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ORIGINAL PAPER

Root colonization and spore abundance of arbuscular mycorrhizal fungi in distinct successional stages from an Atlantic rainforest biome in southern Brazil

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Abstract The influence of plant functional groups and moderate seasonality on arbuscular mycorrhizal (AM) fungal status (root colonization and spore density) was investigated during 13 consecutive months in a chronosequence of succession in southern Brazil, consisting of grassland field, scrub vegetation, secondary forest and mature forest, in a region of transition from tropical to subtropical zones. AM root colonization and spore density decreased with advancing succession and were highest in early successional sites with grassland and scrub vegetation, intermediary in the secondary forest and lowest in the mature forest. They were little influenced by soil properties, but were sufficiently influenced by the fine root nutrient status and fine root traits among different functional plant groups. AM root colonization and spore density were higher during the favourable plant growth season (spring and summer) than during the less favourable plant growth season (autumn and winter). Spore density displayed significant seasonal variation at all sites, whilst root colonization displayed significant seasonal variation in grassland, scrub and secondary forest, but not in mature forest. The data suggest that (1) different plant functional groups display different relationships with AM fungi, influencing their abundance differentially; (2) plant species from early successional phases are more susceptible to AM root colonization and maintain higher AM sporulation than late successional species; (3) fine root traits and nutrient status influence these AM fungal attributes; and (4) higher AM spore production and root colonization is associated with the season of higher light incidence and temperature, abundant water in soil and higher plant metabolic activity.

Keywords Grassland · Seasonality · Root colonization · Spore density · Succession continuum · Symbiosis

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Introduction

Arbuscular mycorrhizal (AM) fungi are essential for terrestrial plant communities, forming mutualistic root associations with most of the herbaceous and woody plants (Smith and Read 2008). Tropical trees belonging to early successional stages, such as pioneer and early secondary trees (fast-growing and light-demanding species), display a high

growth response to AM fungi in addition to a high AM root colonization. In contrast, late secondary and climax trees (slow-growing and shade-tolerant species) typical of mature forests exhibit low AM root colonization and also a low growth response to AM fungi (Siqueira and Saggin-Júnior 2001; Zangaro et al. 2003; Matsumoto et al. 2005; Pasqualini et al. 2007; Lacerda et al. 2011). AM fungal abundance is negatively influenced by soil depth due to a decline in fine root mass and length (Zangaro et al. 2008, 2012a) and is affected by soil properties such as moisture, nutrient availability, organic matter, heavy metals and salinity (Cardoso et al. 2003). The cultivation of non-mycorrhizal crops, intensive tillage and high P applications also negatively influence AM fungi (Smith and Read 2008), whilst natural vegetation with a high plant density and low-input cropping systems tend to favour the propagation of AM fungi (Lekberg et al. 2008). AM fungal abundance is also influenced by plant functional groups. During several years, Zangaro et al. (2012a, b) investigated in sites over tropical successional gradients in Araucaria, Atlantic and Pantanal biomes in Brazil and found that the root colonization intensity and the spore density in the soil decrease with succession advance. They suggested that plant species in the early stages of succession favour the proliferation of AM fungi, leading to a higher potential of the AM inoculum in the soil, and that plant investment in AM fungi decreases in later successional stages so that the potential of the AM inoculum is also reduced. However, the seasonal effects on AM fungi in the Atlantic rainforest biome have never been studied.

In many habitats, AM spore density and root colonization are submitted to severe seasonality, with the main impacts being related to water availability and host phenology (Wilson and Hartnett 1997; Guadarrama and Alvarez-Sanchez 1999; Lugo and Cabello 2002; Lugo et al. 2003; Caproni et al. 2007; Cuenca and Lovera 2010). In tropical or subtropical regions, the highest AM sporulation often occurs during the less favourable plant growth season, which corresponds to dry seasons and coincides with the period when there is no plant flowering or fruiting, whilst AM sporulation is lower in wet seasons, which generally correspond to flowering and fruiting phases when the plant carbon is mobilized to produce reproductive structures. The higher abundance of spores in dry seasons has been associated with plant phenology (Guadarrama and Alvarez-Sanchez 1999), when plants are less photosynthetically active due to leaf fall or stomata closure and decreased carbon flow to the roots (Birhane et al. 2010). Thus, the formation of spores can be stimulated in dry soils as a consequence of low carbon availability in roots (Cardoso et al. 2003; Birhane et al. 2010). AM fungal spore density may also be influenced by root phenology and dynamics since sporulation is inversely linked to fine root production. In general, the decrease in fine roots during the dry season in tropical dry forests (Guadarrama and Alvarez-Sanchez 1999) and in pastures and forests (Picone 2000) stimulates sporulation. During the rainy season, spore germination increases with fine root production, and as a result, an increase in AM root colonization and a decrease in spore abundance are observed (Caproni et al. 2007; Cuenca and Lovera 2010). However, Aidar et al. (2004) reported on the contrary that the density of AM spores in soils was nine times more abundant in the wet season than in the dry season in an Atlantic forest chronosequence in southeastern Brazil. Similarly, Bononi and Trufem (1983), Trufem and Viriato (1990), Silva et al. (2006) and Pagano et al. (2009) observed a higher density of spores and species richness during the wet season than in the dry season at different sites in Brazilian Atlantic forests. In the light of these contrasting results, we monitored during 13 months the influence of moderate seasonality and functional groups of plants on the AM status (spore density and root colonization) in an Atlantic rainforest biome in southern Brazil, which represents a chronosequence of succession of grassland, scrub, secondary forest and mature forest, in a transition from tropical to subtropical zones. Considering the moderate seasonality in the area, we hypothesized that AM sporulation and root colonization would be higher during spring and summer, characterized by rainy, warmer and longer days, in contrast to autumn and winter with drier, cooler and shorter days. We also expected that plant communities from the early stages of succession should display higher AM root colonization and AM fungal spore production than plant communities belonging to later successional stages.

