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Mycorrhizal response and successional status in 80 woody species from south Brazil

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Abstract: Arbuscular mycorrhizal (AM) fungi colonization and response were studied in seedlings of 80 native woody species belonging to different successional groups from the Tibagi River Basin, Paraná State, south Brazil. This study includes data from 43 native woody species already published. The results with 80 species did not differ from the results of the 43 species. The experiment was carried out in a greenhouse in plastic bags filled with a mix of subsoil (85%) and sand (15%), inoculated or not with spores of native AM fungi obtained from rhizosphere soil of different native tree species in an area with natural vegetation dominated by woody pioneer species. The successional groups were represented by 16 pioneer, 20 early secondary, 29 late-secondary and 15 climax species. The AM response and colonization in the greenhouse were 5.9 and 4.2 times greater in the early successional species than in the late-successional species, respectively. Seedlings of 49 woody species were collected in the interior under the canopy of the tropical forest of the Mata dos Godoy State Park and in a cleared area dominated by woody pioneer species. The percentage of AM colonization in the field was 54.9, 40.4, 7.2 and 3.1 for the pioneer, early secondary, late-secondary and climax species, respectively. The response to AM inoculation was strongly and directly related to AM colonization in the greenhouse and field and inversely related to seed weight. The AM colonization in the greenhouse was strongly and directly related to AM colonization in field. The late-successional species showed lower AM colonization and response than early successional species. The accentuated mycotrophism of the early successional species may be involved in their establishment, growth, survival and early forest structuring on low-fertility soils.

Key Words: inoculation, mycorrhizal colonization, native woody species, revegetation, root symbiosis, soil restoration, succession

INTRODUCTION

Tropical deforestation reduces species diversity, increases forest fragmentation and permits the establishment of permanent agriculture, pasture and extensive areas of degraded land. This leads to the loss of biodiversity, decline in soil fertility, deterioration of soil physical and biological properties which are serious obstacles to natural forest regeneration and reforestation programmes (Brown & Lugo 1994). Most of the areas designated for reforestation are made up of low-fertility soil with low inoculum potential of microorganisms beneficial to plants such as the arbuscular mycorrhizal (AM) fungi (Janos 1996). Soil erosion removes the superficial layer and causes a sharp decline in the number of active AM fungi propagules and the root colonization rate (Abbott & Robson 1991). Knowledge about the ability of plant species to form symbiosis with AM fungi is very important for reforestation success and indicates the need for inoculum in plants cultivated in forest nurseries (Perry *et al*. 1987).

AM fungi increase the mineral uptake by plants and contribute to nutrient conservation and maintenance and functioning of ecosystems (Miller & Jastrow 1994). The effect of the AM fungi on plant growth is greater in soils with low P availability (Koide 1991). Plants colonized by AM have increased root and shoot dry matter and greater P concentrations in the host plant tissues (Smith & Gianinazzi-Pearson 1988). AM fungi are predominant in woody plants in the tropics. Janos (1980, 1983) suggested that, for native Costa Rican species, AM fungi are essential for growth especially for those of the mature forest. In an earlier paper Zangaro *et al*. (2000) studied the mycorrhizal response of 43 native woody species, and here we report on 80 species as an extension of the earlier study. The early successional woody species were more strongly colonized and responsive to AM fungi than late-successional species of the mature forest. These results corroborate Siqueira *et al*. (1998) for tropical woody species from south-east Brazil.

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Table 1. Traits for the early and late-successional native woody species.

Parameter	Early successional species	Late-successional species
Shade	Intolerant	Tolerant
Light demand	High	Low
Photosynthetic rate	High	Low
Growth rate	High	Low
Nutritional demand	High	Low
Woody density	Low	High
Flowering time	Early and long	Late and short
Life span	Short	Long
Leaf turnover	Fast	Slow
Seed size	Small	Large
Cotyledon	Photosynthetic	Non-photosynthetic
Root/shoot ratio	Low	High
Regeneration	Seed banks	Seedling banks
Recruitment	Large gaps and forest edge	Small gaps and shade
Geographic range	Wide	Narrow
Plasticity	High	Low

The present study reports on the role of AM fungi symbiosis of 80 native woody species belonging to different successional groups, to answer the following question: is mycorrhizal symbiosis important to early woody succession on the degraded lands in the south of Brazil?

METHODS

The native forest species were placed in traditional successional categories: pioneer, early secondary, late secondary, and climax, according to the general characteristics established by various authors (Barbosa 1997, Bazzaz 1991, Budowski 1965, Chagas e Silva & Soares-Silva 2000, Denslow 1980, Ferretti *et al*. 1995, Kageyama & Viana 1989, Swaine & Whitmore 1988, Whitmore 1991).

Pioneer and early secondary native woody species dominate the earlier stages of succession and are denominated here as early successional species. Late-secondary and climax species dominate the later stages of succession in mature forest and are denominated here as late-successional species. Traits of the early and late-successional species are shown in Table 1, according to authors given above.

