi-microkjeldahl distillation.

Root extraction and measurements

The soil cores were soaked in water and root fragments were separated from soil residues using a 0.25-mm mesh sieve. The sieved materials were hand-sorted in shallow dishes underwater and live fine roots (<2-mm diameter) were separated from coarse roots (>2-mm diameter), dead roots, and organic matter fragments. Only live fine roots (<2-mm diameter) were used in further analysis. Live fine roots were distinguished from the dead roots under a stereomicroscope, according to color, root elasticity, and the degree of cohesion of cortex, periderm, and stele (Röderstein et al. 2005).

The total length of fine fresh roots was determined by the gridline intersection method (Tennant 1975). For analysis of root morphological traits, 0.5 g of fresh fine root segments (<1-mm diameter) were taken in each soil sample and fixed in FAA (5 mL acetic acid, 5 mL formaldehyde, and 90 mL 50% ethanol) and stored until analysis. Fine root diameter was determined in eight segments in three random sites for each sample and soil depth, totalizing 24 measurements of fine root diameter. Root hair length was determined in eight fine root segments in up to 100 root hairs in each sample. The incidence of root hairs was assessed by the presence or absence of root hairs in 100 intersections of roots by a gridline method (Siqueira and Saggin-Júnior 2001; Zangaro et al. 2005) for each sample. Fine root diameter and root hair length were determined using a microscope at ×100 magnification with an ocular micrometer (Manjunath and Habte 1991; Schweiger et al. 1995). The fresh fine root fractions were placed in a drying chamber at 60°C until constant weight to obtain the dry mass. Specific root length (root length per unit of root mass) was derived from root length and root dry mass for each sample. Five samples of fine roots from each depth and quadrant in each site were pooled before nutrient analysis, determined at the Instituto Agronômico do Paraná, Londrina, Paraná.

AM fungal colonization and spore numbers in soil

The percentage of plant roots colonized with AM fungi was estimated microscopically on each sample stained according

Table 1 Mean values (±SE) for soil chemical and physical analysis from samples collected at the top surface (0–10 cm) and subsurface (10–20 cm) in the grass-covered site and secondary and mature forests in southern Brazil (n=3)

	Grass		Secondary		Mature	
Soil depth (cm)	0–10	10–20	0–10	10–20	0–10	10–20
C (g dm^{-3})	6.6±0.59	4.6±0.44	37.4±2.0	22.3±1.03	46.0±2.86	24.4±1.78
N (mg dm^{-3})	2.1±0.12	1.5±0.10	11.1±0.60	7.8±0.25	14.5±0.68	12.2±0.40
P (mg dm^{-3})	0.9±0.10	0.6±0.05	5.4±0.21	2.9±0.15	8.9±0.41	5.2±0.32
Ca (cmol(+) dm^{-3})	3.3±0.22	2.2±0.21	12.3±0.60	9.3±0.74	15.2±0.53	12.5±1.0
Mg (cmol(+) dm^{-3})	1.9±0.08	1.6±0.07	5.0±0.17	5.1±0.13	4.5±0.42	4.6±0.23
K (cmol(+) dm^{-3})	0.4±0.02	0.2±0.01	0.6±0.09	0.4±0.05	1.0±0.04	0.6±0.03
pH (water)	6.0±0.14	5.7±0.16	5.6±0.20	5.5±0.22	5.9±0.15	5.8±0.16
Bulk density (g cm^{-3})	1.25±0.10	1.31±0.07	0.97±0.10	1.1±0.08	0.8±0.07	0.95±0.10
Sand (%)	16±1.21	–	17±1.04	–	22±0.98	–
Loam (%)	17±1.14	–	22±1.45	–	24±1.56	–
Clay (%)	67±3.61	–	61±4.22	–	54±3.52	–

to Phillips and Hayman (1970) using a gridline intersect method (Giovannetti and Mosse 1980). AM fungal spores were extracted from 20 g of soil in each sample using the wet-sieving technique (sieves 710–53 μm), and spores separated by sieving were centrifuged in 60% sucrose (Sieverding 1991). The spores were recovered, washed in water, and spread upon squared filter paper and counted under a dissecting microscope.