Methods

Study sites

Four sites under different plant successional stages were studied in an Atlantic rainforest biome, located in the Londrina municipality, Paraná state, Southern Brazil (23°27′ S, 51°15′ W). The climate is Cfa-mesothermic, with hot summers, an undefined dry season and an average temperature of 21 °C, with 1,600 mm of annual rainfall. The soil has been classified as Rhodic Ferralsol (FAO 1994) at all sites. The first site is covered with grass, located at the campus of The State University of Londrina. The A and B horizons in this area were removed in 1986, when the upper 3 m of the soil layer was removed with a bulldozer and the subsoil remained exposed where graminaceous pioneer plants became established. Currently, the grasses *Paspalum notatum* and *Cynodon* sp. are the dominant vegetation in the area; there are no trees or shrubs. This area represents the first stage of plant succession on a degraded, low-fertility soil. The second site is scrub vegetation formed in 2001 after abandonment of an old agricultural field, which prior to that had most recently been used for soybean cultivation. The

most common regenerated vegetation now found there includes *P. notatum*, *Elionurus candidus*, *Cleome affinis*, *Achyrocline satureoides*, the shrubs *Rosmariunus officinalis* and *Vernonia* sp. and the pioneer woody species *Solanum granuloso leprosum* and *Cecropia pachystachya*. The third site is a secondary forest, regenerated after pasture abandonment in 1987. Pioneer and early secondary woody species such as *Alchornea triplinervia*, *Anadenanthera colubrina*, *Croton floribundus*, *Parapiptadenia rigida* and *Tabernaemontana australis* are the most common tree species. The fourth site is a primary, semi-deciduous mature forest located at the Mata dos Godoy State Park. It is rich in species diversity and shows a complex canopy and structure. 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*. All sites were located within a maximum distance of 10 km from one another.

Data on temperature and rainfall were obtained from the agro-climatologic web of the Instituto Agronômico do Paraná (IAPAR; www.iapar.br); day length was obtained from the National Observatory (www.on.br).

Field sampling and soil characteristics

We established three 100×100-m plots at each site representative of the respective successional phases. Each 100×100-m plot was subdivided into five 20×100-m subplots, and each month, four sampling points were placed at random within each subplot. At each sampling point, we randomly collected four soil cores (45 mm in diameter and 50 mm in depth) at a depth of 0–5 cm because fine roots and AM spores are most dense in the first few centimetres of soil and decline with soil depth (Cardoso et al. 2003; Muleta et al. 2008). One of the four subsamples was utilized for fine root extraction; the three remaining subsamples were pooled to form a composite sample for the assessment of AM fungal spore density because spores can have an aggregate distribution (Koske and Halvorson 1981). For each month, this procedure gave 10 samples per plot, 30 samples per site representative of each successional phase and 120 samples from each biome. Soil samples were taken in the first week of each month, starting in October 2006 and finishing in October 2007. This sampling strategy ensured that samples were independent and representative of each sampling site.

The soil cores for fine root extraction were stored at 5 °C and processed within 10 days of sampling. Five samples containing 20 g of each soil core were dried at 104 °C for 24 h to determine soil water content. The soil core samples for AM spore density and soil fertility were dried at room temperature. Thirteen samples of the soils from each study site were used for chemical analysis, making a total of 52 samples. Chemical analysis of the soils was undertaken by the Soil Fertility Laboratory of the IAPAR. The carbon was oxidized with 2 M $Na_2Cr_2O_7$ in 5 M 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.

Root extraction and AM root colonization

Soil samples were soaked in tap water and root fragments were separated from the soil by sieving through a 0.25-mm mesh. The material retained on the sieve was hand-sorted in shallow dishes underwater, and living fine roots (<2-mm diameter) were separated from coarse roots (>2-mm diameter), dead roots and organic matter. Living fine roots were distinguished from dead roots under a stereomicroscope according to colour, elasticity, and the degree of cohesion of the cortex, periderm and stele. Only living fine roots (<2-mm diameter) were used in further analyses.

AM colonization was estimated in the fine roots obtained from each individual sample from each successional stage. Approximately 1.0 g of fresh fine root segments was fixed in FAA (5 mL formaldehyde, 5 mL acetic acid and 90 mL 50 % ethanol) and stored until analysis. Mycorrhizal colonization was estimated after clarifying (10 % KOH), acidifying (1 % HCl) and staining (0.05 % trypan blue) fine roots according to Brundrett et al. 1996). H_2O_2 (0.5 %) was used after KOH for darkly pigmented root fragments. Total AM colonization was estimated using the magnified intersection method (McGonigle et al. 1990) by observing the presence of different AM fungal structures at ×100 magnification; only aseptate hyphae were considered to be AM fungi in the root cortex.

The fine root traits were obtained for each individual sample from each successional stage. The total length of fine fresh roots was determined by the gridline intersection method. Fine fresh root fractions were dried at 60 °C to obtain the dry mass. Specific root length was derived from the ratio between the fine root length and root dry mass. The means of fine root diameter were determined using the formula: diameter = $2(W/L\pi)^{0.5}$, where W is the fresh root weight and L is the fine root length. The diameter of fine root tips was determined from 0.5 cm of the root coif. Root hair length was determined on eight fine root segments for up to 100 root hairs in each sample. Root hair incidence was assessed for each sample by the presence or absence of root hairs on 100 fine root intersections using a gridline method (Zangaro et al. 2005). Fine root diameter and root hair length were determined using a microscope at ×100 magnification with an ocular micrometer. Fine root tissue density was determined by immersing fresh fine roots in water in a volumetric graduated burette.

Thirteen samples of the dry fine roots from each site were used to determine tissue nutrient concentration, making a total of 52 samples, at the Soil Fertility Laboratory at IAPAR. Briefly, N was determined by the indophenol method after sulphuric acid digestion. The other nutrients were determined in nitric–perchloric digests. P was determined by the molybdenum blue method; K by flame photometry; Ca and Mg by atomic absorption spectrophotometry in the presence of lanthanum; Cu, Zn and Mn by atomic absorption spectrophotometry; and B by azometine-H colorimetry.

AM fungal spore density and species identification

Spores and sporocarps were extracted from 20 g of soil from each composite sample (pool of three subsamples from each plot and successional stage) using the wet-sieving technique (sieves, 710–53 μm) and flotation on sucrose (Brundrett et al. 1996). The spores were recovered, washed in water and spread on filter paper in order to count the apparently healthy AM spores under a dissecting microscope at ×40 magnification. Sporocarps were counted as one spore. For the identification of the AM fungal species, spores were separated into morphotypes under a dissecting microscope (×60) and mounted on permanent glass slides with PVLG and PVLG + Melzer's reagent. Spores were identified under ×400 in a light microscope, based on spore wall structure, comparisons with original descriptions (Schenck and Pérez 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).