The probable position in the different successional groups of the 80 native woody species studied was determined according to studies by Chagas e Silva & Soares-Silva (2000), Dias *et al*. (1998), Ferretti *et al*. (1995), Gandolfi *et al*. (1995), Kageyama (1992), Leitão-Filho (1993) and Salis *et al*. (1994). The criteria used to classify the native woody species in ecological groups are not standardized among the above authors. Based on this literature, we searched for the successional status of the 80 species and eight native woody species included in Zangaro *et al*. (2000) were reclassified in different ecological groups in this study. Analyses of variance and correlation were used to analyse data and treatment means were compared by Tukey–Kramer's test at $\alpha = 0.05$. The levels of significance of the correlation analysis were adjusted with the Bonferroni procedure.

Experimental details are from Zangaro *et al*. (2000).

RESULTS

Seedling growth was affected by AM inoculation, species and by successional group. Pioneer and early secondary species were highly influenced by the AM fungi when compared with late-secondary and climax species (Table 2). AM colonization was only found in inoculated seedlings. All pioneer species responded significantly to the AM fungi inoculation. Amongst early secondary species, only *Anadenanthera macrocarpa* did not respond significantly in root dry biomass. *Colubrina glandulosa* and *Poecilanthe parviflora* showed AM colonization below 50% in the greenhouse. In contrast, amongst late-secondary species, only three, *Campomanesia xanthocarpa*, *Tabebuia roseo-alba* and *Vitex montevidensis* showed significant increase in seedling height, root and shoot dry biomass. All climax species showed AM colonization below 30% and weak response to AM fungi inoculation. The number of species with positive response to AM inoculation diminished with the advance among the successional groups.

The time to cotyledon loss of the non-inoculated plants increased with the advance among the successional groups, where the late-secondary species differed significantly ($P < 0.05$) from the climax species and those from the early secondary and pioneer species, which were similar (Table 3). The seedling height and root and shoot dry matter decreased with the advance among the successional groups, where the pioneer species differed significantly ($P < 0.05$) from the late-secondary and climax species, however the early secondary species did not differ significantly from any other successional group. The response to inoculation and AM colonization in the greenhouse decreased with the advance among the successional

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Table 2. Identification, successional groups and growth characteristics of the native woody species from south Brazil, inoculated and non-inoculated with AM fungi. [a] Time to loss of cotyledons of the non-inoculated seedling. [b] Ratio between inoculated and non-inoculated plants. AM col = AM fungi colonization.

Coty-[a] ledons fall (wk)	Height[b]	Root[b] dry matter	Shoot[b] dry matter	Res-ponse (%)	AM col. green-house (%)	AM col. in field (%)	Seed fresh weight (mg)	Root[b] shoot ratio	Relative[b] growth rate
Pioneer									
Aegiphila sellowiana Cham. (Verbenaceae)									
7	2.96***	10.9***	28.7***	96.5	86.6	54.2	42.0	0.51***	2.89***
Cecropia glaziovii Snethl. (Cecropiaceae)									
4	14.0***	165***	75.2***	93.3	80.2	60.2	1.86	0.47***	2.45***
Cecropia pachystachya Trec. (Cecropiaceae)									
3	17.4***	38.0***	77.5***	98.7	80.0	69.3	1.28	0.49***	4.01***
Cestrum intermedium Semdth. (Solanaceae)									
3	2.7**	36.0***	6.3***	97.6	66.7	51.1	5.65	0.57**	2.59***
Citharexylum myrianthum Cham. *(Verbenaceae)									
6	3.5***	25.0***	50.5***	98.0	92.0		75.2	0.38***	3.58***
Croton floribundus Spreng. (Euphorbiaceae)									
4	3.4***	9.4***	25.9***	94.0	80.0	53.7	34.1	0.35***	2.27***
Croton urucurana Baill. (Euphorbiaceae)									
4	5.7***	52.3***	305***	99.4	72.1		6.99	0.17***	4.20***
Mimosa scabrella Benth. (Mimosaceae)									
5	7.3***	47.1***	79.9***	98.7	72.2		12.0	0.64**	3.69***
Piptocarpha axillaris (Less.) Baker (Asteraceae)									
5	7.2***	62.7***	108***	99.0	97.6		0.9	0.52***	2.98***
Schinus terebinthifolius Raddi (Anacardiaceae)									
4	105***	16.6***	66.2***	97.3	63.4	53.9	16.8	0.26***	3.12***
Senna macranthera (Collad.) H. S. Irwin & Barneby (Caesalpiniaceae)									
4	4.5**	2.0*	13.7***	82.7	77.8	57.2	39.7	0.19***	2.81***
Solanum argenteum Dun. (Solanaceae)									
3	10.8***	5.6***	126***	98.8	81.2	49.4		0.51***	4.52***
Tabernaemontana australis (Müll. Arg.) Miers (Apocynaceae)									
5	3.4***	15.8***	20.9***	95.2	83.1	38.8	64.5	0.48***	2.87***
Trema micrantha (L.) Blume (Ulmaceae)									
3	13***	165***	308***	99.5	80.0	64.6	3.98	0.63***	6.33***
Xylosma ciliatifolium (Clos) Eichler (Flacourtiaceae)									
5	4.4***	27.3**	25.4***	96.0	81.8	52.1	9.2	0.62**	5.12***
Xylosma pseudosalzmannii Sleumer (Flacourtiaceae)									
8	4.3***	20.0***	55.6***	98.2	88.0		17.1	0.45***	2.50***
Early secondary									
Albizia hassleri (Chodat) Burkart (Mimosaceae)									
8	2.6***	36.1***	35.0***	97.2	74.5		20.6	0.49***	1.98***
Anadenanthera colubrina (Vell.) Brenan (Mimosaceae)									
7	2.6***	3.7*	4.5**	78.4	84.6		66.6	0.54***	2.57***
Anadenanthera macrocarpa (Benth.) Brenan (Mimosaceae)									
7	1.9*	1.3 ns	2.1*	30.3	58.2		114.6	0.67**	1.18*
Bastardiopsis densiflora (Hook. & Arn.) Hassl. (Malvaceae)									
10	5.8***	144***	270***	99.6	76.7		8.9	0.51***	2.59***
Bauhinia forficata Link (Caesalpiniaceae)									
5	2.1*	1.9*	3.7**	52.8	84.1		55.2	0.45***	1.96**
Casearia sylvestris Sw. (Flacourtiaceae)									
5	6.1***	24.5***	77.2***	98.7	68.9	44.9	14.9	0.56***	1.65**
Colubrina glandulosa Perk. (Rhamnaceae)									
6	3.0**	2.6*	2.6**	53.1	48.3	24.7	20.9	0.68***	3.12***
Cordia trichotoma (Vell.) Arrab. ex Steud. (Boraginaceae)									
7	4.3***	83.9***	54.7***	98.0	79.0		28.0	0.49***	2.56***

