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Relationships among arbuscular mycorrhizas, root morphology and seedling growth of tropical native woody species in southern Brazil

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Abstract: The relationships between arbuscular mycorrhizal fungi and root morphological characteristics were studied under greenhouse conditions of 78 tropical native woody species and 47 seedling species collected in the field. Seedlings of native woody pioneer and early secondary species that generally exhibited fine roots with a dense cover of long root hairs showed higher mycorrhizal response and root mycorrhizal colonization than late-secondary and climax species with coarse roots with a sparse cover of short root hairs. Root-hair length and incidence decreased with the progression among the successional groups while fine-root diameter increased, both in the greenhouse and in the field. The mycorrhizal response was highly correlated to root mycorrhizal colonization in the greenhouse and in the field. These parameters were inversely correlated with the seed mass and fine-root diameter, but directly correlated with root-hair incidence, both in the greenhouse and in the field. Mycorrhizal response and root mycorrhizal colonization were also directly correlated with the root-hair length and root/shoot ratio of uninoculated plants. The seedling mycorrhizal status of the early successional woody species suggests that the root traits of these fast-growing species can be more receptive to attraction, infection and colonization by arbuscular mycorrhizas than root traits of late-successional species.

Key Words: arbuscular mycorrhizal fungi, ecological successional groups, native woody species, root colonization, root hair, root traits, seed mass, seedling growth, succession, tropical forest

INTRODUCTION

The response of a plant to the colonization of its roots by the hyphae of arbuscular mycorrhizal (AM) fungi is very variable, depending mainly on the plant's nutrient requirements, physiological stage of the life cycle and the root system morphology and absorption capacity (Janos 1987, Koide 1991). A depletion zone is formed around the roots due to the slow diffusion of P in the soil and the size of this zone is determined by the sorption capacity for P from the soil and by the length of the root hairs (Smith & Read 1997). Thin ultimate rootlets and long root hairs allow the plant to exploit a greater volume of soil and consequently increase P uptake (Baon *et al.* 1994, Gahoonia *et al.* 2001). A large absorption area of the root is an inherent property of the plant or can be induced by P or N deficiency (Marschner 1998). An increase in the absorption area of a root to acquire nutrients can also be obtained by formation of mycorrhizas. The external hyphae of the symbiotic fungi can be considered as alternative paths to decrease the distance of the P in the soil to the absorption structures of the plant (Schweiger *et al.* 1995).

The degree to which plant species differ in their growth response, when inoculated with mycorrhizal fungi, is often referred to as mycorrhizal dependency (Gerdemann 1975) or responsiveness (Janos 1988). The amplitude of the response and the degree to which roots are colonized by AM fungi have been related to the morphological properties of the host plant roots. Plant species with low root length per soil volume (Koide & Li 1991, Ryser & Lambers 1995), high root/shoot ratio (Graham & Syvertsen 1985), large root diameter (Graham & Syvertsen 1985, Hetrick *et al.* 1992, Manjunath & Habte 1991, Reinhardt & Miller 1990) and roots with few and short root hairs (Baylis 1975, Schweiger *et al.* 1995, St. John 1980) are more benefited by the AM fungi than those with large root length, small

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root diameter and roots densely cover with long root hairs. In contrast, Saif (1987) reported that tropical grass with long root hairs were more benefited by the AM fungi than the leguminous species with short root hairs. Duponnois *et al.* (2001) showed a positive correlation between tropical leguminous mycorrhizal response and the root-hair density and length. Siqueira & Saggin-Júnior (2001) reported that some tropical native woody species from south-eastern Brazil with thick roots and few root hairs were not responsive to AM fungi, while other woody species with fine roots and abundant root hairs were very responsive. According to Peterson & Farquhar (1996), root hairs exude great quantities of material that attract the hyphae of AM fungi and stimulate colonization. These authors suggested that plant roots with long and numerous hairs tend to exhibit high mycorrhizal colonization, because long root hairs can exude at greater distance large quantities of material that attract more hyphae from the soil and stimulate colonization. The objective of the present study was to assess the relationship between arbuscular mycorrhizas and root morphological characteristics in different tropical native woody species in southern Brazil.

METHODS

Seeds from native woody species were disinfected with 1% sodium hypochlorite, washed in distilled water and placed on sterilized sand to germinate. Seedlings from 78 native woody species belonging to different successional groups from the Tibagi river basin, Paraná state, southern Brazil, were grown in a mix of subsoil (85%) and sand (15%). The mixture was placed in black plastic bags with 2.0-kg capacity and fumigated with methyl bromide. The substratum nutrient concentrations 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 flame photometry. Al were extracted with 1 M KCl and determined by titulometry. P was extracted by Mehlich-1 and determined by colorimetry. K was extracted by Mehlich-1 and determined by flame photometry. Spores of AM fungi were obtained from rhizospheric soil from different native tree species in an area with natural vegetation dominated by early successional woody species. The spores were separated by sieving and decanting, centrifuged in 60% sucrose and disinfected with 1% sodium hypochlorite (Sieverding 1991). Ten individuals of each plant species were inoculated with AM fungi. To inoculate the seedlings about 350 spores of indigenous AM fungi were applied in the planting hole to each cultivation bag. Another 10 individuals of each plant species did not receive spores, being considered as the control group. The original rhizospheric soil was filtered on cellulose filter paper (0.22 μm) and mycorrhizal fungi were retained on it; 100 ml of soil filtrate was added to each bag (Abbott & Robson 1984). The seedlings were transplanted between 6 and 15 d after emergence of the shoot. The successional groups were represented by 16 pioneer, 20 early secondary, 27 late-secondary and 15 climax species. These species were grown for 17, 19, 21 and 26 wk, respectively. The experiment was conducted under greenhouse cover with 50% shading. The percentage of light within the greenhouse was approximately 50% of total sunlight (percentage measured by a luximeter). The plants were grown during the warm season (spring and summer) and under non-controlled temperature conditions. All seedlings were watered once daily.

Table 1. Means (± SE) of soil nutrient concentration of the substratum for seedling growth, early successional area and mature forest of the Mata dos Godoy State Park (n = 3).

	Substratum	Early succession	Mature forest
PH	5.1 ± 0.02	5.2 ± 0.03	4.9 ± 0.03
C (g 100 g^{-1})	1.9 ± 0.06	1.8 ± 0.07	4.2 ± 0.17
P (mg kg^{-1})	1.8 ± 0.03	1.8 ± 0.01	9.96 ± 0.46
Al (meq 100 ml^{-1})	0.08 ± 0.005	0.09 ± 0.007	0.04 ± 0.008
Ca (meq 100 ml^{-1})	5.47 ± 0.21	6.89 ± 0.25	11.7 ± 0.37
Mg (meq 100 ml^{-1})	2.46 ± 0.12	2.77 ± 0.14	3.61 ± 0.15
K (meq 100 ml^{-1})	0.61 ± 0.06	0.52 ± 0.05	0.73 ± 0.05

To estimate the mycorrhizal colonization, a 1-g root sample from each plant was clarified in 10% KOH, acidified with 1% HCl, washed in running water and stained with 0.05% trypan blue in lactoglycerol solution (Brundrett *et al.* 1996). For some darkly pigmented roots, 0.5% H_2O_2 was used after KOH. Segments of fine roots, about 1 cm long, were used, and total colonization of roots was calculated by the grid-line intersection method (Giovannetti & Mosse 1980). Roots and shoots were placed in a drying chamber at 65 °C until they reached a constant weight to obtain the dry mass. Root to shoot ratio was calculated for inoculated and uninoculated plants. Using shoot dry matter data, the degree of response to mycorrhiza (responsiveness) was calculated as being the difference between the biomass of the shoot of inoculated and uninoculated plants and was expressed as a percentage of the dry biomass of inoculated plants (Plenchette *et al.* 1983).