Data analysis

AM root colonization and spore density from each successional site are presented as the means with standard errors. The monthly means (15 samples per month) within the same successional site were submitted to a one-way ANOVA, according to a completely randomized design, followed by means for comparison within the successional site using Tukey's test at the 0.05 level of significance. The means of each successional site (representing 13 months) were also submitted to a one-way ANOVA, followed by means for comparison among successional sites using Tukey's test, again at the 0.05 level of significance. The means of AM root colonization and spore density also were compared between seasons (spring and summer against autumn and winter) using Students' t test at 0.05 of significance level. All data were tested for normal distribution using the Kolmogorov–Smirnov test. Only data for spore density in grass and scrub were log-transformed before analysis. Percentage data were transformed to arcsin of square root values.

Pearson's correlation analyses were performed considering each successional site for all months and were undertaken for both AM fungal spore density and root colonization with air temperature, day length, rainfall and soil water content in grassland, scrub, secondary forest and mature forest. Pearson's correlation analyses were also performed considering all successional sites (succession) and were undertaken for both AM spore density and root colonization with fine root traits (root dry mass, root length, specific root length, root tissue density, total root diameter, root tip diameter, root hair incidence and root-hair length); fine root nutrient concentration; soil properties; and environmental variables (temperature, day length, rainfall and soil water content).

Results

The annual means for rainfall and temperature based on historic records from January 1976 to December 2009 in the Atlantic rainforest biome show that rainfall occurs all through the year, with predominance during spring and summer (Fig. 1a). The highest temperatures occur during the same periods. For the period of the present study, the average day length, temperature and rainfall were highest during spring and summer, in contrast with autumn and winter (Fig. 1b). The average day length was 12.8 h in spring and summer, with a peak in December, and 10.9 h in autumn and winter, with the shortest day in July. The average temperature was 23.9 °C in spring and summer and 19.8 °C in autumn and winter; rainfall averaged 14.2 cm in spring and summer and 5.7 cm in autumn and winter. The annual means for water content in soil was 20.1 % at the grasslands site, 30.2 % under scrub vegetation, 32.8 % in secondary forest and 36.9 % in mature forest (Fig. 2). Although the rainy period predominated in the spring and summer, the precipitation during autumn and winter maintained soil humidity more constant along of the year, suggesting an absence of severe seasonality in this transitional tropical to subtropical zone.

AM root colonization and fungal spore density decreased with successional advance, being highest in the grassland and scrub vegetations, decreasing in the secondary forest and reaching their lowest values in the mature forest (Fig. 3). Fine root mycorrhizal colonization tended to be higher during spring and summer than in the autumn and winter for all the sites (Fig. 3a), but it was only significantly higher in scrub and secondary forest (Fig. 4a). Comparisons among the successional sites showed that AM root colonization differed significantly along the succession, decreasing as the succession advanced and was highest in grassland

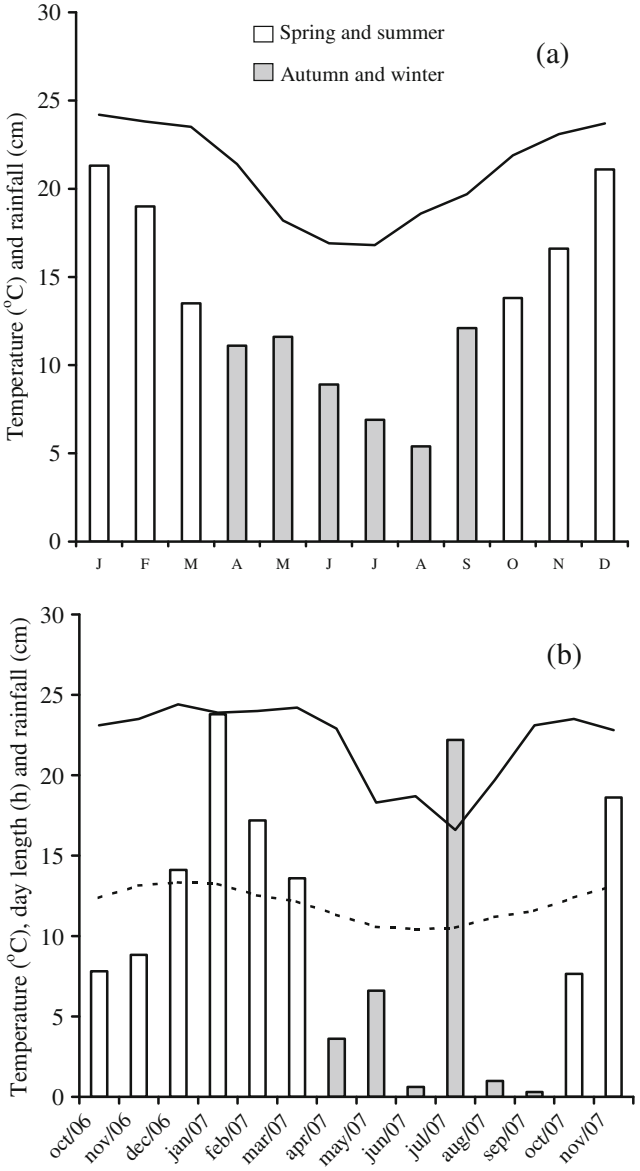

Fig. 1 **a** Historical monthly means of rainfall (*columns*) and temperature (*line*) based on records from January 1976 to December 2009. **b** Monthly means of rainfall (*columns*), temperature (*continuous line*) and light available period (*dotted line*) that correspond to the period of sampling from October 2006 until November 2007 in an Atlantic rainforest biome, located at Londrina municipality, Paraná state, Southern Brazil. Records for rainfall and temperature from Instituto Agronômico do Paraná (www.iapar.br) and light available period from the National Observatory (www.on.br)