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Table 2. *Continued*

Coty-[a] ledons fall (wk)	Height[b]	Root[b] dry matter	Shoot[b] dry matter	Res-ponse (%)	AM col. green-house (%)	AM col. in field (%)	Seed fresh weight (mg)	Root[b] shoot ratio	Relative[b] growth rate
Eugenia uniflora L. (Myrtaceae)									
10	2.2**	6.9**	4.7**	90.5	82.1	39.6	170.1	0.56***	2.87***
Guazuma ulmifolia Lam. (Sterculiaceae)									
3	13.9***	30.3***	159***	98.9	75.5	53.8	5.45	0.19***	3.53***
Heliocarpus americanus L. (Tiliaceae)									
5	10.3***	22.5***	171***	99.8	80.9	37.9	6.99	0.26***	3.11***
Lafoensia pacari A. St. Hil. (Lythraceae)									
8	4.6***	24.9***	43.1***	97.7	93.4		29.2	0.57***	2.54***
Lonchocarpus campestris Mart. & Benth. (Fabaceae)									
6	1.6*	2.4*	6.5**	73.7	70.4		242.8	0.48***	1.73***
Luehea candicans Mart. (Tiliaceae)									
5	5.3**	5.2**	20.6***	92.6	75.2	48.7	5.85	0.41***	1.69***
Luehea divaricata Mart. (Tiliaceae)									
6	7.0***	38.8***	17.5***	98.5	93.6		8.71	0.26***	1.98***
Parapiptadenia rigida (Benth.) Brenan (Mimosaceae)									
4	1.4*	4.0**	2.5*	59.4	67.4	22.3	32.1	0.48***	1.49**
Poecilanthe parviflora Benth. (Fabaceae)									
8	1.7**	4.6***	3.9***	74.8	48.0		419.5	0.59***	3.21***
Pseudobombax grandiflorum (Cav.) A. Robyns (Bombacaceae)									
8	2.4***	10.5***	8.9***	88.2	73.8		54.7	0.68***	1.59***
Sebastiania commersoniana (Baill.) Smith & Downs (Euphorbiaceae)									
8	2.4*	4.3**	10.9***	87.1	72.2	51.6	12.9	0.42***	1.57**
Tabebuia chrysotricha (Mart. ex DC.) Standl. (Bignoniaceae)									
10	3.5***	33.6***	6.1***	82.8	65.5		11.8	0.50***	2.54***
Late secondary									
Acacia polyphylla DC. (Mimosaceae)									
8	1.8*	0.9 ns	1.4 ns	25.4	17.1		78.6	0.52**	1.13 ns
Astronium graveolens Jacq. (Anacardiaceae)									
9	1.1 ns	1.1 ns	1.3 ns	17.3	43.1	11.7	42.4	0.93 ns	1.14 ns
Bougainvillea spectabilis Willd. (Nyctaginaceae)									
12	1.0 ns	1.1 ns	1.0 ns	0	1.3	0	119.9	1.07 ns	1.01 ns
Campomanesia xanthocarpa O. Berg (Myrtaceae)									
8	2.3***	8.6**	10.8***	90.8	85.0	27.3	72.1	0.54***	2.10***
Cedrela fissilis Vell. (Meliaceae)									
7	1.0 ns	0.9 ns	0.9 ns	0	31.6	9.8	45.0	1.04 ns	0.97 ns
Centrolobium tomentosum Guill. ex Benth. (Fabaceae)									
14	1.9*	1.8 ns	1.6 ns	44.6	26.5	7.2	4421	0.98 ns	1.12 ns
Chorisia speciosa St. Hil. (Bombacaceae)									
11	0.7*	0.8 ns	0.7 ns	0	42.3	8.7	230.4	1.11 ns	0.96 ns
Cordia ecalyculata Vell. (Boraginaceae)									
16	1.3 ns	1.7 ns	2.2*	41.5	32.1		292.4	0.91 ns	1.28*
Enterolobium contortisiliquum (Vell.) Morong (Mimosaceae)									
10	0.9 ns	0.9 ns	1.0 ns	0	14.5		316.3	0.98 ns	0.96 ns
Ficus guaranitica Schodat (Moraceae)									
4	1.6*	1.1 ns	1.4*	26.9	15.9	2.1	0.41	0.73 ns	1.03 ns
Genipa americana L. (Rubiaceae)									
15	1.1 ns	0.9 ns	1.0 ns	0	2.5		99.3	0.84 ns	0.98 ns
Inga sessilis (Vell.) Mart. (Mimosaceae)									
9	1.4*	1.6 ns	1.4*	27.8	31.1		408.3	0.72*	0.92 ns
Inga striata Benth. (Mimosaceae)									
10	1.1 ns	1.2 ns	1.1 ns	16.2	17.1	4.2	580.4	0.78 ns	0.99 ns
Jacaranda mimosaefolia D. Don (Bignoniaceae)									
10	0.9 ns	1.0 ns	0.9 ns	0	23.5		6.84	1.12 ns	0.98 ns