Data analysis

Data are presented as means and standard deviation for fine root traits and AM fungal variables. The Pearson's correlation analyses among AM fungal variables, root morphological traits, and soil and fine root nutrient concentration were analyzed considering the means obtained in each quadrant and depth (n=18).

Results

Soil fertility increased with the progress in succession. The mature forest had the maximum fertility levels followed by soils from the secondary forest and grass sites. Higher levels were observed in the 0–10-cm layer than in the 10–20-cm soil layer in all places. The bulk soil density decreased with advance in the succession and increased soil depth (Table 1).

In the same way, the nutrient level in fine roots increased with progress in the succession. This means that the fine root tissues from the mature forest had the maximum nutrient concentration followed by the secondary forest and grass sites, except for Ca where no difference was observed between secondary and mature forests. No differences in depths were observed in root nutrient concentration among the three areas studied (Table 2).

The fine root dry mass was greater in the secondary forest than in the mature forest or grass sites at both soil depths (Fig. 1a). Also, when depth was compared, no differences were observed between secondary forest and grass sites. The total fine root length decreased through the succession progress (Fig. 1b). Considering the 0–10-cm layer, the total root length was high in the grass area and secondary forest and low in the mature forest. At 10–20 cm, the secondary forest showed more total fine root length compared with the other areas. The specific root length decreased with advance in the succession (Fig. 1c) and increased with soil depth. Specific root length was large in the grass area and low in the two forests. The root diameter also increased with the succession progress (Fig. 1d) and did not show variation between depths in all sites. The root hair length and its incidence decreased along the succession progress (Fig. 1e,f) as well as in depth when grass area and secondary forest were compared.

Spore numbers of AM fungi in soil decreased with succession progress and soil depth (Fig. 2a) and were high in the grass area and secondary forest and low in mature forest. The genera *Acaulospora*, *Gigaspora*, *Glomus*, and *Scutellospora* occurred in the mycorrhizal fungal community associated with plants from the secondary and mature forests, where *Acaulospora* and *Glomus* predominated. Only *Acaulospora* and *Glomus* occurred in the grass site, the latter species being more frequent in soil samples. AM root colonization (Fig. 2b) decreased as succession advanced and with soil depth and was high in the grass site, intermediary in secondary forest, and low in mature forest. Hyphal colonization was the most common form of colonization found in the roots from all sites. *Arum*-type and *Paris*-type colonization was observed in root samples, the first being more common in both the grass site and secondary forest, while the latter type was more common in the mature forest. Only AM fungal colonization was found in the root samples of the study sites. No evidence of ectomycorrhizal association was found.

AM root colonization and fungal spores in soil were correlated with some root morphological traits and nutrient concentration in soil and in fine root tissue (Table 3). There was a positive correlation between mycorrhizal root colonization and mycorrhizal fungal spores in soil. The mycorrhizal colonization and spores in soil correlated positively with fine root length, specific root length, root hair length, root hair incidence, and soil bulk density and negatively correlated with fine root diameter and concentration of the majority of nutrients in soil and in root tissue.

Table 2 Mean values (±SE) for nutrient concentrations in fine roots collected at the top surface (0–10 cm) and subsurface (10–20 cm) in the grass-covered site and secondary and mature forests in southern Brazil (n=3)

	Grass		Secondary		Mature	
Soil depth (cm)	0–10	10–20	0–10	10–20	0–10	10–20
N (g kg^{-1})	4.4±0.14	4.3±0.11	14.8±0.11	14.5±0.19	16.9±0.15	16.7±0.24
P (g kg^{-1})	0.3±0.04	0.2±0.03	0.5±0.02	0.4±0.04	0.8±0.03	0.7±0.04
K (g kg^{-1})	1.0±0.02	0.8±0.04	5.5±0.1	5.8±0.1	7.6±0.17	7.4±0.15
Ca (g kg^{-1})	4.7±0.1	4.9±0.09	13.1±0.21	13.4±0.17	13.2±0.25	13.5±0.22
Mg (g kg^{-1})	0.6±0.05	0.5±0.04	1.6±0.09	1.6±0.1	2.2±0.08	2.0±0.09