Seedlings of 47 native woody species were collected in the interior under canopy of the Mata dos Godoy State Park tropical forest (23°27′S, 51°15′W) and in a cleared area used as pasture for 40 y and abandoned for natural recuperation about 15 y ago, dominated by early successional woody species, and adjacent to the forest in Londrina city, Paraná state, Brazil. The description of the mature forest can be found in Chagas e Silva &

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Soares-Silva (2000) and Bianchini *et al.* (2001). The soil nutrient concentrations from the mature forest and early successional area are shown in Table 1. All the seedlings were collected without cotyledons and 30–60 cm in height. Three to five seedlings of each species were collected with their root system, which were washed in running water to remove soil and separate the roots of other plants. The fine roots were stored in FAA, later cleared, stained and root mycorrhizal colonization was calculated.

To analyse root morphological characters, 1 g of finest roots of approximately 1 cm length from each plant species were sampled from the treatments inoculated, uninoculated and field plants. Finest root segments were sampled in all 10 individuals of each plant species under each treatment (uninoculated and inoculated). Finest root segments of the seedlings collected in the field were sampled in 3–5 individuals for each plant species. These samples were, then, separately fixed in FAA (5 ml acetic acid, 5 ml formaldehyde, 90 ml ethanol 50%) and stored for 90 d before subsequent analysis. Root morphological characters were analysed at 12 points in each of four random sites in each sample. Thus, 48 measurements of fine-root diameter, root-hair length and root-hair diameter were taken from each individual of each plant species in each treatment. The same procedure was used for the seedlings collected in the field. Fine-root diameters were determined using a compound microscope fitted with an ocular micrometer at 100× magnification (Manjunath & Habte 1991). Root-hair length and diameter were also measured using a compound microscope fitted with an ocular micrometer at 200× magnification (Schweiger *et al.* 1995). The incidence of root hairs was assessed by recording the presence or absence of root hairs at 100 intersections with a grid line (as used for mycorrhizal colonization) and expressed as per cent of intersections with root hairs (Siqueira & Saggin-Júnior 2001). This procedure were conducted for each individual of each plant species under each treatment.

The probable assignment of each native woody species to the different successional groups and some morphological and physiological traits of the early successional species (pioneer and early secondary) and late-successional species (late-secondary and climax) are from Zangaro *et al.* (2003). Data were tested for normal distribution with Kolmogorov–Smirnov test. Seed mass, fine-root diameter, root-hair length, root-hair diameter and root/shoot ratio were log-transformed before analysis and the percentage values were arcsine-square-root-transformed. Correlation and analyses of variance were used on data analysis. Mean differences between treatments for each plant species were determined using Tukey–Kramer's HSD test at 5%. The means of each plant species were considered as one replicate and the species means were used to compare successional groups by Tukey–Kramer's HSD test at 5%.

RESULTS

The native woody species inoculated, uninoculated and collected in the field presented marked variation in the seed fresh mass, in response to inoculation, mycorrhizal colonization (see Zangaro *et al.* 2003 for the species data), root morphological characteristics and root/shoot ratio.

The root morphological characteristics also varied considerably among the species and were affected by inoculation and growth environment (Appendix 1). The pioneer and early secondary species tended generally to reduce the root-hair length in the presence of AM fungi. The mean length of root hairs varied from 24 μm for *Peltophorum dubium* to 936 μm for *Cestrum intermedium*. The pioneer and early secondary species *Cecropia glaziovii, Cecropia pachystachya, Cestrum intermedium, Citharexylum myrianthum, Croton urucurana, Senna macranthera, Solanum argenteum, Albizia hassleri, Colubrina glandulosa, Eugenia uniflora, Lafoensia pacari, Luehea candicans, Parapiptadenia rigida, Poecilanthe parviflora, Sebastiania commersoniana* and *Tabebuia chrysotricha* presented significantly shorter root-hair length in the presence of mycorrhizal fungi. The other seedling species that belong to these early succession stages did not present differences in root-hair length. Only seedlings of *Vitex montevidensis* among late-secondary species presented significant reduction in the incidence of root hairs in the presence of mycorrhizal fungi. None of the climax species presented differences in root-hair length between treatments. The diameter of root hairs varied from 4 μm for *Lithraea molleoides* to 33 μm for *Copaifera langsdorffii*. Root-hair diameter was significantly reduced in the presence of AM fungi only in the early secondary species *Albizia hassleri, Cordia trichotoma* and *Parapiptadenia rigida*. However, *Croton floribundus* presented a significant increase in root-hair diameter in the presence of AM fungi. Generally, the incidence of root hairs was lower in the presence of mycorrhizal fungi among the woody species of the different ecological groups. The incidence varied from absent in *Enterolobium contortisiliquum, Inga sessilis, Ocotea puberula, Syagrus romanzoffiana* and *Ormosia arborea* to 100% of incidence in *Cestrum intermedium, Croton urucurana, Schinus terebinthifolius, Trema micrantha, Guazuma ulmifolia, Luehea candicans, Luehea divaricata, Sebastiania commersoniana, Tabebuia chrysotricha, Astronium graveolens* and *Aspidosperma polyneuron*. Seedlings of *Aegiphila sellowiana, Croton floribundus, Croton urucurana, Mimosa scabrella, Piptocarpha axillaris, Xylosma pseudosalzmannii, Anadenanthera colubrina, Bauhinia forficata, Cordia trichotoma, Heliocarpus americanus, Luehea divaricata, Parapiptadenia rigida,*

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Acacia polyphylla, Campomanesia xanthocarpa, Strichinus brasiliensis, Holocalyx balansae, Trichilia claussenii and *Trichilia elegans* presented significant reduction in the incidence of root hairs in the presence of mycorrhizal fungi. However, *Cedrela fissilis* presented significant increase on the incidence of root hairs in the presence of AM fungi. The fine-root diameter tended to increase in the presence of symbiotic fungi, varying from 87 μm for *Ficus guaranitica* to 814 μm for *Ocotea puberula*. Seedlings of *Aegiphila sellowiana, Cecropia glaziovii, Croton urucurana, Heliocarpus americanus, Lonchocarpus campestris, Parapiptadenia rigida, Sebastiania commersoniana, Centrolobium tomentosum, Jacaranda puberola* and *Actinostemon concolor* presented significant increases in fine-root diameter in the presence of mycorrhizal fungi. According to Baylis's (1975) concept, *Ocotea puberula, Zeyheria tuberculosa, Guarea kunthiana* and *Holocalyx balansae* are the magnolioid type (fine-root diameter > 560 μm and root-hair length < 100 μm). No roots of the graminoid type (fine-root diameter < 100 μm and densely covered by root hairs, 1000–2000 μm long) occurred among the species studied. St. John (1980) also failed to detect a graminoid type root system in species from the Amazon forest. The other woody species belonged to the intermediate type.

Inoculation with AM fungi changed root/shoot ratio, presenting significant reduction for all the pioneer and early secondary species, except for *Colubrina glandulosa* (Appendix 1). From all the late-secondary species, only *Campomanesia xanthocarpa* and *Vitex montevidensis* presented significant reduction in this ratio. The other late-secondary and climax species did not present changes. The presence of symbiotic fungi in the roots of the pioneer and early secondary species altered the measure of, at least, one of the morphological parameters analysed, except in *Colubrina glandulosa*. For the late-secondary and climax species, alterations of, at least, one morphological root parameter, were detected only in 9 out of the 42 species studied. Alteration of the different root morphological parameters was reported in most of the species that presented high response to inoculation and root mycorrhizal colonization, such as the pioneer and early secondary, and in a few late-secondary species.