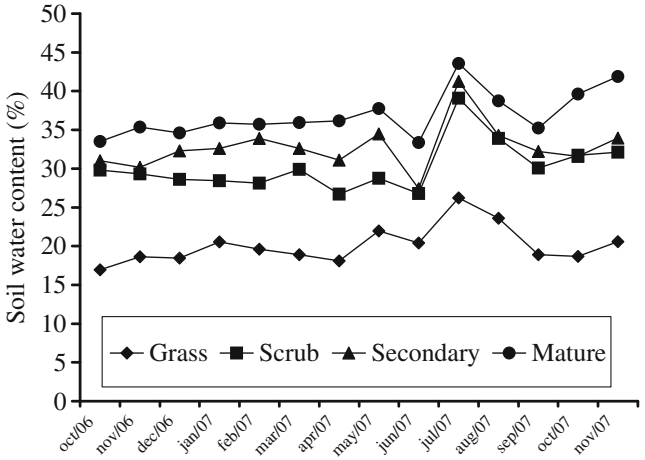

Fig. 2 Soil water content in the grassland, scrub, secondary forest and mature forest from an Atlantic rainforest biome located at Londrina municipality, Paraná state, Southern Brazil. Data range from October 2006 until November 2007 that correspond to the period of sampling

and scrub sites, intermediate in the secondary forest and lowest in the mature forest. AM fungal spore density in soil displayed considerable variation in all successional sites (Fig. 3b) and had a significantly higher abundance during the spring and summer than in autumn and winter at all sites (Fig. 4b). Spore density also differed significantly along the succession and was highest in the grassland and scrub sites, intermediary in secondary forest and lowest in the mature forest.

The fine root dry mass increased with successional advance and was significantly higher in grass and scrub sites in the spring and summer than in the autumn and winter, reflecting a seasonality in fine root turnover (Fig. 5). No statistical differences were detected for secondary and mature forests through the seasons, indicating that the fine root turnover is more constant throughout the year in these biomes.

A total of 68 fungal spore morphotypes were recovered from all successional stages and soils collected monthly in each site (Table 1). Species from the genus *Glomus* were the most abundant (28 species, 41 % of total), followed by *Acaulospora* (19 species, 28 % of total); *Claroideoglomus* (4 species, 6 % of total); *Funneliformis* (3 species, 4 % of total); *Gigaspora* (3 species, 4 % of total); *Scutellospora* (3 species, 4 % of total); *Rhizophagus* (2 species, 3 % of total); and *Archaeospora*, *Diversispora*, *Entrophospora*, *Paraglomus*, *Racocetra* and *Redeckera* (1 species each, 9 % of total). Twenty-nine AM fungal species were present in the four successional sites (frequency of occurrence, FO= 100 %), 6 species were present in three sites (FO=75 %), 15 species were present in two sites (FO=50 %), and 18 species were present in only one site (FO=25 %). All sites displayed high AM fungal species diversity since 43 species were present in the grass site, 52 under scrub, 41 in the secondary forest and 47 in the mature forest.

The soil at the grassland site showed very low fertility in comparison to scrub, secondary forest and mature forest soils (Table 2). The scrub site displayed the highest P levels, whilst the other nutrients did not display any marked difference between scrub and secondary and mature forests. The nutrient concentration in the fine root tissues from grassland was lowest when compared to scrub and secondary and mature forests. In the case of P, K, Mg and Cu, fine roots from the scrub and mature forest displayed higher nutrient

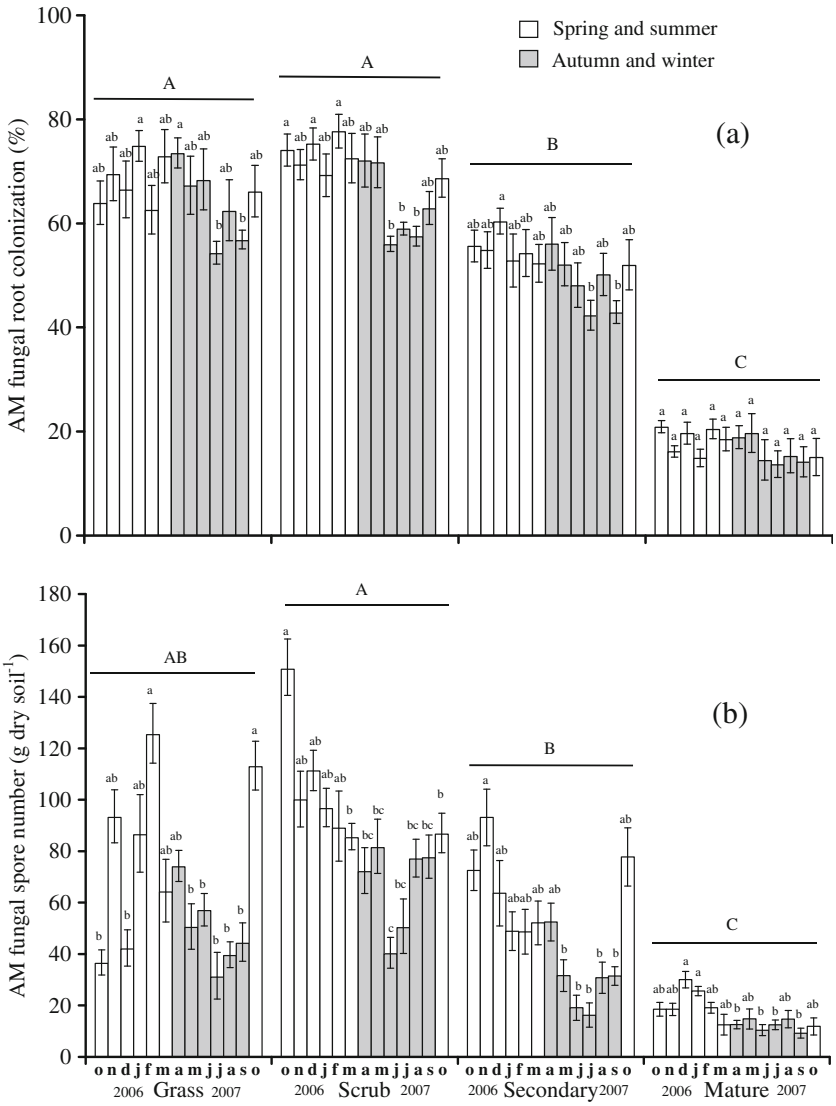

Fig. 3 Mycorrhizal root colonization (**a**) and mycorrhizal spore number (**b**) over several months from grassland, scrub, secondary forest and mature forest of an Atlantic rainforest biome located at Londrina municipality, Paraná state, Southern Brazil. Soils and fine root samples were assessed at 0- to 5-cm depth from October 2006 until November 2007. *Error bars* are ±1 SE. *Means followed by the same letter* are not different by Tukey's test at $P=0.05$. *Small letters* compare means within a same successional site. *Capital letters* compare among successional sites (AM root colonization: $n=13$, $P<0.001$; AM spore number: $n=13$, $P<0.001$)

concentrations than for the secondary forest. However, N concentrations were highest in roots from the secondary forest.

