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Dependency on arbuscular mycorrhizal fungi and responsiveness of some Brazilian native woody species

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Abstract Arbuscular mycorrhiza (AM) associations are of great importance in forest ecology and land rehabilitation in the tropics, but information on AM susceptibility, host dependence, and host responsiveness to the fungi is scarce. The present study was carried out under greenhouse conditions in a low-fertility soil with 29 woody species. There were very large differences between plant species in AM colonization, responsiveness to inoculation, mycorrhizal dependency and efficiency of phosphorus (P) uptake. All of these parameters were influenced by available soil P in solution. AM colonization ranged from zero in several non-mycotrophic species to >60% in the highly mycotrophic ones. Ten species (34% of the total) were found to be mycorrhiza-independent or non-mycotrophic, whereas the rest were highly to very highly dependent. The level of P above which there was no AM effect, defined here as the T′ value, allowed distinction between AM dependence and responsiveness of the host and was very efficient for separating species according to these traits. Mycorrhizal responsiveness and dependency were not related and some species were responsive to increased P in the soil solution only when mycorrhizal. Efficiency of P uptake was affected by AM and by P levels. Some species exhibited a high efficiency independent of AM, while others were very inefficient even at high P. Despite differences between species, in most cases AM growth enhancement was nutritionally mediated. Differences in AM responsiveness and dependency as well as the importance of these concepts for reforestation technology in the tropics are discussed.

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Introduction

Arbuscular mycorrhizae (AM) are highly evolved mutualistic associations determined by features of the host plant and mycorrhizal fungus and regulated by soil and environmental factors. These associations are important for plant growth, succession and the rehabilitation of deforested lands (Haselwandter and Bowen 1996; Janos 1996). They are also highly promising for inoculation of native woody species in low-fertility soils (Perry et al. 1987; Siqueira et al. 1998). Such associations consist of a very complex underground system in a tripartite interaction which determines the symbiotic effectiveness of the fungus and the responsiveness and dependency of the host plant. Even though the majority of plant species are naturally AM, neither plant benefits from this symbiosis nor the factors responsible for different degrees of mycorrhiza formation and host dependency are well defined and understood. It has been suggested that two independent sets of genes control the occurrence of colonization and the degree of benefit to the host from the symbiosis (Duc et al. 1989). Based upon their ability to growth with or without AM at different levels of soil-available phosphorus (P), plants can be separated into two-major groups: non-mycotrophic and mycotrophic. Mycotrophic plants are further distinguished according to their degree of dependence on the fungus, ranging from obligatory to facultative (Stahl 1900; Janos 1980b).

Because enhanced nutrient uptake is the major plant growth benefit, Baylis (1975) hypothesized that mycorrhizal dependency is largely controlled by root system architecture. Plants with coarsely branched roots and with few or no root hairs are expected to be more dependent on mycorrhiza than are plants with finely branched or fibrous roots. This hypothesis is broadly accepted, but not extensively demonstrated. Gerdemann (1975) de-

fined mycorrhizal dependency as "the degree to which a plant species is dependent on the mycorrhizal condition to produce its maximum growth at a given soil fertility". This definition is widely accepted by mycorrhizasts, but its appropriateness and usefulness has been debated. Janos (1988) considered mycorrhiza dependency as an intrinsic property of a plant species or genotype and defined it as the "host inability for growth without mycorrhizae at a given soil fertility." He considered the difference between mycorrhizal and non-inoculated plants "plant responsiveness". Thus, the mycorrhiza dependency indices of Menge et al. (1978) and Plenchette et al. (1983) measure plant responsiveness. However, use of the index of Menge et al. to make comparisons across species or growth conditions is rather difficult. Although the conceptual distinction between responsiveness and dependence is clear, they have often been confused. This distinction is a matter of concern considering that seedling survival is probably more strongly related to dependence than to responsiveness (Janos 1980a). Host responsiveness is affected by the environment (Brundrett 1991) and by plant–fungus relationships, given the varying effects of different fungus isolates on the same host genotype (Saggin-Júnior and Siqueira 1995). Responsiveness relates directly to host-growth rate and internal P demand (Koide 1991), while mycorrhiza dependency is more related to the nutrient absorption ability of a non-colonized plant than to its nutrient requirement. Plant independence of mycorrhiza arises when uptake by roots alone of mineral nutrients at a given level of supply is sufficient (Janos 1996). According to these concepts, an intrinsically slow-growing species cannot be highly responsive to mycorrhiza, but can exhibit high dependence on mycorrhiza for survival and continued growth if its roots do not supply its nutrient requirements.

The degree of plant dependence is of great practical and ecological interest, but studies of this plant attribute have been mostly conducted with cultivated herbaceous crops and rarely with tropical wild species. Habte and Manjunath (1991) suggested that critical P concentrations in soil solution are useful for classifying host species into AM-dependency categories. Although using the Plenchette et al. index (=responsiveness), these authors were dealing at least in part with mycorrhiza dependence, as they considered plant response to AM in deficient and sufficient P supply. Although it was suggested by Janos (1988) that the threshold level of P above which there is no response to AM (T′) measures plant mycorrhiza dependence, this has not been tested experimentally. In the present study, mycorrhiza formation and host responsiveness and dependence were evaluated for seedlings of 29 woody species in a low-fertility Oxisol in Brazil with manipulated P availability.