The seed mass increased with the advance among the successional groups (Figure 1a). The early secondary group did not differ significantly from pioneer and late-secondary ecological groups. Pioneer, late-secondary and climax groups differed significantly amongst each other. The response of the seedlings to mycorrhizal inoculation decreased with the advance among the ecological groups (Figure 1b). The mycorrhizal responses of pioneer and early secondary groups were high and were not different between each other. These groups differed significantly from the late-secondary and climax groups. These two groups presented low response and

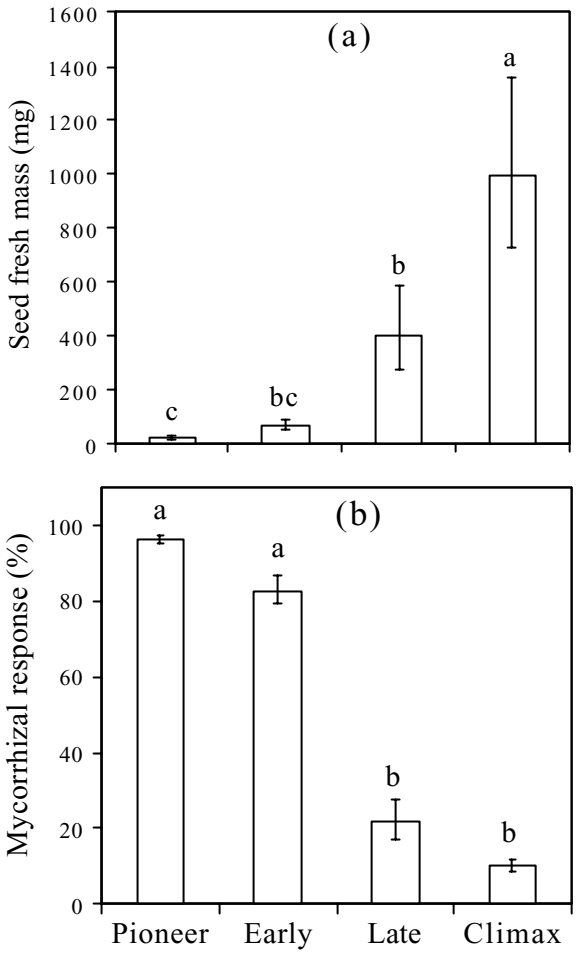

Figure 1. Seed fresh (n = 76) mass (a) and mycorrhizal response (b) of the seedlings belonging to different successional groups. The means were obtained from the values showed in Appendix 1. Error bars represent ± 1 SE. Means followed by the same letter are not different by Tukey–Kramer HSD test at 0.05 level.

no significant difference between each other. The root mycorrhizal colonization, both in the greenhouse and in field, decreased with the progress among the successional groups and was high among the pioneer and early secondary groups, which did not differ significantly from each other (Figure 2a). These groups differed significantly from the late-secondary and climax groups, which presented low root mycorrhizal colonization and did not differ amongst each other. The root/shoot ratio decreased with the advance among the successional groups in seedlings uninoculated (Figure 2b). The pioneer and early secondary groups showed high root/shoot ratio and did not differ significantly from each other. These groups differed significantly from late-secondary and climax groups, which differed significantly between themselves. The pioneer and early secondary groups presented significant reduction in the root/shoot ratio in

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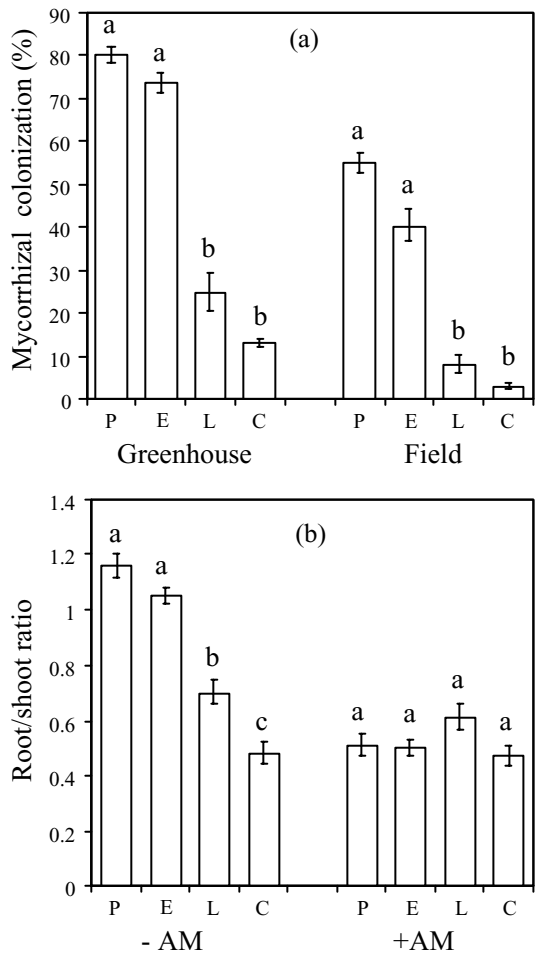

Figure 2. Root mycorrhizal colonization (a) of seedlings grown in greenhouse and seedlings collected in the field. Root/shoot ratio (b) of the seedlings uninoculated (– AM) and inoculated (+ AM) with arbuscular mycorrhizal fungi. The successional groups are classified as pioneer (P), early secondary (E), late-secondary (L) and climax (C). The means were obtained of the values showed in Appendix 1. Error bars represent ± 1 SE. Means followed by the same letter are not different by Tukey–Kramer HSD test at 0.05 level.

the presence of AM fungi, which did not differ from the late-secondary and climax groups.

When compared with the uninoculated plants, mycorrhizal inoculation in the greenhouse and the root mycorrhizal colonization in the field presented a general tendency to increase fine-root diameter and decrease root-hair length and root-hair incidence. Analysis among the ecological groups showed that there were significant differences in the morphological characteristics of the roots and root hairs regardless of mycorrhizal colonization. Fine-root diameter increased with the progress among the ecological groups, being small for the pioneers and early secondary and large in the late-secondary and climax groups of uninoculated, inoculated and field seedlings (Figure 3a). Root-hair length decreased with the progress among the sucessional groups of uninoculated, inoculated and field seedlings (Figure 3b). Generally, the root-hair length was significantly longer in pioneer and early secondary groups than late-secondary and climax groups. Both inoculated and field seedlings presented decrease of root-hair length when compared with uninoculated seedlings, especially among the pioneer and early secondary groups. Root-hair incidence decreased with the progress among the ecological groups of uninoculated, inoculated and field seedlings (Figure 3c). Generally, the root-hair incidence was significantly higher among the pioneer and early secondary than late-secondary and climax groups. Root-hair incidence decreased among pioneer and early secondary groups of seedlings with mycorrhizal colonization both in the greenhouse and the field. Root-hair diameter did not differ among ecological groups (Figure 3d).