Pearson's correlation coefficients between AM fungal spore density in soil and AM root colonization with environmental variables, for each site, showed that day length was the only parameter that correlated positively with AM fungal spore density in all successional sites (Table 3). In addition, spore density was also positively correlated with temperature for the secondary forest and with rainfall for the mature forest. AM root colonization levels were positively correlated with temperature and day length only for the scrub and secondary forest biomes.

A Pearson's correlation analysis was performed considering the fine root morphological traits for all successional sites with the AM root colonization and fungal spore density (Table 4). Root colonization by AM fungi was positively correlated with spore density, and these properties were positively correlated with specific root length, root hair incidence and root hair length and were negatively correlated with fine root dry mass, root tissue density, root diameter and diameter of root tips. AM root colonization and fungal spore density were negatively correlated with N, Ca, Mg and Mn in the fine root tissues and positively correlated with Zn. Considering the soil chemical attributes, root colonization and the density of spores were negatively correlated with C and positively correlated with P levels, whilst fine root colonization was negatively correlated with soil organic matter and Ca levels. Finally, considering all successional sites, AM root colonization and fungal spore density were negatively correlated with soil water content; only spore density was positively correlated with temperature and day length.

Discussion

The results from this study of plant successional stages in an Atlantic rainforest biome showed both higher fine root colonization and spore production by AM fungi in the

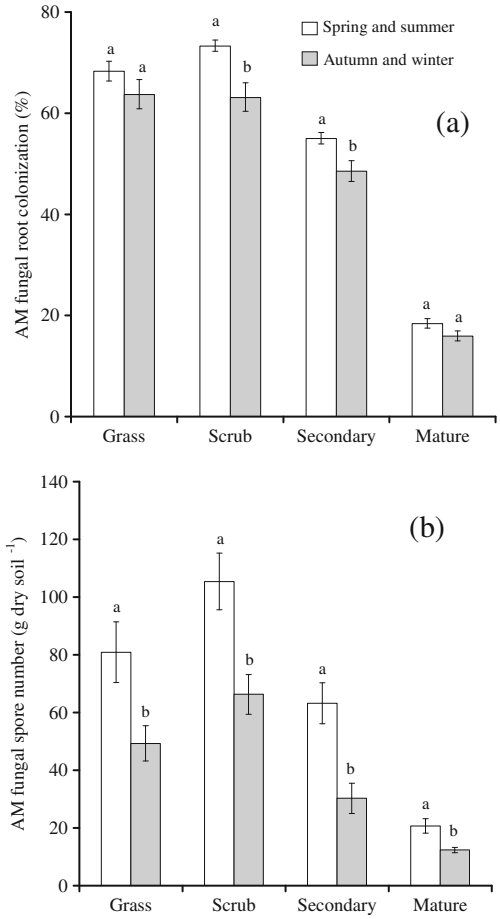

Fig. 4 Means of the AM root colonization in spring and summer (n=7) and autumn and winter (n=6) from grassland (P=0.228), scrub (P=0.009), secondary forest (P=0.026) and mature forest (P=0.128) (**a**) means of the AM spore number in spring and summer (n=7) and autumn and winter (n=6) from grassland (P=0.035), scrub (P=0.008), secondary forest (P=0.004) and mature forest (P=0.011) (**b**) of an Atlantic rainforest biome located at Londrina municipality, Paraná state, Southern Brazil. *Error bars* are ±SE. *Means followed by the same letter* are not different by Student's t test at P=0.05

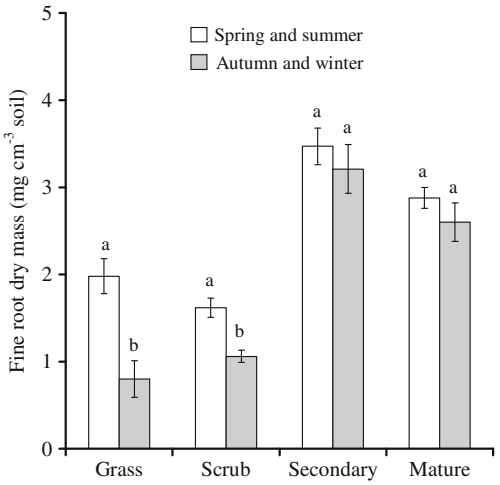

Fig. 5 Means of fine root dry mass of native plants assessed during spring and summer (n=7) and autumn and winter (n=6) from grassland (P=0.003), scrub (P<0.001), secondary forest (P=0.831) and mature forest (P=0.357) of the Atlantic rainforest biome located at Londrina municipality, Paraná state, Southern Brazil. Fine root samples were assessed at 0- to 5-cm depth. *Error bars* are ±1 SE. *Means followed by the same letter* are not different by Student's t test at P=0.05

spring and summer as compared to the autumn and winter in all four successional sites, which is consistent with our first hypothesis. Such higher AM root colonization during the favourable plant growth season was also found by Michelsen et al. (1993) in many forbs and graminoids of tree plantations in Ethiopia and by Lugo et al. (2003) in a natural grassland in Argentina. It may be attributed to the higher metabolic activity of plants, favoured by higher soil moisture and higher temperatures. Higher AM spore density during spring and summer was also reported in other sites in Brazilian Atlantic forests (Bononi and Trufem 1983; Trufem and Viriato 1990; Aidar et al. 2004; Silva et al. 2006; Pagano et al. 2009). In the present study, the highest AM fungal sporulation and root colonization occurred during the season with longer day length, higher temperatures and rainfall. It is known that higher temperatures and higher light intensities may increase the sporulation potential of AM fungi (Hetrick 1984; Guadarrama and Alvarez-Sanchez 1999; Cardoso et al. 2003; Gamage et al. 2004). During the spring and summer seasons, most plant species have photosynthetically active leaves and greater leaf production, and therefore a larger amount of carbon could be fixed and translocated for fine root production and maintenance of the AM fungi (Birhane et al. 2010). However, as observed in this study, sporulation and root colonization are two phenomena that are often closely related so that factors that stimulate or inhibit AM sporulation also do so for AM root colonization (Cardoso et al. 2003). In contrast to studies conducted in habitats with severe seasonality (Wilson and Hartnett 1997; Guadarrama and Alvarez-Sanchez 1999; Lugo and Cabello 2002; Lugo et al. 2003; Caproni et al. 2007; Cuenca and Lovera 2010), plant root phenology and seasonality appeared to be less important factors determining the high levels of AM spores and root colonization across the successional stages of the Atlantic rainforest biome studied here.