Materials and methods

Soil preparation

The present study was conducted in plastic pots filled with a clayey, low-fertility Dark Reddish-Latosol (Oxisol) in a glasshouse at the Soil Science Department of the Federal University of Lavras (UFLA), Minas Gerais State, Brazil. Surface soil (0–50 cm depth) was collected from a non-cultivated field with natural "Cerrado" vegetation, allowed to dry, crushed to pass through a 4-mm sieve and then mixed with dolomitic limestone to raise soil base saturation to 50% of CEC at pH 7.0. After liming, a basal nutrient solution was applied and was thoroughly mixed with the soil. Nutrients were supplied at the following rates of mg kg^{-1} of dry soil: 35 N, 100 K, 7.5 S, 5 Cu, 10 Zn, 10 B and 0.5 Mo. Nutrient solutions were prepared with analytical grade sources of the following: NH_4NO_3, KCl, $CuSO_4.5H_2O$, $ZnSO_4.7H_2O$, H_3BO_3 and $Na_2MoO_4.2H_2O$. The fertilized soil was transferred to a fumigation brick box and treated with Bromex (methyl bromide 98% + chloropicrin 2%) at a rate of 196 $ml \cdot m^{-3}$ of soil, according to the manufacturer's instructions. At this stage, soil had a water pH (1:2.5) of 5.4; P and K by Mehlich I extraction of 1 and 144 mg dm^{-3} of soil, respectively, and 17, 8 and 1 $mmol_c$ dm^{-3} of Ca, Mg and Al extractable by 1 M KCl solution (Thomas 1982). Extracted P and K were determined by colorimetry and flame photometry, respectively, and the other elements by titrimetry according to routine analysis in this laboratory.

Treatments

The experiment consisted of six treatments in a two-way factorial combination comprising 3 P levels and inoculated (AM) or non-inoculated (Ni) plants. These treatments with 10 replicates were tested separately on each species for a total of 60 pots per species. Thus, the total for all species in the experiment involved 1,740 pots, each containing 1.25 kg of dry soil with one seedling in each pot. Pots were arranged on glasshouse benches in a completely randomized design for each species. The three P levels in the soil solution (0.002 mg l^{-1} as the natural extractable P, 0.02 and 0.2 mg l^{-1}) were established as described by Manjunath and Habte (1990) using a KH_2PO_4 solution applied individually to each pot and thoroughly mixed with the soil. Before planting, extractable P (Mehlich I) concentrations were 1, 2 and 28 mg dm^{-3} of soil for the three P levels, respectively.

Uniform and healthy 1-week-old seedlings of 28 native species (Table 1) and *Leucaena leucocephala* were obtained from surface-disinfected seeds supplied by the Seed Laboratory of The Forest Science Department of UFLA. Seeds for all native species were collected from forest fragments on low-fertility soil in southeastern Brazil and germinated on germ-test paper or vermiculite according to seed size. Seed disinfection was by 1% sodium hypochlorite for 5 min followed by three washings with sterile water. Mycorrhizal inoculation was done at transplantation using 3 ml of whole-soil inoculum containing about 75 spores of *Glomus etunicatum* Becker and Gerdemann per ml of inoculum in addition to hyphae and mycorrhizal root pieces. This *G. etunicatum* isolate was originally from coffee in Varginha County and had been maintained in culture with *Brachiaria decumbens* for several years at the Glomalean culture collection of UFLA. For counting, spores were extracted according to Gerdemann and Nicolson (1963). The inoculum was mixed with soil in the planting hole. Ten milliliters of a mycorrhiza-free inoculum filtrate was applied per pot to all non-inoculated pots to standardize microbiota among treatments. The filtrate was prepared by passing soil inoculum infusion through a 53-µm sieve followed by filtering through paper filter. Mycorrhizal inoculum was obtained from a 5-month-old brachiaria grass pot culture. *G. etunicatum* was used in this study because of its widespread occurrence (Siqueira et al. 1989) and known effectiveness in several plant species tested in our laboratory, including wild woody species (Siqueira et al. 1998). Nodulating leguminous species were also inoculated with specific rhizobial peat-inoculum provided by Embrapa Agrobiologia, Seropédica, RJ. After transplanting to pots with treatments, plants were allowed to grow in a glasshouse until the experiment was terminated (Table 1). The growth period ranged from 58 to 262 days, according to the growth rate of each species. Plants were harvested when they reached a size considered adequate for transplanta-

Table 1 Scientific and common names, family or subfamily, successional group, growth period in the experiment, maximal plant height at harvest and seed weight of woody species used in the study. *Leucaena leucocephala* (Lam.) de Wit was included as a reference type species according to Habte and Manjunath (1991). The succession is according to Whitmore (1988)