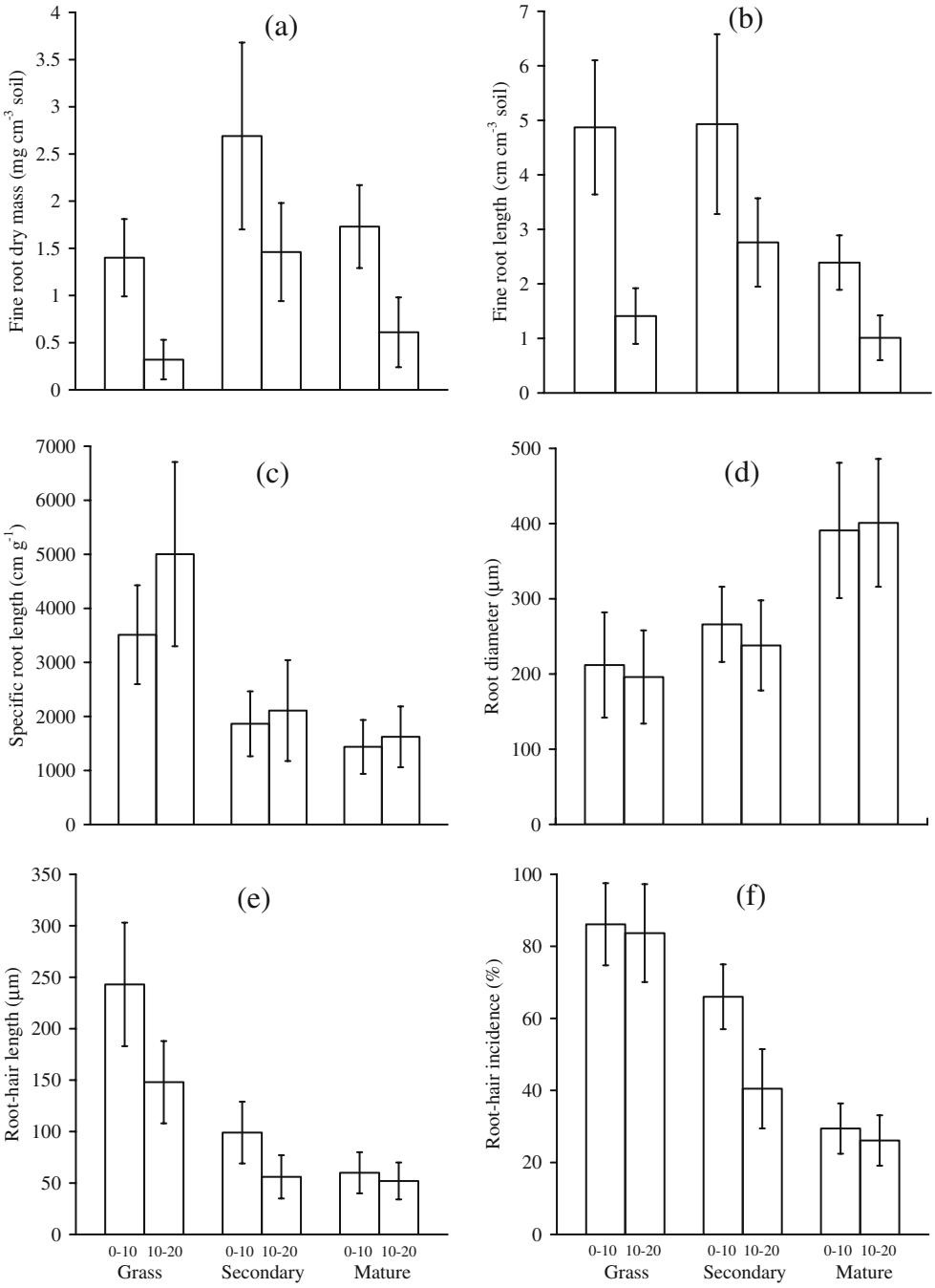

Fig. 1 Fine root dry mass (**a**), fine root length (**b**), specific root length (**c**), fine root diameter (**d**), root hair length (**e**), and root hair incidence (**f**) of native plants from the grass-covered site and secondary and mature forests in southern Brazil. Roots were taken at 0–10 and 10–20-cm soil depth. *Error bars* represent ±1 SD

The nutrient concentration in root tissue and in soil was correlated with root morphological traits (Table 3). Only C and Ca in soil were positively correlated with fine root dry mass. The nutrient concentration in root tissue and in soil was positively correlated with fine root diameter and negatively correlated with specific root length, root hair length, and root hair incidence. The soil bulk density was negatively correlated with fine root diameter and positively correlated with specific root length, root hair length, and root hair incidence.