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Table 2. *Continued*

Coty-[a] ledons fall (wk)	Height[b]	Root[b] dry matter	Shoot[b] dry matter	Res-ponse (%)	AM col. green-house (%)	AM col. in field (%)	Seed fresh weight (mg)	Root[b] shoot ratio	Relative[b] growth rate
Jacaranda puberula Cham. (Bignoniaceae)									
9	1.5*	1.3 ns	1.3 ns	26.6	32.1	12.1	6.36	0.87 ns	1.06 ns
Jacaratia spinosa (Aubl.) A. DC. (Caricaceae)									
7	1.0 ns	1.2 ns	1.2 ns	16.2	12.7	0	28.2	1.01 ns	1.12 ns
Lonchocarpus muehlbergianus Hassl. (Fabaceae)									
11	0.9 ns	0.9 ns	0.8 ns	0	10.6	3.3	841.7	1.08 ns	0.97 ns
Machaerium minutiflorum Tul. (Fabaceae)									
9	0.9 ns	0.9 ns	1.0 ns	0	27.0		229.4	0.84 ns	1.05 ns
Machaerium stipitatum (D.C.) Vogel (Fabaceae)									
8	1.1 ns	1.1 ns	1.0 ns	3.5	12.3	3.1	45.8	1.06 ns	1.01 ns
Ocotea puberula (Reich.) Ness (Lauraceae)									
8	1.5 ns	1.9 ns	2.3*	44.5	33.6	8.7	370.9	0.80 ns	1.12 ns
Peltophorum dubium (Spreng.) Taub. (Caesalpiniaceae)									
9	0.7*	0.6*	0.5*	0	0	0	46.0	1.02 ns	0.91 ns
Prunus sellowii Hoehne (Rosaceae)									
5	1.0 ns	0.7 ns	0.9 ns	0	7.4	0.8	230.1	0.78 ns	0.96 ns
Pterogyne nitens Tul. (Caesalpiniaceae)									
8	1.0 ns	0.8 ns	0.9 ns	0	4.2	1.1	98.0	0.95 ns	1.10 ns
Ruprechtia laxiflora Meisn. (Polygonaceae)									
8	0.9 ns	0.7*	0.7*	0	2.9	0	13.0	1.12 ns	0.95 ns
Strichinus brasiliensis (Spreng.) Mart. (Styracaceae)									
14	1.3 ns	1.2 ns	1.5*	26.0	12.3	5.1	700.8	0.85 ns	1.11 ns
Syagrus romanzoffiana (Cham.) Glassm. (Arecaceae)									
17	0.9 ns	0.7 ns	1.2 ns	0	2.5	1.9	1383	1.13 ns	1.00 ns
Tabebuia roseo-alba (Ridl.) Sand. (Bignoniaceae)									
7	3.3**	30.1***	42.3***	97.6	83.6		6.4	0.61***	1.81***
Vitex montevidensis Cham. (Verbenaceae)									
9	1.8*	3.3*	9.5**	71.3	53.2	37.3	158.1	0.34***	1.75**
Zeyheria tuberculosa (Vell.) Bureau (Bignoniaceae)									
7	1.0 ns	0.8 ns	0.6 ns	0	0		76.1	0.98 ns	0.97 ns
Climax									
Actinostemon concolor (Spreng.) Müll. Arg. (Euphorbiaceae)									
13	1.4*	1.3 ns	1.6*	30.6	26.5	4.1		0.84 ns	1.12 ns
Aspidosperma polyneuron Müll. Arg. (Apocynaceae)									
11	1.2 ns	1.1 ns	1.1 ns	0	0	0	85.1	0.77 ns	1.01 ns
Cariniana estrellensis (Raddi) Kuntze (Lecythidaceae)									
20	1.1 ns	1.7 ns	1.2 ns	17.6	12.3		79.6	1.12 ns	0.92 ns
Copaifera langsdorffii Desf. (Caesalpiniaceae)									
12	0.9 ns	1.1 ns	1.1 ns	8.9	15.8		501.0	0.96 ns	1.01 ns
Euterpe edulis Mart. (Arecaceae)									
14	1.1 ns	1.2 ns	1.2 ns	11.4	14.3	6.5	1134	0.87 ns	1.14 ns
Guarea kunthiana A. Juss. (Meliaceae)									
16	1.2 ns	1.1 ns	1.0 ns	6.3	4.8	1.3	1324	1.01 ns	1.00 ns
Holocalyx balansae Micheli (Rabaceae)									
15	1.1 ns	0.9 ns	1.3 ns	13.5	11.4	3.1	2621	0.95 ns	0.98 ns
Hymenaea courbaril L. (Caesalpiniaceae)									
9	0.9 ns	1.0 ns	0.9 ns	0	6.2		4093	0.98 ns	0.99 ns
Ocotea indecora Schost. (Lauraceae)									
14	1.3*	1.0 ns	1.2 ns	21.0	15.3	5.6	826	1.14 ns	1.02 ns
Ormosia arborea (Vell.) Harms (Mimosaceae)									
11	1.1 ns	1.3 ns	1.1 ns	13.8	22.6		716.8	1.22 ns	0.95 ns