Scientific name	Common name	Family or subfamily	Succession	Growth period (days)	Plant height (cm)	Mean seed weight (mg)
Platyciamus regnellii Benth.	Pau-pereira	Faboideae	Light demanding climax	186	18.3	625.00
Ormosia arborea (Vell.) Harms.	Tento	Faboideae	Light demanding climax	150	10.5	735.29
Caesalpinia peltophoroides Benth.	Sibipiruna	Caesalpinioideae	Light demanding climax	101	15.5	250.00
Platypodium elegans Vog.	Jacarandá-branco	Faboideae	Light demanding climax	120	30.7	1190.48
Macherium stipitatum (DC.) Vogel	Jacarandá-roxo	Faboideae	Shade tolerant climax	108	27.0	117.65
Myroxylon peruiferum L.f.	Óleo-bálsamo	Faboideae	Shade tolerant climax	160	13.0	632.91
Hymenaea courbaril L.	Jatobá	Caesalpinioideae	Light demanding climax	113	25.6	4761.90
Dendropanax cuneatum (DC.) Dcne.e Planch	Maria-mole	Araliaceae	Light demanding climax	195	5.1	5.09
Ceiba speciosa (St. Hil.) Gibbs e Semir	Paineira-rosa	Bombacaceae	Light demanding climax	75	25.3	169.49
Tabebuia roseo-alba (Rid.) Sandw.	Ipê-branco	Bignoniaceae	Light demanding climax	85	11.7	14.15
Solanum granuloso-leprosum Dun.	Gravitinga	Solanaceae	Pioneer	58	8.9	1.15
Lithraea molleoides (Vell.) Engl.	Aroeira-branca	Anacardiaceae	Pioneer	90	18.7	31.75
Trema micrantha (L.) Engler.	Trema	Ulmaceae	Pioneer	70	42.8	3.60
Luehea grandiflora Mart.	Açoita-cavalo	Tiliaceae	Light demanding climax	93	36.3	4.24
Senna spectabilis (A.DC.) Irw. Et Barn.	Cássia-carnaval	Caesalpinioideae	Light demanding climax	90	16.5	33.11
Croton floribundus Spreng	Capixingui	Euphorbiaceae	Pioneer	101	12.8	41.15
Tibouchina granulosa Cogn.	Quaresmeira-roxa	Melastomataceae	Light demanding climax	144	13.3	0.03
Cecropia pachystachya Trec.	Embaúba-cinzenta	Cecropiaceae	Pioneer	98	17.3	0.67
Cordia trichotoma (Vell.) Arrab. Ex. Steud	Louro	Boraginaceae	Light demanding climax	90	11.2	28.74
Leucaena leucocephala (Lam.) de Wit.	Leucena	Mimosoideae	Light demanding climax	136	20.4	54.17
Senna macranthera (Collad) Irw. Et Barn.	Fedegoso	Caesalpinioideae	Light demanding climax	120	23.2	55.56
Cedrella fissilis Vell.	Cedro	Meliaceae	Light demanding climax	96	38.2	35.84
Caesalpinia ferrea Mart.	Pau-ferro	Caesalpinioideae	Light demanding climax	97	51.4	97.28
Myrsine umbellata Mart.	Pororoca-branca	Myrsinaceae	Light demanding climax	111	11.4	16.86
Tabebuia impetiginosa (Mart.) Standl.	Ipê-roxo	Bignoniaceae	Light demanding climax	84	10.1	212.77
Sapindus saponaria L.	Saboneteira	Sapindaceae	Shade tolerant climax	116	28.9	769.23
Tabebuia serratifolia (Vahl) Nichols.	Ipê-amarelo	Bignoniaceae	Shade tolerant climax	129	16.3	67.11
Aspidosperma parvifolium A.DC.	Guatambu	Apocynaceae	Light demanding climax	180	20.1	167.22
Copaifera langsdorffii Desf.	Óleo-copaíba	Caesalpinioideae	Light demanding climax	262	21.3	454.55

tion (Table 1) of each species. During the pot experiment, soil moisture was maintained at 60–70% of the total soil pore space occupied by water through daily irrigation.

Measurements and statistics

Plants were harvested and dry weight determined after drying roots and shoots at 68°C in a forced air dryer for 1 week. Dry matter was used for calculating the mycorrhizal dependency index (=responsiveness) of Plenchette et al. (1983) and for P analysis. Using the best-fit regression lines for the response of mycorrhizal and non-mycorrhizal plants to P levels, the T′ value (Janos 1988) was estimated by the intersection of the two lines and considered as an indicator of host dependency. T′ as a measure of host dependency on mycorrhiza corresponds to the soil P level above which there was no mycorrhiza benefit.

Samples of lateral fresh root were randomly taken from all replicate plants to assess AM colonization and from only 4 plants of each treatment for root characteristic assessment. Fresh subsamples were mounted on microscope slides and used for measurements of root diameter and the diameter, length and density of root hairs along root segments. For AM colonization assessments, subsamples were clarified and stained according to Koske and Gemma (1989) and mounted on microscope slides with 24×50-mm cover slips. These were examined by light microscopy at 200× magnification; at least 150 intersections were analyzed for total, arbuscular, vesicular and hyphal colonization following the protocol of McGonigle et al. (1990). All heavily stained coenocytic hyphae were counted as AM fungus. Root hair incidence was assessed in cleared and stained root subsamples as used for AM colonization and expressed as percent of intersects with root hairs. After plant harvesting, soil samples were taken for spore extraction (Gerdemann and Nicolson 1963) and counting.

Plant dry tissue was ground to pass a 30-mesh screen and subjected to a nitro-percloric digestion for P analysis by colorimetry with molybdophosphate (Sarruge and Haag 1974). Efficiency of P uptake (EPU) was estimated according to Blair (1993) as the ratio of total P uptake per plant divided by total root dry weight. Growth rates (mg day^{-1}) were obtained by dividing maximal dry matter yield of a given species by its growth period. Daily P demand was calculated by multiplying plant growth rate by the mean P concentration in the shoot at a P level of 0.2 mg l^{-1} and expressed as mg day^{-1} of P. Treatment effects consisted of inoculation with AM fungi and P within species. Data were analyzed for each species as a completely randomized design using ANOVA procedures of the SANEST program (Federal University of Pelotas, RS). When treatment effects were significant ($P \leq 0.05$), means were compared with Tukey's test at 0.01. Regression analyses were carried out with TableCurve 3.01 (Jandel Corporation, USA). Pearson product-moment correlation coefficients between different parameters were examined using SigmaStat 1.0 (Jandel Corporation, USA) with Bonferroni-corrected probabilities.