The number of AM fungal species found in the present plant successional system showed high diversity (41–52), especially in the early successional stage under shrub. The genera *Glomus* and *Acaulospora* predominated in the AM fungal community in all the biomes, which is in accordance with other findings for tropical forests (Louis and Lim 1987; Trufem and Viriato 1990; Guadarrama and Alvarez-Sanchez 1999). It has been suggested that AM fungal species belonging to the genera *Glomus* and *Acaulospora* prevail after soil disturbances because their spores are resistant to the

Table 1 FO of AM fungal species for each successional site represented by grass, scrub, secondary forest and mature forest in southern Brazil

	Grass	Scrub	Secondary	Mature	FO (%)
Acaulospora colombiana (Spain & Schenck) Kaonongbua, Morton & Bever		+		+	50
Acaulospora colossica Schultz, Bever & Morton	+	+	+	+	100
Acaulospora delicata Walker, Pfeiffer & Bloss	+	+	+	+	100
Acaulospora foveata Trappe & Janos	+	+	+	+	100
Acaulospora koskei Blaszkowski	+			+	50
Acaulospora laevis Gerdemann & Trappe	+	+			50
Acaulospora longula Spain & Schenck				+	25
Acaulospora mellea Spain & Schenck	+	+	+	+	100
Acaulospora morrowiae Spain & Schenck	+	+	+	+	100
Acaulospora rehmii Sieverding & Toro		+			25
Acaulospora rugosa Morton	+	+	+	+	100
Acaulospora scrobiculata Trappe	+	+	+	+	100
Acaulospora spinosa Walker & Trappe		+	+	+	75
Acaulospora tuberculata Janos & Trappe	+	+	+	+	100
Acaulospora sp. 1				+	25
Acaulospora sp. 2		+	+	+	75
Acaulospora sp. 3		+	+		50
Acaulospora sp. 4	+	+	+	+	100
Acaulospora sp. 5	+	+			50
Archaeospora trappei (Ames & Linderman) Morton & Redecker		+	+		50
Claroideoglomus claroideum (Schecnk & Smith) Walker & Schuessler	+	+	+	+	100
Claroideoglomus etunicatum (Becker & Gerdemann) Walker & Schuessler	+	+	+	+	100
Claroideoglomus lamellosum (Dalpé, Koske & Tews) Walker & Schuessler		+			25
Claroideoglomus luteum (Kennedy, Stutz & Morton) Walker & Schuessler	+	+	+	+	100
Diversispora spurca (Pfeiffer, Walker & Bloss) Walker & Schuessler	+	+			50
Entrophospora infrequens (Hall) Ames & Schneider	+	+	+	+	100
Funneliformis constrictus (Trappe) Walker & Schuessler	+	+	+	+	100
Funneliformis geosporus (Nicolson & Gerdemann) Walker & Schuessler	+	+	+	+	100
Funneliformis mosseae (Nicolson & Gerdemann) Walker & Schuessler	+	+	+	+	100
Gigaspora decipiens Hall & Abbott	+	+			50
Gigaspora gigantea (Nicolson & Gerdemann) Gerd. & Trappe	+				25
Gigaspora margarita Becker & Hall			+	+	50
Glomus albidum Walker & Rhodes	+	+	+	+	75
Glomus clavisporum (Trappe) Almeida & Schenck	+		+	+	75
Glomus coremioides (Berk. & Broome) Redecker & Morton		+			25
Glomus glomerulatum Sieverding		+	+		50
Glomus hoi Berch & Trappe	+	+	+	+	100
Glomus invermaium Hall	+	+	+	+	100
Glomus macrocarpum Tulasne & Tulasne	+	+	+	+	100
Glomus microaggregatum Koske, Gemma & Olexia	+	+	+	+	100
Glomus microcarpum Tulasne & Tulasne	+	+	+	+	100
Glomus sinuosum (Gerdemann & Bakshi) Almeida & Schenck	+	+	+	+	100
Glomus tortuosum Schenck & Smith		+			25
Glomus sp. 1	+	+	+	+	100
Glomus sp. 2	+	+	+	+	100
Glomus sp. 3				+	25
Glomus sp. 4		+		+	50
Glomus sp. 5	+				25
Glomus sp. 6		+	+	+	75

Table 1 (continued)

	Grass	Scrub	Secondary	Mature	FO (%)
Glomus sp. 7	+				25
Glomus sp. 8	+	+	+	+	100
Glomus sp. 9	+	+	+	+	100
Glomus sp. 10	+	+	+	+	100
Glomus sp. 11			+	+	50
Glomus sp. 12		+		+	50
Glomus sp. 13	+				25
Glomus sp. 14				+	25
Glomus sp. 15			+	+	50
Glomus sp. 16	+				25
Glomus sp. 17		+			25
Paraglomus occultum (Walker) Morton & Redecker	+	+	+	+	100
Racocetra verrucosa (Koske & Walker) Oehl, Souza & Sieverding				+	25
Redeckera fulvum (Berk. & Broome) Walker & Schuessler		+			25
Rhizophagus clarus (Nicolson & Schenck) Walker & Schuessler	+	+			50
Rhizophagus diaphanus (Morton & Walker) Walker & Schuessler	+	+	+	+	100
Scutellospora calospora (Nicolson & Gerdemann) Walker & Sanders				+	25
Scutellospora heterogama (Nicolson & Gerdemann) Walker & Sanders		+			25
Scutellospora pellucida (Nicolson & Schenck) Walker & Sanders	+	+	+		75
Total species occurrence	43	52	41	47	

The AM fungal species represent the total in the assembly of soils collected monthly in each site in October 2006 and November 2007

FO frequency of occurrence

effects of the modified ecosystems (Picone 2000; Silva et al. 2006; Zangaro and Moreira 2010).