The mycorrhizal response of the seedlings in the greenhouse was strongly and positively correlated with root mycorrhizal colonization in greenhouse ($r = 0.94$, $P < 0.001$, $n = 78$) and in field ($r = 0.95$, $P < 0.001$, $n = 47$). Root mycorrhizal colonization in the greenhouse was strongly and positively correlated with root mycorrhizal colonization in the field ($r = 0.93$, $P < 0.001$, $n = 47$). Seed mass was negatively correlated with mycorrhizal response ($r = -0.32$, $P < 0.01$, $n = 76$), root mycorrhizal colonization in the greenhouse ($r = -0.38$, $P < 0.01$, $n = 76$), root mycorrhizal colonization in the field ($r = -0.35$, $P < 0.05$, $n = 47$), root-hair incidence of uninoculated seedlings ($r = -0.29$, $P < 0.05$, $n = 76$), inoculated seedlings ($r = -0.26$, $P < 0.05$, $n = 76$), seedlings from the field ($r = -0.33$, $P < 0.01$, $n = 47$), and root/shoot ratio of uninoculated seedlings ($r = -0.41$, $P < 0.01$, $n = 76$). The seed mass was positively correlated with fine-root diameter of uninoculated seedlings ($r = 0.27$, $P < 0.05$, $n = 76$), inoculated seedlings ($r = 0.36$, $P < 0.01$, $n = 76$), and seedlings from the field ($r = 0.44$, $P < 0.01$, $n = 76$). The mycorrhizal response ($r = 0.32$, $P < 0.01$, $n = 78$), root mycorrhizal colonization in the greenhouse ($r = 0.27$, $P < 0.05$, $n = 78$), and root mycorrhizal colonization in the field ($r = 0.35$, $P < 0.05$, $n = 47$) were positively correlated with root-hair length only in uninoculated seedlings. The mycorrhizal response ($r = 0.56$, $P < 0.001$, $n = 78$), root mycorrhizal colonization in the greenhouse ($r = 0.56$, $P < 0.001$, $n = 78$), and root mycorrhizal colonization in the field ($r = 0.62$, $P < 0.001$, $n = 47$) were positively correlated with root-hair incidence of the uninoculated seedlings. These correlations were also positive for the inoculated seedlings and those from field. The mycorrhizal response ($r = -0.31$, $P < 0.05$, $n = 78$), root mycorrhizal colonization in the greenhouse ($r = -0.38$, $P < 0.01$, $n = 78$), and root mycorrhizal colonization in the field ($r = -0.34$, $P < 0.01$, $n = 47$) were negatively correlated with fine-root diameter of

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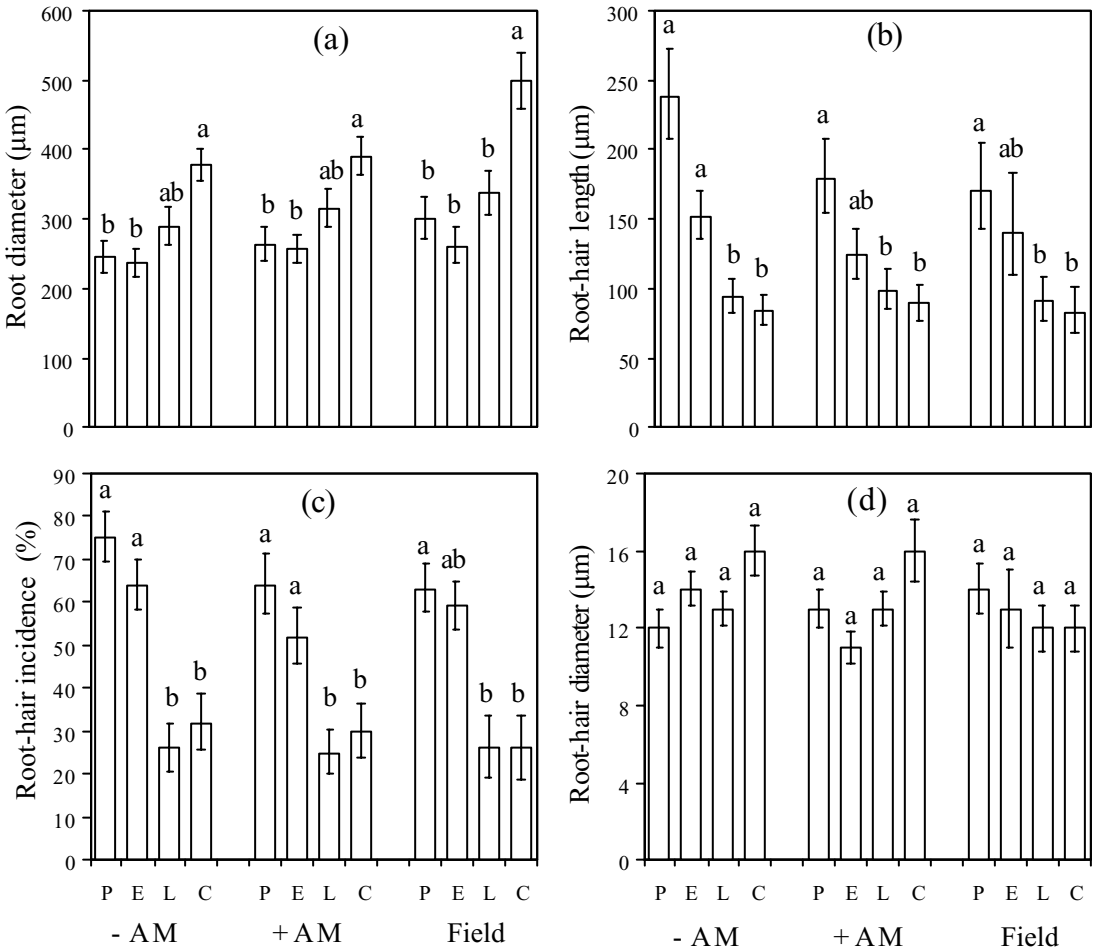

Figure 3. Root diameter (a), root-hair length (b), root-hair incidence (c) and root-hair diameter (d) of seedlings uninoculated (– AM) and inoculated (+ AM) with arbuscular mycorrhizal fungi and seedlings collected in the field. The successional groups are as described for Figure 2. The means were obtained of the values showed in Appendix 1. Error bars represent ± 1 SE. Means followed by the same letter are not different by Tukey–Kramer HSD test at 0.05 level.

the uninoculated seedlings. These correlations were also negative for the inoculated seedlings and those from the field. The mycorrhizal response ($r = 0.72$, $P < 0.001$, $n = 78$), root mycorrhizal colonization in the greenhouse ($r = 0.73$, $P < 0.001$, $n = 78$), and root mycorrhizal colonization in the field ($r = 0.68$, $P < 0.001$, $n = 47$) were positively correlated with root/shoot ratio only for uninoculated seedlings.

DISCUSSION

Root morphology and arbuscular mycorrhizas

Typically, seedlings of early successional woody species presented higher mycorrhizal response, higher degree of root mycorrhizal colonization, smaller fine-root diameter, longer and more plentiful root hairs than seedlings of late-successional woody species. The mycorrhizal status and root morphological properties exhibited for these seedlings are in accordance to studies that have noted that some tropical plant species with long and abundant root hairs and small fine-root diameter (Duponnois *et al.* 2001, Saif 1987, Siqueira & Saggin-Júnior 2001) benefit more from AM fungi than plant species with short and few root hairs and large fine-root diameter (Baylis 1975, Graham & Syvertsen 1985, Hetrick *et al.* 1992, Manjunath & Habte 1991, Reinhardt & Miller 1990, Schweiger *et al.* 1995, St. John 1980).