Results

AM colonization parameters were affected by P level and varied markedly between plant species (Table 2). At the highest P level, colonization of several species was

Table 2 AM hyphal, arbuscular, vesicular and total colonization (as percent of root segments) and spore density (number per 50 ml) in woody species after growth in a low-fertility oxisol at three levels of phosphorus (P) in the soil solution (0.002, 0.02 and 0.2 mg l^{-1}). Means followed by the same letters in a row for each species are not different by Tukey's test at P=0.01 (*nf* not found – colonization present but assessment not possible because of difficulty in clearing and staining roots)

Species	Hyphal			Arbuscular			Vesicular			Total			Spore density		
	0.002	0.02	0.2	0.002	0.02	0.2	0.002	0.02	0.2	0.002	0.02	0.2	0.002	0.02	0.2
P. regnellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. arborea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. peltophoroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. elegans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. stipitatum	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	2a	1a
M. peruiferum	<1a	1a	1a	<1a	2a	1a	<1a	1a	<1a	1a	2a	2a	2a	3a	1a
H. courbaril	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	<1a	1a	<1a	<1b	<1b	8a
D. cuneatum	<1a	1a	<1a	<1a	2a	<1a	<1a	1a	<1a	<1a	2a	<1a	1a	7a	<1a
C. speciosa	<1b	2a	<1b	<1a	<1a	<1a	<1a	<1a	<1a	<1b	3a	<1b	3a	4a	3a
T. roseo-alba	3a	5a	1a	3a	5a	4a	<1a	1a	<1a	6a	10a	5a	0	0	0
S. gran.-leprosum	3ab	7a	2b	32a	49a	4b	15a	19a	2b	36a	57a	5b	2b	98a	1b
L. molleoides	<1a	2a	1a	3b	24a	9ab	<1a	<1a	1a	3b	27a	11ab	3a	4a	4a
T. micrantha	1ab	2a	<1b	9b	31a	1c	1b	7a	<1b	10b	32a	1c	4b	97a	6b
L. grandiflora	1a	2a	2a	6a	19a	9a	<1b	5a	1b	8a	21a	11a	18ab	58a	11b
S. spectabilis	nf	nf	nf	8b	63a	30a	<1a	<1a	1a	8b	63a	30a	9c	347a	90b
C. floribundus	6a	7a	5a	26a	39a	18a	1b	20a	3b	33a	48a	23a	123b	614a	126b
T. granulosa	5a	4a	5a	3a	15a	12a	nf	nf	nf	10a	20a	17a	77b	412a	27b
C. pachystachya	2a	3a	2a	47ab	57a	23b	1a	4a	5a	50ab	62a	24b	63b	725a	101b
C. trichotoma	–	–	–	–	–	–	–	–	–	–	–	–	21b	286a	46b
L. leucocephala	28a	5b	1b	33a	14ab	3b	1a	1a	<1a	61a	17ab	3b	98a	39b	21b
S. macranthera	nf	nf	nf	6a	20a	13a	<1a	<1a	1a	6a	20a	13a	21a	30a	23a
C. fissilis	5ab	10a	2b	47a	57a	18a	11ab	16a	4b	58a	70a	20b	238b	471a	18c
C. ferrea	nf	nf	nf	2b	30a	11a	<1a	<1a	<1a	2b	30a	11a	14a	93a	58a
M. umbellata	9a	11a	3a	7b	40a	26ab	<1a	1a	<1a	15a	52a	29a	44ab	116a	11b
T. impetiginosa	6a	4a	1a	19a	37a	27a	1a	2a	1a	25a	41a	29a	17a	20a	17a
S. saponaria	5b	23a	8b	<1a	1a	<1a	<1a	<1a	<1a	5b	24a	9b	3b	20a	15a
T. serratifolia	7a	9a	3a	68a	62a	50a	13a	13a	12a	76a	72a	54a	63a	169a	42a
A. parvifolium	–	–	–	–	–	–	–	–	–	–	–	–	4a	3a	<1a
C. langsdorffii	–	–	–	–	–	–	–	–	–	–	–	–	29a	114a	101a

Table 3 Root characteristics, plant growth rate (dry matter) and estimated P demand for 29 woody species

Species	Root morphology					Plant growth rate ($mg \cdot day^{-1}$)	Plant P demand ($\mu g \cdot day^{-1}$)
	Root diameter (µm)	Root hair density (per mm)	Root hair diameter (µm)	Root hair length (µm)	Root hair incidence (%)		
P. regnellii	683	7	19	40	5	8.3	4.35
O. arborea	602	13	21	42	<1	9.3	7.40
C. peltophoroides	367	6	7	34	<1	16.0	23.20
P. elegans	533	7	14	22	4	8.6	8.02
M. stipitatum	333	34	9	39	3	7.6	6.63
M. peruiferum	462	5	29	88	<1	3.1	2.88
H. courbaril	354	26	15	62	43	25.7	31.24
D. cuneatum	414	31	14	95	79	0.8	0.79
C. speciosa	490	140	8	107	100	24.2	37.55
T. roseo-alba	356	84	8	63	74	6.6	6.27
S. gran.-leprosum	388	37	9	265	98	36.2	109.85
L. molleoides	290	24	6	113	86	16.5	34.30
T. micrantha	248	115	9	145	96	49.3	235.63
L. grandiflora	275	39	8	123	96	31.0	62.54
S. spectabilis	408	41	15	175	61	34.7	43.71
C. floribundus	644	16	14	83	72	24.4	33.29
T. granulosa	450	8	13	158	5	12.9	23.80
C. pachystachya	264	53	8	123	99	39.3	84.30
C. trichotoma	499	16	14	92	25	19.0	42.95
L. leucocephala	323	26	15	138	76	18.3	20.20
S. macranthera	385	29	17	61	40	26.6	24.50
C. fissilis	421	53	7	79	73	30.2	34.66
C. ferrea	337	13	11	44	3	40.4	36.08
M. umbellata	360	57	7	86	94	13.6	1.64
T. impetiginosa	382	142	8	124	90	11.0	17.11
S. saponaria	280	52	10	78	79	17.1	23.79
T. serratifolia	458	152	7	164	100	23.8	26.41
A. parvifolium	610	51	8	119	99	6.5	3.91
C. langsdorffii	471	29	16	72	94	8.5	8.03