Mycorrhizal root colonization and AM fungal spore density were inversely related to the plant successional trajectory of the Atlantic rainforest biome, which is consistent with our second hypothesis and does not sustain the view that plant species in mature forests are more susceptible and display higher levels of AM colonization than pioneer species (Janos 1980). Our results indicate that different functional plant groups may display different relationships with AM fungi, influencing differentially their abundance (Bever et al. 1996; Zangaro and Moreira 2010). The density of AM fungal spores was positively correlated with AM root colonization, which has also been found in other studies (McGonigle et al. 1990; Gange et al. 1993; Cardoso et al. 2003; Zangaro et al. 2008, 2012a, b). The higher values for these AM fungal attributes in grassland and scrub vegetation have also been observed in wild plants in natural early successional phases worldwide (Mangan et al. 2004; Lekberg et al. 2008; Zangaro et al. 2008, 2012a, b; Kalinhoff et al. 2009; Stürmer and Siqueira 2011). The high levels of root colonization and sporulation in the early successional plant community can be related to favourable climatic conditions (high light incidence due to longer days, higher temperature, higher soil moisture) improving the photosynthetic capacity (Reich et al. 1998; Khurana and Singh 2006; Lusk et al. 2008; Poorter and Rozendaal 2008) and, as a result, increasing the amount of photoassimilates exported to roots (Nielsen et al. 1998; Lynch and Ho 2005). In contrast, the lower abundance of AM fungi in the mature forest may be connected to the lower nutrient requirements of tree species due to their intrinsically slower growth rates, lower light requirements, lower photosynthetic potential and lower metabolic demands (Walter and Reich 1996, Zangaro et al. 2003). Plant communities in mature forests have denser canopies and experience shaded environments with high competition for light (Lusk et al. 2008), so that low light availability may decrease photosynthesis and carbon translocation rate towards roots (Grayston et al. 1996, Gamage et al. 2004) and therefore limit carbon availability to AM fungi (Bennett and Bever 2009). Therefore, plant species and habitat characteristics can negatively influence both AM root colonization levels and sporulation in mature forest.

Greater fine root production occurred in spring and summer and coincided with the higher levels of AM root colonization and sporulation for all the sites studied, and these corresponded with both the maximum pulse of available soil nutrients and the period for highest plant growth. During the successional advance from grassland to mature forest, fine

Table 2 Mean values (±SD, $n=13$) for soil chemical fertility attributes and concentrations of nutrients in fine roots from grass, scrub, secondary and mature forests in southern Brazil

	Successional stage			
	Grass	Scrub	Secondary	Mature
Soil chemical attributes				
P ($mg\,dm^{-3}$)	1.72±0.24 c	16.5±6.81 a	5.23±1.02 b	4.66±0.68 b
C ($mg\,dm^{-3}$)	9.84±3.19 c	44.6±7.11 b	51.4±1.73 a	51.7±5.72 a
OM ($g\,dm^{-3}$)	46.8±5.69 c	96.5±13.4 b	107±7.65 ab	112±10.4 a
pH ($Ca\,Cl_2$)	5.43±0.18 a	5.76±0.39 a	5.45±0.18 a	5.47±0.43 a
Al ($cmol_c\,dm^{-3}$)	0	0	0	0
H+Al ($cmol_c\,dm^{-3}$)	3.66±0.35 b	4.42±0.72 ab	4.99±0.56 a	5.51±1.83 a
Ca ($cmol_c\,dm^{-3}$)	2.53±0.64 b	10.4±2.48 a	10.9±1.65 a	9.83±1.93 a
Mg ($cmol_c\,dm^{-3}$)	2.20±0.21 c	4.13±0.23 a	4.02±0.35 a	3.29±0.57 b
K ($cmol_c\,dm^{-3}$)	0.38±0.10 c	0.84±0.23 a	0.64±0.21 b	0.51±0.13 bc
S ($cmol_c\,dm^{-3}$)	5.11±0.83 b	15.4±2.56 a	15.6±1.75 a	13.6±2.42 a
T ($cmol_c\,dm^{-3}$)	8.75±0.93 b	19.8±2.12 a	20.6±1.46 a	19.1±1.54 a
V (%)	58.1±4.54 b	76.5±6.05 a	76.4±2.76 a	71.9±9.68 a
Root nutrient concentration				
N ($g\,kg^{-1}$)	4.51±1.22 d	11.3±2.51 c	16.7±1.79 a	13.7±1.71 b
P ($g\,kg^{-1}$)	0.27±0.05 c	0.97±0.22 a	0.52±0.11 b	0.55±0.06 b
K ($g\,kg^{-1}$)	1.77±1.01 c	8.54±2.50 a	4.92±1.71 b	8.66±2.82 a
Ca ($g\,kg^{-1}$)	4.64±0.97 d	8.49±0.67 c	10.1±1.03 b	11.7±1.50 a
Mg ($g\,kg^{-1}$)	0.90±0.12 c	2.12±0.54 ab	2.04±0.36 b	2.47±0.32 a
Cu ($mg\,kg^{-1}$)	142±33.8 a	152±38.6 a	125±47.1 a	135±22.1 a
Zn ($mg\,kg^{-1}$)	22.3±5.65 b	78.3±11.6 a	63.8±28.2 a	25.1±28.1 b
B ($mg\,kg^{-1}$)	27.2±6.63 a	37.8±12.3 a	39.2±15.6 a	37.1±10.6 a
Mn ($mg\,kg^{-1}$)	124±17.8 c	154±21.6 bc	184±39.4 b	258±43.6 a

Means followed by the same letter are not different by Tukey's test at the 0.05 level

Table 3 Pearson's correlation coefficients, considering each successional site, among AM fungal spore density in soil and AM root colonization with temperature, day length, rainfall and soil water content in grassland, scrub, secondary forest and mature forest from southern Brazil

	Successional stage			
	Grassland	Scrub	Secondary	Mature
AM spore density				
Temperature	0.51	0.50	**0.73**	0.28
	$P=0.0755$	$P=0.0798$	***P*=0.0046**	$P=0.3612$
Day length	**0.54**	**0.57**	**0.79**	**0.64**
	***P*=0.0494**	***P*=0.0413**	***P*=0.0012**	***P*=0.0196**
Rainfall	0.22	0.08	0.07	**0.58**
	$P=0.4678$	$P=0.7857$	$P=0.8262$	***P*=0.0381**
Soil water content	−0.35	−0.17	−0.42	0.29
	$P=0.2478$	$P=0.5688$	$P=0.1560$	$P=0.3346$
AM root colonization				
Temperature	0.14	**0.56**	**0.67**	0.37
	$P=0.6539$	***P*=0.0456**	***P*=0.0126**	$P=0.2081$
Day length	0.11	**0.56**	**0.70**	0.28
	$P=0.7240$	***P*=0.0478**	***P*=0.0078**	$P=0.3572$
Rainfall	0.17	0.28	0.14	0.06
	$P=0.5896$	$P=0.3504$	$P=0.6580$	$P=0.8546$
Soil water content	−0.21	−0.51	−0.34	−0.42
	$P=0.4976$	$P=0.0734$	$P=0.2520$	$P=0.1516$