Discussion

In the present study, the reduction in AM fungal root colonization and spore density below 10-cm depth is correlated with incidence of fine roots in this horizon, in agreement with other field studies (Abbott and Robson 1991; Brown and Bledsoe 1996; Ingleby et al. 1997; Muthukumar et al. 2003; Powers et al. 2005). AM root colonization and number of spores in the soil showed a positive correlation, reflecting the mycelial biomass of AM

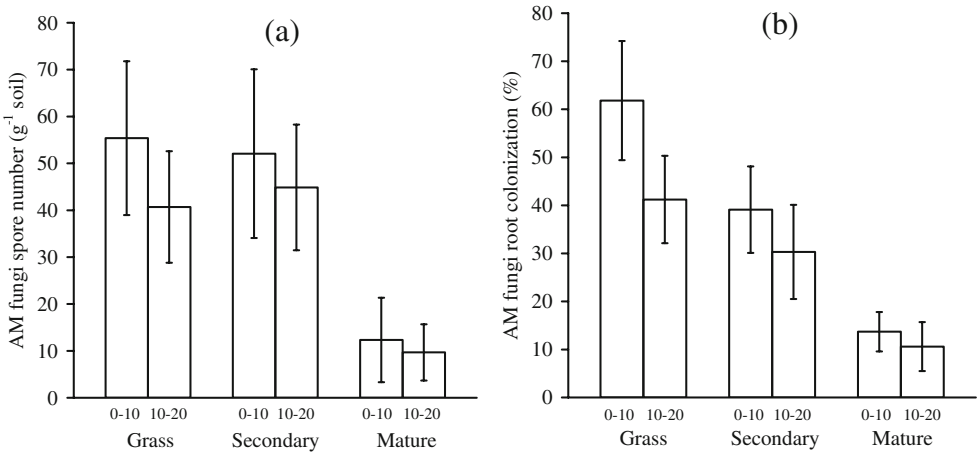

Fig. 2 Spore numbers of AM fungi in soils (**a**) and root colonization by AM fungi (**b**) of native plants from the grass-covered site and secondary and mature forests in southern Brazil. Soil samples were taken at 0–10- and 10–20-cm depth. *Error bars* represent ±1 SD

fungi present in the soil of the different study areas. Since the abundance of AM fungi in soil is often correlated with the degree of root colonization (McGonigle et al. 1990; Gange et al. 1993), the higher number of AM fungal spores in soils could be linked to a greater fine root production (Picone 2000). The mycorrhizal root colonization and spores in soil decreased with the progress in plant succession. Thus, these results reflect the greater investment in the AM symbiosis by grasses and early successional woody species (fast-growing species) as compared to native woody species of a mature forest (slow-growing species). Several studies corroborate this view. AM fungal spores were more abundant in pasture soil compared to dry jarrah forest in Australia (Jasper et al. 1991), humid secondary forest in Costa Rica (Fischer et al. 1994), dry forest in Mexico (Allen et al. 1998), lowland evergreen forest in Nicaragua and Costa Rica (Picone 2000), and tropical forest in southern Brazil (Zangaro and Andrade 2002). Zangaro et al. (2000) found a low density of AM fungi spores and low root colonization in plants from a mature forest in southern Brazil and suggested that slow-growing species are less able to maintain AM fungi due to their low metabolic activity, growth in relative high soil fertility, and shading. Aidar et al. (2004) found decreases in AM fungal root colonization in the chronosequence of an Atlantic forest in southeast Brazil and suggested that AM fungal colonization decreases with increasing soil fertility. Powers et al. (2005) reported that the amount of AM mycorrhizal hyphae in the soil of four tropical forests in Central and South America was quite low and suggested that such

Table 3 The Pearson correlation coefficient (r) among AM fungal variables, nutrient concentration in fine root tissue and soils, and fine root traits collected at 0–10- and 10–20-cm depth (n=18) from the grass-covered site and secondary and mature forests in southern Brazil