inhibited. This effect was most pronounced in species exhibiting a high degree of colonization. Colonization was completely absent in only four species (*Platyciamus regnellii*, *Ormosia arborea*, *Caesalpinia peltophoroides* and *Platypodium elegans*) whereas in three others (*Cordia trichotoma*, *Aspidosperma parvifolium* and *Copaifera langsdorffii*) fungal structures were observed in the roots, but colonization was not quantified because of difficulties in root clarification and staining. Several species (*Macherium stipitatum*, *Myroxylon peruiferum*, *Hymenaea courbaril*, *Dendropanax cuneatum*, *Ceiba speciosa* and *Tabebuia roseo-alba*) were mycorrhizal, but colonization was very low. Hyphal colonization was low in most species and reached a maximum of 28% in *Leucaena leucocephala*. Arbuscular colonization also varied considerably between species. Values ≥ 49% of the root segments with arbuscules were found in *Tabebuia serratifolia*, *Cedrella fissilis*, *Cecropia pachystachya*, *Senna spectabilis* and *Solanum granuloso-leprosum*. Vesicular colonization was generally low, except for *Tabebuia serratifolia*, *Cedrella fissilis*, *Croton floribundus* and *Solanum granuloso-leprosum*, where vesicles were most frequently found. P levels affected colonization, but not for all species. In general, colonization was favored by the intermediate P level (0.02 mg l^{-1}) and moderately inhibited at the highest level, except for *Solanum granuloso-leprosum*, *Trema micrantha* and *Leucaena leucocephala*. The colonization results indicate interspecific variability of AM susceptibility among these plants. Total root colonization was highly correlated ($r \geq 0.98$; $P < 0.01$) with arbuscular colonization and thus provides information on mycorrhiza functionality. Species with high growth rates (Table 3) tended to exhibit high levels of arbuscular colonization at 0.02 mg l^{-1} P in solution. As found for colonization, spore density in the rhizosphere also differed substantially between species. It was highest in species with a high degree of colonization and at a P level favoring colonization. In general, high P was more inhibitory to sporulation than to root colonization.

Root parameters also varied considerably between plant species but were not much affected by the treatments. For this reason, overall means for individual species are presented in Table 3. Root hair density ranged from 5 per mm for *Myroxylon peruiferum* to 152 per mm of root for *Tabebuia serratifolia*. Similar variation between species was found for root hair diameter and length. Root hair incidence varied from very rare to 100% incidence in some species. Root mean diameter ranged from 248 µm for *Trema micrantha* to 683 µm for *Platyciamus regnellii*. Root hairs were relatively frequent in roots of some species, but were generally short.

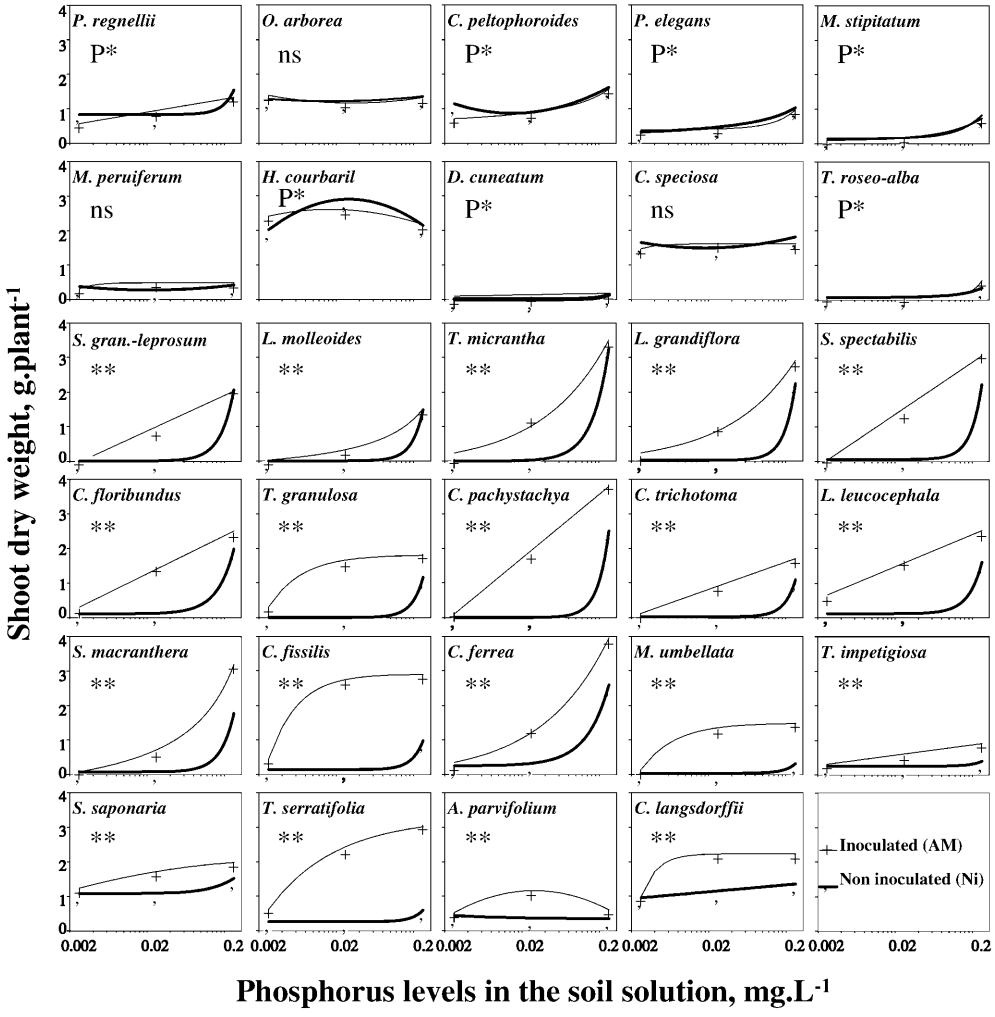

Fig. 1 Shoot dry mass of woody species seedlings, inoculated or non-inoculated with an arbuscular mycorrhizal (AM) fungus (*Glomus etunicatum*) in soil with three levels of P in solution. Regression lines of the best fit according to TableCurve 3.01 are shown (*ns* non-significant effect, *P** significant effect for P only, ** significant effect for AM, P and AM by P)

Hair length was as low as 22 µm for *Platypodium elegans* to as high as 265 µm for *Solanum granuloso-leprosum*. According to one concept (Baylis 1975), roots of *Platyciamus regnellii*, *Croton floribundus*, *Aspidosperma parvifolium* and *Ormosia arborea* are of the magnolioid type (root diameter >560 µm and hair length <100 µm). No graminoid-like roots (root diameter <100 µm) were found in these species, most of them being roots of the intermediate type.