Data for comparisons ($n=13$) are monthly means. Correlations with $P<0.05$ are in bold

Table 4 Pearson's correlation coefficients, considering all successional sites, among AMS and AMC with fine root traits (RDM, RL, SRL, RTD, MRD, DRT, RHI and RHL), fine root nutrient concentration, soil properties and some environment variables

Root traits									
	AMS	RDM	RL	SRL	RTD	MRD	DRT	RHI	RHL
AMS		**−0.33**	0.21	**0.55**	**−0.38**	**−0.55**	**−0.66**	**0.75**	**0.63**
		***P*=0.017**	*P*=0.134	***P*<0.0001**	***P*=0.0058**	***P*<0.0001**	***P*<0.0001**	***P*<0.0001**	***P*<0.0001**
AMC	**0.79**	**−0.49**	0.15	**0.68**	**−0.49**	**−0.73**	**−0.94**	**0.92**	**0.83**
	***P*<0.0001**	***P*=0.0002**	*P*=0.304	***P*<0.0001**	***P*=0.0002**	***P*<0.0001**	***P*<0.0001**	***P*<0.0001**	***P*<0.0001**
Root nutrient concentration									
	N	P	K	Ca	Mg	Cu	Zn	B	Mn
AMS	**−0.42**	0.15	−0.20	**−0.43**	**−0.38**	0.22	**0.35**	0.22	**−0.45**
	***P*=0.0019**	*P*=0.2933	*P*=0.1526	***P*=0.0014**	***P*=0.0051**	*P*=0.1139	***P*=0.0121**	*P*=0.1101	***P*=0.0009**
AMC	**−0.50**	0.15	**−0.38**	**−0.67**	**−0.56**	0.13	**0.35**	0.06	**−0.80**
	***P*<0.0001**	*P*=0.2896	***P*=0.0053**	***P*<0.0001**	***P*<0.0001**	*P*=0.3440	***P*=0.0108**	*P*=0.6908	***P*<0.0001**
Soil chemical properties									
	P	C		OM	pH	Ca	Mg		K
AMS	**0.37**	**−0.28**		−0.24	0.12	−0.18	0.13		0.25
	***P*=0.0063**	***P*=0.0487**		*P*=0.0813	*P*=0.3688	*P*=0.2078	*P*=0.3594		*P*=0.0751
AMC	**0.38**	**−0.50**		**−0.54**	0.19	**−0.31**	−0.001		0.24
	***P*=0.0059**	***P*<0.0001**		***P*<0.0001**	*P*=0.1889	***P*=0.0233**	*P*=0.9931		*P*=0.0862
Environmental variables									
	Temperature		Day length		Rainfall		Soil moisture		
AMS	**0.34**		**0.37**		0.10		**−0.45**		
	***P*=0.0128**		***P*=0.0064**		*P*=0.4759		***P*=0.0008**		
AMC	0.09		0.09		0.04		**−068**		
	P=0.5098		*P*=5278		*P*=0.7923		***P*<0.0001**		

Data for comparisons are the monthly means of the four successional sites (n=52). Correlations with P<0.05 are in bold

AMS AM spore density, *AMC* AM root colonization, *RDM* root dry mass, *RL* root length, *SRL* specific root length, *RTD* root tissue density, *MRD* means of root diameter, *DRT* diameter of root tips, *RHI* root hair incidence, *RHL* root hair length

root dry mass, diameter and tissue density displayed a progressive increase, whilst root length, specific length, root hair length and root hair incidence decreased (data not shown). As a result, AM root colonization and fungal spore density displayed positive correlations with fine root morphology, suggesting that root traits strongly influence the AM association. The combination of fine root production and high AM root colonization among the plant species from grassland and scrub contributes to the efficient exploitation of a large soil volume for greater nutrient acquisition (Zangaro et al. 2012a), in agreement with the intrinsically higher metabolism of plant species typical of the early phases of succession (Reich et al. 1998; Khurana and Singh 2006; Kuijk et al. 2008). In addition, the spread of their fine root morphology may increase the likelihood of contact with AM propagules, increasing the probability of AM development (Zangaro et al. 2005). In contrast, the lower investment in fine root morphological traits and AM colonization among plant species from mature forests is possibly associated with a lower demand for nutrients, a feature corresponding with the inherently low metabolism typical of such plant functional groups (Zangaro et al. 2003; Poorter and Rozendaal 2008). Additionally, such reduced fine root morphology possibly decreases the likelihood of contact with AM propagules, therefore contributing to lower mycorrhizal development. Consequently, plants in subtropical to tropical biomes investing in fine root morphological traits for effective soil exploration become colonized by AM fungi to a greater extent than plant species less able to invest in fine root morphology, as previously reported by Zangaro et al. (2005, 2007) and Flores (2010) for seedlings of tropical woody species and by Zangaro et al. (2008, 2012a, b) for tropical adult plants in the field.

Overall positive correlations between soil P and AM root colonization and fungal spore density were found in the present study. It is generally considered that high soil P availability decreases the level of AM fungal colonization and sporulation, but this depends also on soil texture, and the suppressive effect of P on AM colonization occurs at much higher levels (Smith and Read 2008) than those found in the present study. On the other hand, fine root nutrient concentration, especially N, K, Ca, Mg and Mn, was

inversely correlated with AM root colonization and spore density. In this and in previous studies (Zangaro et al. 2000, 2008, 2012a, b), higher levels of these AM attributes were always associated with the early succession stages irrespective of the level of soil fertility. Due to the differential effects that plant species can have on spore production and root colonization (Bever et al. 1996; Bever 2002), the AM association in these transitional tropical to subtropical sites could be more related to plant functional groups and their fine root nutrient content than to the natural soil fertility.

In summary, the higher levels of root colonization and spore production by AM fungi in the spring and summer seasons of distinct successional stages in the Atlantic rainforest biome in southern Brazil suggest a synchronization between higher plant photosynthetic potential and the production of fine roots colonized by active AM fungi for efficient nutrient uptake, which plays an ecological significant role in the establishment, growth and survival of species in different plant functional groups.

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