The results of this study support the view that plant roots with long and numerous hairs tend to exhibit high mycorrhizal colonization (Peterson & Farquhar 1996). Root hairs exude a sizeable quantity of polysaccharides (Smith and Read 1997) and longer root hairs exude material more distant than short hairs, which allows to amplify the interface contact with soil hyphae, increasing the chance of the attraction of symbiotic fungi. The chemical components found in the host plant exudates

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increased lengthening and ramification of fungal hyphae (Giovannetti *et al.* 1996). Plants with P shortage increase exudate production, promoting the proliferation of the hyphal ramifications and increasing the chance of contact with the root surface of the host plant (Bécard *et al.* 1997). Seedlings of the early successional woody species that grew without AM fungi showed an increase in root-hair length and root-hair incidence, which increased even more the possibility of roots encountering symbiotic fungi. Furthermore, Zangaro *et al.* (2003) observed that these same pioneer and early secondary species inoculated with AM fungi, presented 2.2 times more P in the leaves than uninoculated plants. The increase of root absorption area (high incidence of long root hairs) of these species, in absence of AM fungi, was not enough to take up the necessary quantity of minerals to promote their growth. These results suggest that the AM fungi provided greater effects in nutrient uptake than in the increase of root absorption area per se, and the attraction of the symbiotic fungi by the increase of root surface from seedlings of early successional species is essential to improving nutrient uptake, when these are limited as in naturally poor or degraded soils.

Root morphology and succession

The species belonging to the different sucessional groups showed differences in root morphology. This influences the uptake of minerals available in the soil (Baylis 1975, Hetrick *et al.* 1992). Root nutrient acquisition is influenced more by root length or root surface area than mass, and root length increases with the decrease in root diameter (Eissenstat 1992). Root diameter influences the P influx rate of root surface, since as root diameter decreased, P influx increased (Eissenstat 1992, Itoh & Barber 1983). The root surface area increases with the increase in root-hair length and incidence (Föehse *et al.* 1991, Gahoonia *et al.* 2001) and with mycorrhizal colonization (Marschner 1998). In this study, there was strong reduction in root-hair length and incidence (decrease in root surface area) and increase in fine-root diameter (decrease in the P absorption capacity) with the advance among the successional groups, regardless of mycorrhizal colonization, both in the greenhouse and the field. This reduction of the root surface and P absorption capacity is probably related to the difference of root longevity, plant metabolic demand and adaptation to the different species habitats. Root life span is related to root morphology and mineral uptake capacity. Root death and re-growth in new areas and roots of fast-growing species with high P uptake capacity reach maximum lifetime efficiency sooner than roots of slow-growing species, due to faster P acquisition (Comas *et al.* 2002). Roots of fast-growing species may have shorter life span and higher P uptake capacity than slow-growing species (Eissenstat 1992). The species belonging to the early successional stages are most frequent in open environments with high light incidence and present rapid growth and high demand for minerals (Brown & Lugo 1994). These fast-growth species occur on a wide range of soil fertilities and are also frequently found growing abundantly on infertile soils with high root mycorrhizal colonization (Zangaro *et al.* 2003). The high growth rates express the great metabolic demand of fast-growing species, which corresponded well to their great root mycorrhizal colonization and mycorrhizal response, long and plentiful root hairs and smaller root diameter.

Seedlings of pioneer and early secondary species inoculated with AM fungi presented a general tendency to reduce root-hair length and incidence and to increase fine-root diameter, when compared with control plants without symbiotic fungi. These results indicate that, during seedling establishment on soils with low P availability and absence of AM fungi, the increase in the root-hair length, root-hair incidence, and reduced fine-root diameter may be mechanisms used by most woody species, characteristic of the early stage of succession, to increase the root absorption area as strategies for acquiring soil resources. These results agree with those of Föehse & Jungk (1983) who reported reduction in root-hair length and incidence in three vegetables with increase in P and N addition. They also agree with Hetrick *et al.* (1991) who reported that warm-season grasses responded to mycorrhizal colonization with increases in root diameter and decreases in specific root length and degree of root ramification.

Low mineral availability in soil generally leads to an increase in specific root length and to a decrease in root diameter (Ryser & Lambers 1995). In contrast, plants growing in soils with high mineral availability exhibit low specific root length and roots with large diameter. The fine-root diameter of seedlings of late-successional species from the forest was bigger than the same uninoculated seedlings that grew in poor soil (control) in the greenhouse, which suggests that the forest soil probably supplies sufficient minerals for the growth of seedling species that dominate in mature forest. Plant species with slow growth present low P requirements due to low metabolic demands (Comas *et al.* 2002), and may be less benefited by AM fungi (Koide 1991, Manjunath & Habte 1991). The native woody species of late-successional stages dominate the mature forest and their seedlings generally occur in shaded places. These seedlings exhibit low mineral demand and frequently present slow growth in forest soils with both adequate mineral availability and low root mycorrhizal colonization (Zangaro & Andrade 2002, Zangaro *et al.* 2000). During seedling establishment of late-successional species, the forest shading and the relatively fertile soils

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presumably selected traits that led these slow-growth species to combine reduced root surface area with low root mycorrhizal colonization. Therefore, a high AM fungi colonization by seedlings of late-successional woody species to increase their root surface area may be limited by their low metabolic demand and slow growth, both in the greenhouse and in forest.

Root morphology and seed reserves

Seed mass was inversely related to root-hair incidence and directly related to the fine-root diameter, both in the presence and absence of mycorrhizal fungi. This relationship indicates that the root morphological characteristics were probably influenced by the seed reserves during initial growth of the seedlings in soils with mineral deficiency. The low reserves of small seeds are insufficient to support the growth of the seedlings of early successional species in the absence of AM fungi. Although the root systems of these species show an increase in root-hair length and incidence and a decrease of fine-root diameter when uninoculated, the adequate P supply for their growth and establishment can only be obtained through root mycorrhizal colonization. In contrast, the apparently inefficient absorption system of the roots of late-successional species may be compensated by the high nutrient content of the seed reserve that promotes the initial seedling growth in the absence of AM fungi in poor soils. Therefore, the lack of abundant root mycorrhizal colonization on seedlings of late-successional species is possibly related to both seed reserve and low metabolic rate, ensuring that the major part of plant carbohydrates is not lost to the symbiotic fungi.

The significant correlation of the uninoculated treatment among the root/shoot ratio with response to inoculation, root mycorrhizal colonization, seed weight, and root morphological characteristic, can be related to the low availability of mineral nutrients in the soil and nutritional content of the seed reserve. In the inoculated treatment, where the mycorrhizal fungi provided the seedlings of the early successional species with greater access to P, these relationships disappeared, indicating the nutritional effect of the symbiont. In the absence of mycorrhizal colonization, the woody species that start succession combined greater investment in the biomass allocated to the roots with a sharp increase in their root surface area. This relationship between biomass and root area was common for the roots of these species. Thus, the extensive root mycorrhizal colonization of the pioneer and early secondary seedling species as a strategy for mineral acquisition in poor soils is clear.

In summary, seedlings of pioneer and early secondary species combined a high incidence of long root hairs, small fine-root diameter and roots with large absorption area, seeds with low nutritional reserves, short root life span, occurring in open environments and presented great root mycorrhizal colonization and mycorrhizal response. Seedlings of the late-secondary and climax species combined few and short root hairs, large fine-root diameter with reduced absorption area, presented seeds with high nutritional reserves, long root life span, dominate the mature stage of the forest and presented little or no root mycorrhizal colonization and mycorrhizal response. These great differences among tropical native woody species belonging to early and late-successional groups are related to differences in their root morphological characteristics as strategies for acquiring nutrients from soil. The large variation in root traits and mycorrhizal colonization among plant species belonging to different ecological groups was presumably selected by adaptation to different light environmental conditions.

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LITERATURE CITED

ABBOTT, L. K. & ROBSON, A. D. 1984. The effect of VAM mycorrhizas on plant growth. Pp. 113–130 in Powell, C. C. & Bagyaraj, D. S. (eds). *VA mycorrhizas*. CRC Press, Florida.

BAON, J. B., SMITH, S. E. & ALSTON, A. M. 1994. Growth response and phosphorus uptake of rye with long and short root hairs: interactions with mycorrhizal infection. *Plant and Soil* 167:247–254.