	RDM	RL	SRL	RD	RHL	RHI	AMC	AMS
AMC	−0.30 ns	0.68**	0.54*	−0.66**	0.64**	0.66**	–	0.78***
AMS	−0.31 ns	0.63**	0.51*	−0.69***	0.62**	0.65**	0.78***	–
Root								
N	0.32 ns	−0.12 ns	−0.90***	0.76***	−0.90***	−0.90***	−0.62**	−0.59*
P	0.02 ns	−0.37 ns	−0.75***	0.89***	−0.76***	−0.87***	−0.83***	−0.87***
K	0.24 ns	−0.19 ns	−0.87***	0.82***	−0.89***	−0.91***	−0.71***	−0.70**
Ca	0.40 ns	−0.03 ns	−0.90***	0.67**	−0.92***	−0.86***	−0.51*	−0.46 ns
Mg	0.28 ns	−0.21 ns	−0.88***	0.84***	−0.88***	−0.92***	−0.74***	−0.72**
Soil								
C	0.54*	−0.12 ns	−0.86***	0.86***	−0.72***	−0.64**	−0.54*	−0.52*
N	0.35 ns	−0.17 ns	−0.79***	0.92***	−0.66**	−0.72***	−0.63**	−0.65**
P	0.39 ns	−0.04 ns	−0.82***	0.96***	−0.70**	−0.70**	−0.64**	−0.66**
Ca	0.63**	−0.23 ns	−0.87***	0.55*	−0.78***	−0.66**	−0.21 ns	−0.17 ns
Mg	0.45 ns	−0.06 ns	−0.89***	0.58*	−0.86***	−0.81***	−0.39 ns	−0.34 ns
K	0.13 ns	−0.12 ns	−0.65**	0.93***	−0.38 ns	−0.53*	−0.60*	−0.69**
Density	−0.42 ns	0.01 ns	0.90***	−0.91***	0.77***	0.79***	0.64**	0.65**

Levels of significance were corrected by the Bonferroni procedure

AMC mycorrhizal root colonization, *AMS* AM fungal spores in soil, *RDM* root dry mass, *RL* root length, *SRL* specific root length, *RD* root diameter, *RHL* root hair length, *RHI* root hair incidence, *ns* $P>0.05$

*$P<0.05$; **$P<0.01$; ***$P<0.001$

plants might rely on fine roots instead of AM fungi for nutrient uptake.

The distribution of fine root biomass down the soil depth was similar among the three sites. More than 50% of fine roots occurred in the upper soil layer (Hendrick and Pregitzer 1996; Muthukumar et al. 2003; Powers et al. 2005) which is intensively explored by a higher concentration of fine roots to absorb nutrients (Hodge 2004; Lynch and Ho 2005). The fine root biomass and length were lower in the mature forest than in the secondary forest. These results are in agreement with other studies stating that the fine root biomass and length in a secondary forest may be similar or greater than that found in a mature forest (Cavalheiro and Nepstad 1996; Cavelier et al. 1996).

Based on the results regarding fine root length, specific root length, fine root diameter, root hair length, root hair incidence, and the high level of AM colonization, it is suggested that plant species of the grass area and early successional woody species of the secondary forest display both maximum effectiveness of carbon use for building fine root systems and more effective soil exploration than woody species of a mature forest. Fine root morphology influences soil nutrient uptake potential (Baylis 1975; Hetrick et al. 1992; Wright and Westoby 1999; Raghothama and Karthikeyan 2005) with root surface area influencing more than root mass (Eissenstat 1992), and therefore P uptake by plants is dependent on the surface area of their absorbing structures in the soil (Marschner 1998). Specific root length, as an indicator of root architecture, reflects both the potential for the acquisition of resources from the soil (Wright and Westoby 1999; Hodge 2004) and the capacity of root proliferation (Eissenstat 1992). The fine root diameter influences the P influx rate at the root surface, since P influx increases as root diameter decreases (Itoh and Barber 1983; Eissenstat 1992). The root surface area increases with the increase in root hair length and incidence (Föehse et al. 1991; Gahoonia and Nielsen 1998; Gahoonia et al. 2001; Raghothama and Karthikeyan 2005) and with AM root colonization (Marschner 1998), also influencing P uptake potential. In addition, root hairs represent a low metabolic cost to be produced and maintained by the plant (Lynch and Ho 2005) and the cost of producing AM hyphae is about two orders of magnitude less expensive than for root construction (Smith and Read 1997). Therefore, fine root morphology and AM root colonization exhibited by plant species in the grass area and secondary forest permit the plant to increase the soil volume explored while investing less biomass in fine roots. Indeed, AM root colonization and the effect on plant growth are greater both in soils with low availability and plants with low P content in tissues (Smith and Read 1997). In this study, the grass site had a low-fertility soil, lower nutrient concentration in roots, and high AM root colonization while soil from the mature forest was more fertile; fine roots presented higher nutrient concentrations and AM root colonization was low.