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Table 2. *Continued*

Coty-[a] ledons fall (wk)	Height[b]	Root[b] dry matter	Shoot[b] dry matter	Res-ponse (%)	AM col. green-house (%)	AM col. in field (%)	Seed fresh weight (mg)	Root[b] shoot ratio	Relative[b] growth rate
Plinia rivularis (Cambess.) Rotman (Myrtaceae)									
13	1.2 ns	0.8 ns	1.1 ns	9.6	13.9	3.2	1284	1.00 ns	1.09 ns
Sorocea bonplandii (Baill.) Burg. Lanj. & Boer (Moraceae)									
14	1.2 ns	1.0 ns	1.1 ns	6.9	10.8	2.7	462.3	0.90 ns	1.03 ns
Trichilia casaretti C. DC. (Meliaceae)									
19	0.9 ns	0.8 ns	1.1 ns	6.6	12.1		324.1	0.85 ns	0.98 ns
Trichilia claussenii C. DC. (Meliaceae)									
16	1.0 ns	1.0 ns	1.1 ns	8.5	5.2	0.3	194.5	1.07 ns	1.02 ns
Trichilia elegans A. Juss. (Meliaceae)									
12	1.1 ns	1.0 ns	1.0 ns	3.5	22.1	4.1	289.4	1.1 ns	1.01 ns

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

Table 3. Means of values for the successional groups. The means were obtained of the values showed in Table 1.

Succe-ssional groups	Cotyle-dons fall (wk)	Height	Root dry matter	Shoot dry matter	Res-ponse	AM col. green-house (%)	AM col. in field (%)	Seed weight (Mg)	Root shoot ratio	Relative growth rate
P	4.56 [c]	13.1 [a]	43.7 [a]	85.5 [a]	96.4 [a]	80.2 [a]	54.9 [a]	22.1 [b]	0.45 [b]	3.49 [a]
ES	6.81 [c]	4.24 [ab]	24.3 [ab]	45.2 [ab]	82.6 [a]	73.6 [a]	40.4 [b]	66.5 [b]	0.49 [b]	2.27 [b]
LS	9.62 [b]	1.27 [b]	2.41 [b]	3.19 [b]	19.9 [b]	23.4 [b]	7.22 [c]	377 [a]	0.89 [a]	1.12 [c]
C	13.9 [a]	1.11 [b]	1.09 [b]	1.13 [b]	10.7 [b]	12.9 [b]	3.09 [c]	995 [a]	0.98 [a]	1.02 [c]

Means within a column followed by same superscript letter are not different by Tukey–Kramer HSD test at 0.05 level. P = pioneer, ES = early secondary, LS = late-secondary and C = climax.

groups. The pioneer and early secondary species did not differ but differed significantly ($P < 0.05$) from the late-secondary and climax species, which were similar. The AM colonization in the field and relative growth rate decreased with the advance of the successional groups, where the pioneer species differed significantly ($P < 0.05$) from the early secondary species and those from the late-secondary and climax species, which were similar. The seed weight and root/shoot ratio increased with the advance among the successional groups, where the pioneer and early secondary species did not differ but differed significantly ($P < 0.05$) from the late-secondary and climax species, which were similar (Table 3).