BAYLIS, G. T. S. 1975. The magnolioid mycorrhiza and mycotrophy in root systems derived from it. Pp. 373–389 in Sanders, F. E. B., Mosse, B. & Tinker, P. B. (eds). *Endomycorrhizas*. Academic Press, New York.

BÉCARD, G., BEGUIRISTAIN, T. & NAGAHASHI, G. 1997. Signaling in plants and root-infecting fungi associations. Pp. 164–177 in Flores, H. E., Lynch, J. P. & Eissenstat, D. (eds). *Radical biology: advances and perspectives on the function of plant roots*. American Society of Plant Physiologists, Rockville.

BIANCHINI, E., PIMENTA, J. A. & SANTOS, F. A. M. 2001. Spatial and temporal variation in the canopy cover in a tropical semi-deciduous forest. *Brazilian Archives of Biology and Technology* 44:269–276.

BROWN, S. & LUGO, A. E. 1994. Rehabilitation of tropical lands: a key to sustaining development. *Restoration Ecology* 2:97–111.

BRUNDRETT, M., BOUGHER, N., DELL, B., GROVE, T. & MALAJCZUK, N. 1996. *Working with mycorrhizas in forestry and agriculture*. ACIR Monograph, Canberra. 374 pp.

CHAGAS e SILVA, F. & SOARES-SILVA, L. H. 2000. Arboreal flora of the Godoy Forest State Park, Londrina, PR. Brazil. Edinburgh *Journal of Botany* 57:107–120.

COMAS, L. H., BOUMA, T. J. & EISSENSTAT, D. M. 2002. Linking root traits to potential growth rate in six temperate tree species. *Oecologia* 132:34–43.

DUPONNOIS, R., PLENCHETTE, C. & BÂ, A. M. 2001. Growth stimulation of seventeen fallow leguminous plants inoculated with *Glomus aggregatum* in Senegal. *European Journal of Soil Biology* 37:181–186.

EISSENSTAT, D. M. 1992. Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition* 15:763–782.

FÖEHSE, D. & JUNGK, A. 1983. Influence of phosphate and nitrate supply on root hair formation of rape, spinach and tomato plants. *Plant and Soil* 74:359–368.

FÖEHSE, D., CLAASSEN, N. & JUNGK, A. 1991. Phosphorus efficiency of plants II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species. *Plant and Soil* 132:261–271.

GAHOONIA, T. S., NIELSEN, N. E., JOSHI, P. A. & JAHOOR, A. 2001. A root hairless barley mutant for elucidating genetics of root hairs and phosphorus uptake. *Plant and Soil* 235:211–219.

GERDEMANN, J. W. 1975. Vesicular-arbuscular mycorrhizae. Pp. 575–591 in Torrey, J. G. & Clarkson, D. T. (eds). *The development and function of roots*. Academic Press, London.

GIOVANNETTI, M. & MOSSE, B. 1980. An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infections in roots. *New Phytologist* 84:489–500.

GIOVANNETTI, M., SBRANA, C., CITERNESI, A. S. & AVIO, L. 1996. Analysis of factors involved in fungal recognition responses to host-derived signals by arbuscular mycorrhizal fungi. *New Phytologist* 133:65–71.

GRAHAM, J. H. & SYVERTSEN, J. P. 1985. Host determinants of mycorrhizal dependency of citrus rootstock seedlings. *The New Phytologist* 101:667–676.

HETRICK, B. A. D., WILSON, G. W. T. & LESLIE, J. F. 1991. Root architecture to warm- and cool-season grasses: relationship to mycorrhizal dependence. *Canadian Journal of Botany* 69:112–118.

HETRICK, B. A. D., WILSON, G. W. T. & TODD, T. C. 1992. Relationships of mycorrhizal symbiosis, root strategy, and phenology among tallgrass prairie forbs. *Canadian Journal of Botany* 70:1521–1528.

ITOH, S. & BARBER, S. A. 1983. Phosphorus uptake by six plant species as related to root hairs. *Agronomy Journal* 75:457–461.

JANOS, D. P. 1987. VA mycorrhizas in humid tropical ecosystems. Pp. 107–134 in Safir, G. R. (ed). *Ecophysiology of VA mycorrhizal plants*. CRC Press, Boca Raton.

JANOS, D. P. 1988. Mycorrhiza applications in tropical forestry: are temperate-zone approaches appropriate? Pp. 133–188 in Ng, F. S. P. (ed). *Trees and mycorrhiza*. Forest Research Institute, Kuala Lumpur.

KOIDE, R. T. 1991. Nutrient supply, nutrient demand and plant response to mycorrhizal infection. *New Phytologist* 117:365–386.

KOIDE, R. T. & LI, M. 1991. Mycorrhizal fungi and the nutrient ecology of three oldfield annual plant species. *Oecologia* 85:403–412.

MANJUNATH, A. & HABTE, M. 1991. Root morphological characteristics of host species having distinct mycorrhizal dependency. *Canadian Journal of Botany* 69:671–676.

MARSCHNER, H. 1998. Role of root growth, arbuscular mycorrhiza, and root exudates for efficiency in nutrient acquisition. *Field Crops Research* 56:203–207.

PETERSON, R. L. & FARQUHAR, M. L. 1996. Root hairs: specialized tubular cells extending root surfaces. *The Botanical Review* 62:1–40.

PLENCHETTE, C., FORTIN, J. A. & FURLAN, V. 1983. Growth response of several plants species to mycorrhiza in a soil of moderate P fertility. I. Mycorrhizal dependency under field conditions. *Plant and Soil* 70:191–209.

REINHARDT, D. R. & MILLER, R. M. 1990. Size classes of root diameter and mycorrhizal fungal colonization in two temperate grassland communities. *New Phytologist* 116:129–136.

RYSER, P. & LAMBERS, H. 1995. Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant and Soil* 170:251–265.

SAIF, S. R. 1987. Growth responses of tropical forage plant species to vesicular-arbuscular mycorrhizae. *Plant and Soil* 97:25–35.

SCHWEIGER, P. F., ROBSON, A. D. & BARROW, N. J. 1995. Root hair length determines beneficial effect of a *Glomus* species on shoot growth of some pasture species. *New Phytologist* 131:247–254.

SIEVERDING, E. 1991. *Vesicular arbuscular mycorrhiza management in tropical agrosystems*. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Eschbon. 372 pp.

SIQUEIRA, J. O. & SAGGIN-JÚNIOR, O. J. 2001. Dependency on arbuscular mycorrhizal fungi and responsiveness of some Brazilian native woody species. *Mycorrhiza* 11:245–255.

SMITH, S. E. & READ, D. J. 1997. *Mycorrhizal symbiosis*. Academic Press, London. 605 pp.

St JOHN, T. V. 1980. Root size, root hairs and mycorrhizal infection: a re-examination of Baylis's hypothesis with tropical trees. *New Phytologist* 84:483–487.

ZANGARO, W. & ANDRADE, G. 2002. Micorrizas arbusculares em espécies arbóreas nativas da bacia do rio Tibagi. Pp. 171–210 in Medri, M. E., Bianchini, E., Pimenta, J. A. & Shibata, O. (eds). *A bacia do rio Tibagi*. Edição dos editores, Londrina.

ZANGARO, W., BONONI, V. L. R. & TRUFEN, S. B. 2000. Mycorrhizal dependency, inoculum potential and habitat preference of native woody species in South Brazil. *Journal of Tropical Ecology* 16:603–621.

ZANGARO, W., NISIZAKI, S. M. A., DOMINGOS, J. C. B. & NAKANO, E. M. 2003. Mycorrhizal response and successional status in 80 woody species from south Brazil. *Journal of Tropical Ecology* 19: 315–324.