Plant growth measured as shoot dry matter was highly affected by P and AM in most species (Fig. 1). The majority of species grew very poorly in the soil with the original P level (0.002 mg l^{-1}), even when inoculated with the AM fungus. In 10 species (*Platyciamus regnellii*, *Ormosia arborea*, *Caesalpinia peltophoroides*, *Platypodium elegans*, *Macherium stipitatum*, *Myroxylon peruiferum*, *Hymenaea courbaril*, *Dendropanax cuneatum*, *Ceiba speciosa*, *Tabebuia roseo-alba*) no significant ($P \leq 0.05$) effect of AM or AM by P interaction was found. In addition, the response of these species to P was either absent ($P \geq 0.05$) or barely significant. The remaining species (66% of the total) responded differently to both factors and exhibited significant AM by P interactions. Phosphorus effects on non-inoculated plants varied from none in *Ormosia arborea* to a very high response in *Cecropia pachystachya* and *Trema micrantha*. Many species were more responsive to P at the intermediate P level in soil solution when they were mycorrhizal (Fig. 1). Response to AM inoculation was highly differentiated by plant species and affected by P level. *Cecropia pachystachya* and *Tibouchina granulosa* had a positive response to inoculation as high as 8,000% at 0.02 mg l^{-1} P, but no significant effect was found at the highest P level. At the two lowest P levels, most plant species exhibiting a high response to inoculation also responded to applied P. Under a higher P in the soil solution, such a relationship was not found. Therefore, most of the species studied responded to both factors when P in soil was insufficient for growth but not under high P (at 0.2 mg l^{-1}). Some species, such as *Myrsine umbellata*, *Tabebuia impetiginosa*, *Sapindus saponaria*, *Tabebuia serratifolia*, *Aspidosperma parvifolium* and *Copaifera langsdorffii* were only responsive to P when mycorrhizal. This indicates a synergistic effect of P and AM on these species when P is limiting plant growth. The mycotrophic habit of this group of species under the

conditions of our experiment was also evident, in spite of their low responsiveness to AM fungi. Thus, the distinction between responsiveness and dependency is clear here. Plant species exhibiting no response to mycorrhiza did not have an AM by P interaction, even when they were responsive to P. These species had a low degree of colonization (Table 2) and some did not even form AM with *Glomus etunicatum*. In contrast, AM-responsive species had an AM by P interaction, a high degree of colonization with an average of 40% for total colonization at 0.02 mg l^{-1} P and were mostly very responsive to P.

Shoot P concentration was also highly affected by the treatments (Table 4). Several species were so severely affected by P deficiency at 0.002 and 0.02 mg l^{-1} that the dry matter produced was insufficient for nutrient analysis. Increasing soil P availability had no effect on P concentration of several species. This was found primarily in species with reduced or no response to either P or AM. P concentration was maximal in *Trema micrantha* reaching 5.04 mg kg^{-1} and minimal in *Myrsine umbellata* at 0.05 mg kg^{-1} dry matter. In general, increments of P concentration were affected by increasing soil P and were greater for mycorrhizal than for non-inoculated plants. Significant mycorrhiza beneficial effects on uptake were found only at 0.02 and 0.2 mg l^{-1} P. Species that had a mycorrhiza effect at 0.02 did not necessarily have one at 0.2, indicating the complex interaction between P and mycorrhizae effects on those species. These interactions were affected by host genotype and soil-available P, as is well known for cultivated plants. It is interesting to note that in the case of *Hymenaea courbaril* mycorrhizal plants had lower P than non-mycorrhizal plants at 0.02 mg l^{-1} P. With insufficient soil P for plant growth (0.002 and 0.02 mg l^{-1}), differences in P concentration in AM plants were correlated with differences in response to inoculation (r=0.75; P<0.01 and r=0.60; P<0.01 for 0.002 and 0.02 mg l^{-1} P); under sufficient P, such a relationship was not found. These results indicate that growth of several non-inoculated species was severely limited by P deficiency and that mycorrhizal growth enhancement of most species was nutritionally-mediated. Moreover, species non-responsive to AM were also little or not at all affected by increasing P supply in the soil (Fig. 1).

Treatments affected the EPU but not to a great extent (Table 4). In general EPU increased with increasing P level and was affected by AM in a number of species. At the lowest P level, only *Leucaena leucocephala* was favored by AM. The EPU of twice as many plants was significantly enhanced by AM at 0.02 mg l^{-1} than at 0.2, i.e. only few plant species had EPU enhanced by AM at an adequate P supply (0.2 mg l^{-1}). These species are themselves inefficient in taking up P, even under high P availability and are, thus, dependent on AM fungi for P uptake whether or not they respond in their growth. As some of these species may have obtained the P required for normal growth at 0.2 mg l^{-1} P, the enhanced P uptake may only represent superfluous consumption. In fact with *Ceiba speciosa* and *Lithraea molleoides*, no AM effect on growth was found at this P level. EPU values varied from as low as 0.13 in *Myrsine umbellata* to 7.46 mg of accumulated shoot P per g of roots in *Trema micrantha*, the latter being very efficient in taking up soil P. *Myrsine umbellata* may compensate for its low P uptake efficiency by a low P demand (Table 3). Certain species, such as *Ceiba speciosa*, exhibited high EPU independent of AM. For most of the responsive species, mycorrhizal effects on EPU were significant (P≤0.05) and of great magnitude. For instance, in *Leucaena leucocephala* at 0.02 mg l^{-1} P, EPU was increased 67-fold due to mycorrhizae, confirming the high level of mycotrophy of this species (Habte and Manjunath 1987).