The cotyledon fall of the non-inoculated plants was inversely related to the response to inoculation in height and root and shoot dry matter. AM colonization in the greenhouse and field and relative growth rate were also inversely related with cotyledon fall but were positively related to the seed weight and root/shoot ratio (Table 4). The height of the seedlings was positively related to the shoot dry matter, inoculation response, AM colonization in the greenhouse and field and relative growth rate, and inversely related to the root/shoot ratio. The root and shoot dry matter were positively related to the response to inoculation, AM colonization in the greenhouse and field and relative growth rate, and inversely related to the root/shoot ratio. The response to inoculation was positively related to the AM colonization in the greenhouse and field and relative growth rate, and inversely related to the seed weight and root/shoot ratio. The AM colonization in the greenhouse was positively related to the AM colonization in field and these were positively related to the relative growth rate but inversely related to the seed weight and root/shoot ratio. The seed weight was positively related to the root/shoot ratio but inversely related to the relative growth rate. The root/shoot ratio was inversely related to the relative growth rate (Table 4).

The concentration and content of the macronutrients in the leaves of the pioneer and early secondary species increased with inoculation (Table 5). When non-inoculated, the pioneers and early secondary species had lower concentrations of the macronutrients than the species belonging to late-successional groups. With inoculation, the P, Ca and K concentrations increased 2.3 and 1.7 times in the pioneer and early secondary species, but did not increase in the other groups, which caused the disappearance of the differences among all the successional groups for P and Ca, and a significant increase in the K concentration in the pioneer and early secondary species when compared with the late-secondary and climax species. Inoculation significantly increased the content of minerals in the pioneer and early secondary species, but there was no difference in the late-secondary and climax species. The pioneer, early secondary and late-secondary

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Table 4. The Pearson correlation coefficients (r) among different parameters of the inoculated and uninoculated native woody species. Level of significance corrected with the Bonferroni procedure. AM col. = AM fungi colonization.

	Height	Root dry matter	Shoot dry matter	Response	AM col. green-house	AM col. in field	Seed weight	Root shoot ratio	Relative growth rate
Cotyledon fall	–0.29*	–0.35**	–0.40***	–0.62***	–0.65***	–0.72***	0.41***	0.67***	–0.61***
Height		0.19ns	0.26*	0.31*	0.23ns	0.39**	–0.11ns	–0.34**	0.33**
Root dry matter			0.73***	0.53***	0.48***	0.55***	–0.19ns	–0.38**	0.58***
Shoot dry matter				0.54***	0.47***	0.60***	–0.19ns	–0.48***	0.70***
Response					0.94***	0.94***	–0.32**	–0.86***	0.79***
AM col. greenhouse						0.93***	–0.37**	–0.83***	0.74***
AM col. in field							–0.36**	–0.85***	0.82***
Seed weight								0.36**	–0.29*
Root/shoot ratio									–0.66***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

Table 5. Leaf nutrient concentrations and contents of pioneer (P), early secondary (ES), late secondary (LS) and climax (C) of woody seedling species from south Brazil inoculated (inoc) and non-inoculated (n-inoc) with AM fungi. Nutrient concentration ratio between inoc / n-inoc: NCR[1]. Nutrient content ratio between inoc / n-inoc: NCR[2].