Appendix 1. Identification, ecological groups and root morphological characters of the native woody species from southern Brazil uninoculated (U) and inoculated (I) with arbuscular mycorrhizas, root-hair length (n = 10), root-hair diameter (n = 10), root-hair incidence (n = 10), root diameter (n = 10) and root/shoot ratio (n = 10). Field (F) seedlings collected (n = 3–5).

Root hair length (μm)			Root hair diameter (μm)			Root hair incidence (%)			Root diameter (μm)			Root/shoot ratio	
U	I	F	U	I	F	U	I	F	U	I	F	U	I
Pioneer													
Aegiphila sellowiana Cham. (Verbenaceae)													
116a	86a	108a	16a	15a	18a	81a	59ab	42b	323b	524a	486ab	1.48a	0.76b
Cecropia glaziovii Snethl. (Cecropiaceae)													
171a	105a	72b	17a	16a	19a	70a	65a	54a	153b	225ab	279a	1.11a	0.52b
Cecropia pachystachya Trec. (Cecropiaceae)													
297a	282a	161b	8a	8a	6a	86a	98a	82a	176a	109a	169a	1.00a	0.49b
Cestrum intermedium Semdth. (Solanaceae)													
936a	721ab	646b	18a	20a	14a	100a	100a	83a	306a	325a	386a	1.10a	0.62b
Citharexylum myrianthum Cham. (Verbenaceae)													
368a	160b	–	8a	10a	–	58a	47a	–	316a	291a	–	1.38a	0.56b
Croton floribundus Spreng. (Euphorbiaceae)													
96a	64a	108a	12b	15ab	18a	61a	37b	46ab	477a	396a	461a	1.27a	0.44b
Croton urucurana Baill. (Euphorbiaceae)													
194a	136b	–	12a	10a	–	100a	68b	–	127b	198a	–	1.50a	0.25b
Mimosa scabrella Benth. (Mimosaceae)													
167a	149a	–	21a	21a	–	51a	26b	–	322a	280a	–	1.04a	0.66b
Piptocarpha axillaris (Less.) Baker (Asteraceae)													
192a	157a	–	8a	10a	–	46a	24b	–	227b	285a	–	1.00a	0.52b
Schinus terebinthifolius Raddi (Anacardiaceae)													
262a	270a	192a	9a	10a	10a	100a	100a	94a	225a	190a	217a	1.23a	0.32b
Senna macranthera (Collad.) H. S. Irwin & Barneby (Caesalpiniaceae)													
178a	101b	109b	14a	17a	18a	12a	12a	26a	256a	284a	329a	1.38a	0.31b
Solanum argenteum Dun. (Solanaceae)													
172a	79b	87b	13a	12a	12a	98a	86a	73a	131b	176ab	208a	1.05a	0.54b
Tabernaemontana australis (M. Arg.) Miers (Apocynaceae)													
191a	157a	107a	8a	11a	10a	54a	63a	57a	271a	313a	294a	1.19a	0.56b
Trema micrantha (L.) Blum. (Ulmaceae)													
176a	138a	170a	9a	8a	12a	100a	94a	63b	179a	163a	196a	1.00a	0.63b
Xylosma ciliatifolium (Clos) Eichler (Flacourtiaceae)													
186a	165a	119a	12a	16a	15a	96a	96a	74a	222a	234a	276a	0.94a	0.58b
Xylosma pseudosalzmannii Sleumer (Flacourtiaceae)													
100a	97a	–	10a	11a	–	92a	57b	–	217a	210a	–	0.98a	0.44b
Early Secondary													
Albizia hassleri (Chodat) Burkart (Mimosaceae)													
148a	84b	–	15a	10b	–	21a	14a	–	225a	191a	–	1.11a	0.54b
Anadenanthera colubrina (Vell.) Brenan (Mimosaceae)													
86a	101a	–	10a	10a	–	62a	21b	–	177a	206a	–	0.95a	0.51b
Anadenanthera macrocarpa (Benth.) Brenan (Mimosaceae)													
114a	123a	–	8a	8a	–	17a	19a	–	206a	184a	–	0.96a	0.63b
Bastardiopsis densiflora (Hook. & Arn.) Hassl. (Malvaceae)													
71a	67a	–	13a	14a	–	52a	71a	–	266a	287a	–	1.08a	0.54b
Bauhinia forficata Link. (Caesalpiniaceae)													
120a	138a	–	11a	10a	–	46a	13b	–	167b	214a	–	1.14a	0.51b
Casearia sylvestris Sw.													
301a	306a	249a	8a	7a	6a	72a	87a	66a	268a	291a	331a	0.86a	0.47b
Colubrina glandulosa Perk. (Rhamnaceae)													
576a	517a	348b	21a	20a	23a	87a	68a	76a	301a	315a	326a	0.79a	0.53a
Cordia trichotoma (Vell.) Arrab. ex Steud. (Boraginaceae)													
86a	51a	–	18a	11b	–	51a	27b	–	384a	374a	–	1.24a	0.64b
Eugenia uniflora L. (Myrtaceae)													
162a	91b	114ab	10a	10a	8a	69a	61a	57a	203a	195a	294a	1.09a	0.62b
Guazuma ulmifolia Lam. (Sterculiaceae)													
116a	71a	93a	13a	11a	13a	100a	84a	61a	179a	166a	198a	1.02a	0.19b
Heliocarpus americanus L. (Tiliaceae)													
177a	202a	130a	14a	15a	16a	81a	53ab	49b	131b	210ab	226a	1.33a	0.35b
Lafoensia pacari A. St. Hil. (Lythraceae)													
165a	108b	–	14a	9a	–	76a	59a	–	287a	284a	–	1.18a	0.67b

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Appendix 1. Continued.