The indices of Plenchette et al. (1983) are presented in Table 5. At low soil P (0.002 mg l^{-1}), the values were zero except for *L. leucocephala* and *Tabebuia serratifolia*, which exhibited mycorrhizal responsiveness at this P level. At 0.02 mg l^{-1} P, 19 species showed significant mycorrhizal responsiveness while, at the highest P level (0.2 mg l^{-1}), many species were still responsive to AM. For instance, *Tabebuia serratifolia*, *Tabebuia impetiginosa*, *Myrsine umbellata* and *Cedrella fissilis* had a Plenchette et al. index greater than 50% at the highest P level, indicating their high degree of mycotrophy. This index was correlated with total root colonization (r=0.67; P<0.01, r=0.80; P<0.01, and r=0.82; P<0.01) and similarly with arbuscular colonization (r=0.56; n.s., r=0.80; P<0.01, and r=0.80; P<0.01) for 0.002; 0.02 and 0.2 mg l^{-1} P, respectively. In general, species exhibiting a high degree of root colonization were also mycorrhiza responsive. Correlation analysis for Plenchette et al. indices and root characteristics showed no relationship between these variables, except for root hair length, which was positively correlated (r=0.61; P<0.01) with this index at 0.02 mg l^{-1} P. By applying the categories of host dependency formulated by Habte and Manjunath (1991) (Table 5), we found 10 AM-independent species, 12 very highly dependent, one highly dependent and six species that did not fit well into their categorization. Several species were responsive to mycorrhiza even at high P supply and were otherwise also very highly dependent. Others such as *Solanum granuloso-leprosum*, *Lithraea molleoides*, *Trema micrantha*, *Tabebuia impetiginosa*, *Sapindus saponaria* and *Copaifera langsdorffii* did not fit the Habte and Manjunath categorization but were AM dependent. Janos (1988) T′ values are also shown in Table 5. For non-responsive hosts, T′ values were considered to be 0.002 mg l^{-1} because there was no AM effect even at this the lowest P level tested. For the responsive hosts, estimated values ranged from 0.198 for *Solanum granuloso-leprosum* to higher than 0.464 mg l^{-1} P for *Copaifera langsdorffii*. Species were distributed in a continuous way according to this parameter, which indicates the appropriateness of T′ as measure of AM dependence. As was the case for the Plenchette et al. index, T′ was also correlated with total root colonization (r=0.56; n.s.; r=0.77; P<0.01; r=0.74; P<0.01 for all three P

Table 4 Shoot P concentration (mg·kg^{-1}) and efficiency of P uptake (EPU, mg of accumulated P per g of roots) of mycorrhizal (*AM*) and non-mycorrhizal (*Ni*) woody species grown in a low-fertility Oxisol with three levels of P in solution. Means followed by the same letters (lower case for P levels and upper case for inoculation) indicate no difference within plant species by Tukey's test at P=0.01 (*OP* overall P effect; M by P ns). – not determined due to insufficient plant material)