Successional	Nutrient concentration (mg 100 mg^{-1})			Nutrient content (mg per leaf)		
groups	n-inoc	inoc	NCR[1]	n-inoc	inoc	NCR[2]
Phosphorus						
P	0.06 $^{b\,B}$	0.16 $^{a\,A}$	2.67	0.31 $^{b\,B}$	5.29 $^{a\,A}$	17.1
ES	0.08 $^{b\,B}$	0.14 $^{a\,A}$	1.75	0.64 $^{b\,B}$	4.79 $^{a\,A}$	7.48
LS	0.13 $^{a\,A}$	0.16 $^{a\,A}$	1.23	2.34 $^{a\,A}$	3.21 $^{a\,A}$	1.37
C	0.15 $^{a\,A}$	0.14 $^{a\,A}$	0.93	1.08 $^{a\,B}$	1.18 $^{a\,B}$	1.09
Calcium						
P	0.31 $^{b\,B}$	0.59 $^{a\,A}$	1.90	1.67 $^{b\,B}$	19.6 $^{a\,A}$	11.7
ES	0.37 $^{b\,B}$	0.53 $^{a\,A}$	1.43	3.81 $^{b\,B}$	15.7 $^{a\,A}$	4.12
LS	0.53 $^{a\,A}$	0.56 $^{a\,A}$	1.06	10.1 $^{a\,A}$	14.1 $^{a\,A}$	1.39
C	0.60 $^{a\,A}$	0.60 $^{a\,A}$	1.00	4.72 $^{a\,B}$	5.67 $^{a\,B}$	1.20
Potassium						
P	0.71 $^{b\,B}$	1.57 $^{a\,A}$	2.21	4.51 $^{b\,C}$	54.6 $^{a\,A}$	12.1
ES	0.82 $^{b\,B}$	1.45 $^{a\,A}$	1.77	10.2 $^{b\,A}$	39.4 $^{a\,B}$	3.86
LS	1.12 $^{a\,A}$	1.17 $^{a\,B}$	1.04	15.3 $^{a\,A}$	20.7 $^{a\,B}$	1.35
C	1.11 $^{a\,A}$	1.19 $^{a\,B}$	1.07	8.11 $^{a\,B}$	9.41 $^{a\,C}$	1.16

Means followed by the same superscript letter (small in row and capital in column) are not different by Tukey–Kramer HSD test at 0.05 level.

species accumulated similar amounts of P and Ca, which were significantly greater than those of the climax species. Regarding K, the pioneers accumulated greater quantities than the early and late-secondary species and even more than the climax species. In presence of AM fungi, the nutrient content for all the successional groups showed that the accumulation potential for the three elements was, on average, 13.6 times for the pioneer species, 5.2 times for the early secondary species, 1.4 times for the late-secondary and 1.2 times for the climax species.

DISCUSSION

The results with 80 native woody species corroborate the results of Zangaro *et al*. (2000). The pioneer and early secondary woody species inoculated with AM fungi had high AM colonization and responsiveness, high relative growth rate, low root/shoot ratio and high P concentration in the leaves. These species have a slow growth rate, high root/shoot ratio and low P content in the leaves in the absence of AM fungi, which are characteristics of a manifestation of the great dependence on the AM fungi in low-fertility soils (Smith & Gianinazzi-Pearson 1988). AM-colonized plants frequently have higher P concentrations in the tissues than non-colonized plants and allocate a smaller proportion of the biomass to the root (Smith & Read 1997). The inverse correlation between the seed weight and AM colonization and responsiveness and the direct correlation with the time of cotyledon fall of non-inoculated plants indicates that, in soils with low nutrient availability, the initial growth of the seedlings which have small seeds is only possible when they are AM colonized. The seeds of the early successional species have small nutritional reserves and at 3–10 wk of slow growth the

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seedlings which are not AM inoculated lose their cotyledons, stop growing and most die at 4–6 mo of age. The seedlings become dependent on the uptake capacity of their roots to obtain minerals from the soil with the emptying of the reserves in the cotyledons and the absence of symbionts. The interruption in growth after the fall of the cotyledons, the low concentration and accumulation of the nutrients in the leaves and low survival, indicate limited uptake capacity in the roots for nutrient acquisition by the pioneer and early secondary species under stress conditions, such as in poor soil and without AM colonization. Seedlings of pioneer and early secondary species inoculated with AM fungi had extremely fast growth, increase in mineral concentration and content and the cotyledons of most of the species remained linked and active until the end of the experiment, showing the importance of AM colonization in improving the mineral nutrition and increasing the survival of all the early successional species.

High rates of P uptake are necessary to support the extremely fast growth of the tropical species which belong to the initial phases of tree succession and the high dependence and mycorrhizal colonization generally are associated with species which have fast growth and high P demands (Koide 1991). The problem of low nutritional content and of P in their small seeds (Allsopp & Stock 1992) and in the internal pools of the seedlings may be solved by quick mycorrhizal colonization, giving adequate P supply to the seedlings. The high demand for P may also be necessary when the plant is recruited (Fitter *et al*. 1996), or during flower and seed production (Koide 1991). The abundant content (accumulation) of P in the tissues of the early successional species colonized by the AM fungi, can be a great advantage to these plants, where the nutrient pool can be mobilized in the periods of greatest demand or when uptake is prevented (Smith & Read 1997). The high growth rates of the AM-colonized pioneer and early secondary species, allied to adaptation to environments with high light intensity, can represent the production of high quantities of photosynthate, where some can be available for the symbiont as a strategy for the development of colonization and sporulation, and for enhanced nutrient acquisition.