Root hair length (μm)			Root hair diameter (μm)			Root hair incidence (%)			Root diameter (μm)			Root / shoot ratio	
U	I	F	U	I	F	U	I	F	U	I	F	U	I
Lonchocarpus campestris Mart. & Benth. (Fabaceae)													
147a	119a	–	12a	13a	–	40a	44a	–	144b	260a	–	1.06a	0.51b
Luehea candicans Mart. Zucc. (Tiliaceae)													
132a	61b	79ab	11a	7a	7a	100a	73a	61a	186a	115a	171a	1.04a	0.42b
Luehea divaricata Mart. (Tiliaceae)													
63a	55a	–	12a	8a	–	100a	41b	–	190a	201a	–	1.22a	0.34b
Parapiptadenia rigida (Benth.) Brenan (Mimosaceae)													
71a	34b	38ab	16a	8b	14ab	29a	5b	16ab	101b	154ab	199a	0.91a	0.41b
Poecilanthe parviflora Benth. (Fabaceae)													
147a	45b	–	19a	14a	–	28a	32a	–	254a	287a	–	1.12a	0.64b
Pseudobombax grandiflorum (Cav.) A. Robyns (Bombacaceae)													
104a	137a	–	14a	12a	–	61a	78a	–	444a	380a	–	0.92a	0.63b
Sebastiania commersoniana (Baill.) Smith & Downs (Euphorbiaceae)													
139a	95ab	76b	22a	21a	17a	100a	100a	74a	158b	355a	346a	1.01a	0.41b
Tabebuia chrysotricha (Mart. ex DC.) Standl. (Bignoniaceae)													
122a	66b	–	10a	10a	–	80a	100a	–	445a	448a	–	0.99a	0.49b
Late secondary													
Acacia polyphylla DC. (Mimosaceae)													
56a	72a	–	22a	21a	–	19a	3b	–	374a	312a	–	0.63a	0.34a
Astronium graveolens Jacq. (Anacardiaceae)													
88a	81a	60a	17a	12a	16a	100a	100a	100a	221a	276a	363a	0.68a	0.64a
Campomanesia xanthocarpa O. Berg (Myrtaceae)													
70a	57a	46a	10a	10a	12a	32a	16b	21ab	203a	180a	274a	0.63a	0.36a
Cedrela fissilis Vell. (Meliaceae)													
59a	68a	47a	8a	8a	6a	18b	32a	49a	308a	281a	336a	1.16a	1.21a
Centrolobium tomentosum Guill. ex Benth. (Fabaceae)													
36a	41a	49a	5a	6a	5a	12a	17a	21a	121b	285a	317a	0.41a	0.40a
Chorisia speciosa St. Hil. (Bombacaceae)													
99a	97a	81a	8a	9a	9a	61a	94a	76a	310a	367a	398a	0.63a	0.71a
Cordia ecalyculata Vell. (Boraginaceae)													
139a	108a	–	11a	8a	–	6a	4a	–	362a	366a	–	0.83a	0.74a
Enterolobium contortisiliquum (Vell.) Morong (Mimosaceae)													
–	–	–	–	–	–	0	0	–	209a	292a	–	0.57a	0.54a
Ficus guaranitica Schodat (Moraceae)													
479a	590a	431a	10a	11a	14a	61a	41a	56a	92a	87a	123a	1.45a	1.09a
Genipa americana L. (Rubiaceae)													
60a	57a	–	18a	18a	–	28a	27a	–	447a	431a	–	0.64a	0.54a
Inga sessilis (Vell.) Mart. (Mimosaceae)													
–	–	–	–	–	–	0	0	–	273a	336a	–	0.75a	0.55a
Inga striata Benth. (Mimosaceae)													
53a	62a	67a	16a	14a	12a	8a	13a	5a	203a	226a	291a	0.58a	0.42a
Jacaranda mimosaefolia D. Don (Bignoniaceae)													
209a	191a	–	9a	10a	–	70a	68a	–	179a	156a	–	0.59a	0.65a
Jacaranda puberula Cham. (Bignoniaceae)													
198a	227a	176a	8a	7a	5a	41a	52a	30a	265b	281ab	356a	0.85a	0.74a
Jacaratia spinosa (Aubl.) A. DC. (Caricaceae)													
45a	48a	56a	17a	19a	21a	6a	6a	3a	481a	496a	509a	0.86a	0.87a
Lithraea molleoides (Vell.) Engl. (Anacardiaceae)													
71a	60a	86a	7a	7a	4a	96a	89a	74a	236a	223a	261a	0.33a	0.35a
Lonchocarpus muehlbergianus Hassl. (Fabaceae)													
63a	78a	59a	18a	16a	14a	8a	15a	10a	289a	460a	367a	1.21a	1.39a
Machaerium stipitatum (DC) Vog. (Fabaceae)													
79a	67a	–	16a	17a	–	27a	14a	–	210a	238a	–	0.63a	0.53a
Ocotea puberula (Reich.) Ness (Lauraceae)													
–	–	–	–	–	–	0	0	0	814a	708a	736a	0.56a	0.45a
Peltophorum dubium (Spreng.) Taub. (Caesalpiniaceae)													
31a	24a	36a	12a	10a	16a	4a	2a	9a	227a	196a	171a	0.44a	0.45a
Prunus sellowii Hoehne (Rosaceae)													
76b	85ab	108a	11a	11a	8a	11a	5a	7a	236a	281a	360a	0.37a	0.29a
Pterogyne nitens Tul. (Caesalpinaceae)													
49a	61a	69a	19a	17a	16a	3a	8a	5a	267a	291a	272a	0.78a	0.76a

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Appendix 1. Continued.

Root hair length (μm)			Root hair diameter (μm)			Root hair incidence (%)			Root diameter (μm)			Root / shoot ratio	
U	I	F	U	I	F	U	I	F	U	I	F	U	I
Strichinus brasiliensis (Spreng.) Mart. (Styracaceae)													
71a	84a	61a	17a	18a	17a	16a	3b	4b	196a	344a	312a	0.51a	0.43a
Syagrus romanzoffiana (Cham.) Glassm. (Arecaceae)													
–	–	–	–	–	–	0	0	0	354a	295a	383a	0.43a	0.48a
Tabebuia roseo-alba (Ridl.) Sand. (Bignoniaceae)													
29a	26a	–	20a	17a	–	23a	27a	–	177a	246a	–	0.75a	0.47a
Vitex montevidensis Cham. (Verbenaceae)													
69a	52a	31b	15a	14a	12a	14a	12a	6a	149a	157a	226a	0.91a	0.32b
Zeyheria tuberculosa (Vell.) Bureau (Bignoniaceae)													
43a	51a	–	10a	10a	–	31a	36a	–	605a	700a	–	0.69a	0.68a
Climax													
Actinostemon concolor (Spreng.) M. Arg. (Euphorbiaceae)													
49a	62a	50a	18a	17a	15a	39a	32a	21a	310b	396ab	547a	0.56a	0.47a
Aspidosperma polyneuron M. Arg. (Apocynaceae)													
289a	306a	302a	11a	10a	10a	100a	100a	86a	405a	381a	490a	0.69a	0.58a
Cariniana estrellensis (Raddi) Kuntze (Lecythidaceae)													
35a	31a	–	20a	20a	–	48a	42a	–	306a	259a	–	0.74a	0.85a
Copaifera langsdorffii Desf. (Caesalpiniaceae)													
64a	79a	–	29a	33a	–	20a	12a	–	314a	363a	–	0.71a	0.68a
Euterpe edulis Mart. (Arecaceae)													
87a	102a	69a	13a	12a	10a	76a	61a	50a	426a	411a	517a	0.46a	0.40a
Guarea kunthiana A. Juss. (Meliaceae)													
61a	57a	41a	20a	19a	15a	30a	37a	21a	547a	602a	726a	0.50a	0.51a
Holocalyx balansae Micheli (Fabaceae)													
67a	88a	61a	11a	12a	13a	41a	46a	12b	602a	598a	679a	0.39a	0.37a
Hymenaea courbaril L. (Caesalpiniaceae)													
47a	42a	–	16a	18a	–	12a	12a	–	335a	431a	–	0.50a	0.49a
Ocotea indecora Schost. (Lauraceae)													
48a	61a	44a	15a	13a	14a	40a	36a	34a	409a	436a	497a	0.43a	0.48a
Ormosia arborea (Vell.) Harms (Mimosaceae)													
–	–	–	–	–	–	0	0	–	359a	347a	–	0.25a	0.29a
Plinia rivularis (Cambess.) Rotman (Myrtaceae)													
79a	77a	60a	18a	19a	19a	6a	10a	14a	363a	339a	378a	0.34a	0.35a
Sorocea bonplandii (Baill.) Burger, Lanj. & Boer (Moraceae)													
69a	56a	41a	16a	16a	14a	17a	21a	12a	422a	431a	441a	0.35a	0.32a
Trichilia casaretti C. DC. (Meliaceae)													
89a	74a	–	17a	15a	–	12a	7a	–	265a	363a	–	0.61a	0.53a
Trichilia claussenii C. DC. (Meliaceae)													
83a	91a	80a	11a	11a	8a	26a	22a	11b	326a	351a	367a	0.26a	0.28a
Trichilia elegans A. Juss. (Meliaceae)													
108a	121a	80a	9a	8a	6a	8a	8a	2b	265a	234a	328a	0.41a	0.42a

Means followed by same letter are not significantly different by a Tukey–Kramer's HSD test at 0.05 level, for each group of measurements.

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