In recent publications, Siqueira and Saggin-Júnior (2001) and Zangaro et al. (2005, 2007) verified that AM fungi root colonization is essential for both nutrient acquisition and plant survival in tropical seedlings of early successional woody species with apparent root morphology for high uptake capacity but not able to ensure adequate nutrition to maintain their inherent fast growth rate. Low soil P availability is an important limiting factor for plant growth in tropical ecosystems (Vitousek 1984; Brundrett 2002) and high rates of P uptake are necessary to support the extremely fast growth of tropical species belonging to the initial phases of succession. Since the AM association increases the root uptake potential (Smith and Read 1997; Brundrett 2004), the combination of AM hyphae and fine root traits in the early successional grasses and woody species permits the plants to both explore an extensive soil volume with high effectiveness and maintain a high growth rate. Thus, there is an adequate carbon investment in the fine roots, root hairs, and AM fungi, in order to improve the nutrient uptake effectiveness typical of fast-growing species.

Biomass allocation in plant communities changes in different successional stages. In plant species belonging to early successional stages, relatively more biomass is allocated to structures used for resource acquisition, like fine roots and leaves. On the other hand, in plants from later successional stages, more biomass is allocated to structural organs like stems and thicker roots (Guariguata and Ostertag 2001). Zangaro et al. (2005, 2007) suggested that roots interfacing with more contact with soil (more total root length, specific root length, long and dense root hairs) may have more chance to find AM fungi inocula to colonize the root. In addition, the large nutritional demand by the early successional species results in a high photosynthetic capacity and more investment in leaf production (Lusk et al. 2008), thus increasing the amount of the photoassimilates that can be exported to roots (Nielsen et al. 1998; Lynch and Ho 2005) and made available for the maintenance of mycorrhizal fungi in roots. As a consequence, fast-growing species show high AM colonization in the field and young seedlings display very high growth responses in the greenhouse, suggesting that the greater aggressiveness exhibited by early successional species during establishment in open and disturbed tropical areas can be due to a high degree of AM mycotrophy (Zangaro et al. 2003). Thus, AM fungi may be considered the main biotic factor for the establishment, survival, and growth acceleration of the native woody species that lead for initial tropical forest structuring (Zangaro et al. 2000).

In the later successional stages, root architecture changes with increasing fine root diameter and decreasing total root length, specific root length, root hair length, root hair

incidence, mycorrhizal root colonization, and spore density in the soil. These root morphological traits and AM colonization levels could result in both a lower potential for the acquisition of resources from the soil and a lower capacity for root proliferation than in early successional grasses and woody species. Several features such as shading, slow growth rate of woody species, lower metabolic demand, low root interface to contact with AM fungi, high soil fertility, and the routing of most part of the carbon fixed photosynthetically to structural organs may result in less available carbohydrates to AM fungi in roots and consequently less mycorrhizal root colonization and sporulation in the mature forest. In the meantime, plant species in mature forest conditions experience low light intensity and can be more carbon-limited, limiting carbohydrate supply to AM fungi. The increased soil fertility of the mature forest may either reduce or increase AM colonization in a wide range of plant species (Gamage et al. 2004), suggesting that the low levels of AM fungi in the mature forest could be due to high carbon cost for maintenance of the AM symbiosis rather than to nutrient availability in soils. Therefore, low plant metabolic demand and low light availability appear to be important factors determining the low AM fungal colonization and sporulation in the mature forest. In addition, lipid-rich spores and fungal hyphae being subject to predation by a wide range of soil animals (Rabatin and Stinner 1988; Stürmer et al. 2006) and increases in soil organism populations during succession (Coleman et al 2004) may also contribute to the decrease in AM fungal populations in soils of mature forests.

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