The late-secondary and climax species had heavy seeds which hold large reserves, low AM colonization and responsiveness, low growth rate, high root/shoot ratio, and the AM inoculum did not modify the concentration or accumulation of minerals in their leaves nor did it prolong the persistence time of the cotyledons. These results indicate that the large seed reserve was extremely important for the seedling nutrition and promoted their initial growth, which may justify the low responsiveness and AM colonization in the greenhouse and the field. The loss of the cotyledons of the late-successional species decreased the quantity of minerals inside the plants, which could stimulate AM colonization as a form of obtaining a continuous source of minerals in soils where these are not easily available. However, Zangaro *et al*. (2000) observed that after cotyledon fall from five woody species of the late stages of succession no increase in the AM colonization or responsiveness was found. The low performance among most of the late-secondary and climax species and the limited capacity of the AM fungi to provide an increase in the growth of these species in low-fertility soil may be due to evolutionary factors, such as the low demand for minerals due to their slow growth and/or for the low supply of carbohydrates to the AM fungi.

The pioneer and early secondary woody species are hosts with a high degree of AM mycotrophy, which makes these symbionts important components of the roots of these trees, helping them in their establishment, growth and survival, especially in the most critical phases, which are the initial growth phases of the plants in the soils with few available nutrients. The high degree of mycotrophy observed in these species may explain their great aggressiveness during establishment in open and disturbed areas, and the AM may be the main biotic factor for the establishment and progress of succession on low-fertility soils (Zangaro *et al*. 2000). The percentage of AM colonization in the field was strongly correlated with colonization in the greenhouse and both were correlated with responsiveness. This indicates the functionality of the symbiosis in the localities with native woody species, enabling the use of the pioneer and early secondary AM-colonized species in programmes of revegetation.

Disturbance disrupts the soil AM fungi and reduces the inoculum density for seedling establishment (Allen *et al*. 1998, Janos 1996). The desirable partnership among early successional woody species with AM fungi may be applied in programmes to recuperate degraded soils. The development of the fungus–plant combination may exercise at least three different effects in the disturbed environment. (1) The abundant growth of the roots and the shoots of AM-colonized pioneer and early secondary species leads to a quick immobilization of nutrients in the biomass of the plants and the symbiotic fungi, becoming one of the main mechanisms of nutrient conservation, allowing minimal losses and contributing to atmospheric CO_2 fixation (Allen 1991). (2) Shading produced by the early successional species hinders direct irradiation on the soil. The attenuation causes extremely important modifications in the microclimate through the reduction of heat fluctuation and increase in the relative humidity (Vazquez-Yanes & Orozco-Segovia 1985). (3) The rapid growth of the mycotrophic pioneer and early secondary species, provides production and later decomposition of a great quantity of litter, providing a continuous organic enrichment of the soil

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and improving the soil structure, which is guaranteed by the quick leaf production and root turnover (Uhl *et al*. 1982). Decomposition of soil organic matter produced by these species is important because of its critical role in the cycling of essential plant nutrients. This is regulated by the supply of above- and below-ground litter quality, quantity and timing of inputs as well as abiotic factors, such as soil moisture, temperature and texture (Chen & Stark 2000). In soil, microbial decomposition and microfaunal grazing of the organic matter release nutrients which become available for plant uptake (Degens *et al*. 2000). This provides the increase of the assimilable P in the soil (Jordan 1991). The maintenance of P solubility through decomposing litter produced by mycotrophic pioneer and early secondary woody species (with high P accumulation in the tissues) may have important implications for the mechanism of P mobilization and availability to take up this essential mineral.

These transformations above and below ground provided by early successional species colonized by AM fungi, can make the soil suitable for subsequent establishment and growth of seedlings that will go on to dominate in mature forests (late-successional species). These species show superficial absorbing roots that grow in forest soil and are adapted to low mineral requirements due to their slow growth and shaded habitats that contribute to low carbohydrate production. This may be the cause of the low AM fungi colonization and responsiveness in the greenhouse and field in these species. Low light intensity reduces the AM colonization because of the decrease of C fixation, leading to low exudation by the roots (Modjo *et al*. 1987). Plants colonized by AM can be more limited to the C than mineral nutrients in localities with low light intensity (Son & Smith 1988). Based on some studies of mineral cycling in the tropical forests of south-eastern and south Brazil, Zangaro *et al*. (2000) suggested that lack of nutrient conservation mechanisms before the fall of the plant constituents and the high rates of microbial litter decomposition lead to the high content of nutrients readily available for plant uptake in the soil. The high availability of P in soil reduces or can eliminate the AM colonization because of the low soluble carbohydrate concentration available to the AM fungi (Peterson & Farquhar 1996). Tropical late-successional woody species may have developed, through their evolutionary process, the ability to establish in forest conditions with little or no colonization by AM and therefore avoid the C cost of the root symbiosis.

In summary, woody species at the initial succession stages are expected to be essential partners of the AM fungi on low-fertility soil to obtain a continuous mineral source. Mycorrhizal symbiosis may be considered as being the main tool to be used in revegetation projects with early successional woody species. This combination may act directly in the recuperation of degraded soils, making the environment suitable for later installation of woody species belonging to the later succession stages, in the tropical environments of the south of Brazil.

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