Species		Shoot P										EPU								
		0.002			0.02			0.2				0.002			0.02			0.2		
P. regnellii	OP	0.45	a		0.50	a		0.52	a		OP	0.44	a		0.38	a		0.32	a	
O. arborea	OP	0.43	b		0.45	b		0.80	a		OP	1.07	b		1.09	b		3.25	a	
C. peltophoroides	OP	0.80	b		0.78	b		1.45	a		OP	0.91	b		0.86	b		2.55	a	
P. elegans	AM	0.69	a	A	0.81	a	A	0.95	a	A	AM	0.93	a	A	0.88	a	A	1.09	a	A
	Ni	0.76	ab	A	0.53	b	A	0.90	a	A	Ni	0.89	ab	A	0.58	b	A	1.36	a	A
M. stipitatum	OP	0.58	ab		0.51	b		0.87	a		AM	0.51	b	A	0.55	ab	A	1.11	a	A
											Ni	0.37	b	A	0.31	b	A	1.48	a	A
M. peruiferum	AM	0.90	a	A	1.06	a	A	0.85	a	A	AM	1.36	a	A	1.94	a	A	1.58	a	A
	Ni	0.84	a	A	0.86	a	A	1.03	a	A	Ni	1.24	a	A	1.29	a	A	2.24	a	A
H. courbaril	AM	0.99	a	A	1.08	a	B	1.44	a	A	AM	1.63	a	A	1.58	a	A	2.12	a	A
	Ni	1.19	a	A	1.63	a	A	1.07	a	A	Ni	1.35	a	A	2.36	a	A	1.14	a	A
D. cuneatum	AM	– (2)			0.76	a		0.98	a	A	AM	–			0.72	b		1.44	a	A
	Ni	–			–			1.08		A	Ni	–			–			1.59		A
C. speciosa	AM	0.91	c	A	1.25	b	A	1.84	a	A	AM	2.99	b	A	4.33	b	A	7.26	a	A
	Ni	0.89	b	A	0.93	b	B	1.27	a	B	Ni	3.05	a	A	3.22	a	A	4.29	a	B
T. roseo-alba	OP	0.59	a		0.55	a		0.95	a		OP	1.21	a		0.98	a		1.74	a	
S. gran.-leprosum	AM	–			2.20	b		3.04	a	A	AM	–			2.25	b		3.70	a	A
	Ni	–			–			3.34		A	Ni	–			–			4.29		A
L. molleoides	AM	1.20	a		1.71	a		2.08	a	A	AM	3.96	a		5.34	a		7.15	a	A
	Ni	–			–			1.02		B	Ni	–			–			3.14		B
T. micrantha	AM	–			2.66	b		4.78	a	A	AM	–			7.46	a		13.62	a	A
	Ni	–			–			5.04		A	Ni	–			–			16.57		A
L. grandiflora	AM	1.23	a		1.59	a		2.02	a	A	AM	3.26	b		3.92	b		7.06	a	A
	Ni	–			–			1.50		A	Ni	–			–			4.33		A
S. spectabilis	AM	0.94	b	A	1.12	b	A	1.54	a	A	OP	1.19	b		1.13	b		2.25	a	
	Ni	0.83	ab	A	0.60	b	B	0.98	a	B										
C. floribundus	AM	0.83	b	A	1.01	b	A	1.73	a	A	AM	0.48	c	A	0.86	b	A	1.62	a	A
	Ni	0.63	b	A	0.56	b	B	1.00	a	B	Ni	0.32	b	A	0.29	b	B	0.70	a	B
T. granulosa	AM	0.30	c		0.74	b		1.85	a	A	AM	0.42	c		1.74	b		4.69	a	A
	Ni	–			–			1.20		B	Ni	–			–			1.61		B
C. pachystachya	AM	–			–			2.14		A	AM	–			–			3.56		A
	Ni	–			–			2.08		A	Ni	–			–			3.36		A
C. trichotoma	AM	1.21	b		1.27	b		2.26	a	A	AM	1.54	a		1.42	a		1.87	a	A
	Ni	–			–			1.19		B	Ni	–			–			0.94		B
L. leucocephala	AM	0.47	c	A	0.72	b	A	1.66	a	A	AM	0.47	b	A	0.47	b	A	0.99	a	A
	Ni	0.35	ab	A	0.15	b	B	0.54	a	B	Ni	0.17	b	B	0.07	b	B	0.34	a	B
S. macranthera	OP	0.53	a		0.63	a		0.92	a		AM	0.54	b	A	0.93	b	A	3.11	a	A
											Ni	0.47	a	A	0.48	a	A	1.37	a	B
C. fissilis	OP	0.69	a		0.94	a		1.15	a		AM	2.07	b	A	3.90	a	A	5.53	a	A
											Ni	0.81	a	A	0.63	a	B	1.69	a	B
C. ferrea	AM	0.96	a	A	0.84	a	A	1.07	a	A	AM	1.04	b	A	1.61	ab	A	2.09	a	A
	Ni	0.93	a	A	0.85	a	A	0.72	a	B	Ni	0.84	a	A	0.79	a	B	1.34	a	B
M. umbellata	AM	0.03	b		0.09	ab		0.12	a	A	AM	0.05	b		0.13	ab		0.17	a	A
	Ni	–			–			0.05		B	Ni	–			–			0.06		B
T. impetiginosa	AM	0.57	c	A	1.39	b	A	2.14	a	A	AM	0.39	b	A	1.26	b	A	2.25	a	A
	Ni	0.88	a	A	0.74	a	B	0.77	a	B	Ni	1.22	a	A	0.64	a	A	0.54	a	B
S. saponaria	AM	0.74	c	A	1.37	b	A	1.81	a	A	AM	1.07	c	A	2.58	b	A	3.51	a	A
	Ni	0.70	a	A	0.67	a	B	0.88	a	B	Ni	1.03	a	A	0.88	a	B	1.41	a	B
T. serratifolia	AM	0.68	c	A	1.06	b	A	1.53	a	A	AM	0.59	b	A	1.54	b	A	3.13	a	A
	Ni	0.57	a	A	0.57	a	B	0.69	a	B	Ni	0.26	a	A	0.27	a	B	0.72	a	B
A. parvifolium	OP	0.66	a		0.58	a		0.61	a		OP	0.60	a		0.65	a		0.52	a	
C. langsdorffii	AM	0.55	c	A	0.89	b	A	1.43	a	A	AM	0.36	b	A	0.96	a	A	1.30	a	A
	Ni	0.41	a	A	0.41	a	B	0.51	a	B	Ni	0.23	a	A	0.24	a	B	0.41	a	B

Table 5 Indices (%) according to Plenchette et al. (1983), AM-dependence categories of Habte and Manjunath (1991) and estimated T′ values of 29 woody species grown in a low-fertility soil with three levels of P in the soil solution (0.002; 0.02; 0.2 mg l^{-1})

Species	Index			Category	T′ value
	0.002	0.02	0.2		
P. regnellii	0	0	0	Independent	0.002
O. arborea	0	0	0	Independent	0.002
C. peltophoroides	0	0	0	Independent	0.002
P. elegans	0	0	0	Independent	0.002
M. stipitatum	0	0	0	Independent	0.002
M. peruiferum	0	0	0	Independent	0.002
H. courbaril	0	0	0	Independent	0.002
D. cuneatum	0	0	0	Independent	0.002
C. speciosa	0	0	0	Independent	0.002
T. roseo-alba	0	0	0	Independent	0.002
S. gran.-leprosum	0	99	0	Highly dependent? [a]	0.198
L. molleoides	0	97	0	Highly dependent?	0.202
T. micrantha	0	98	0	Highly dependent?	0.210
L. grandiflora	0	98	22	Very highly dependent	0.222
S. spectabilis	0	95	29	Very highly dependent	0.225
C. floribundus	0	92	20	Very highly dependent	0.229
T. granulosa	0	100	37	Very highly dependent	0.231
C. pachystachya	0	100	35	Very highly dependent	0.232
C. trichotoma	0	98	36	Very highly dependent	0.235
L. leucocephala	81	92	35	Very highly dependent	0.246
S. macranthera	0	87	45	Very highly dependent	0.293
C. fissilis	0	95	66	Very highly dependent	0.297
C. ferrea	0	76	34	Very highly dependent	0.322
M. umbellata	0	98	79	Very highly dependent	0.346
T. impetiginosa	0	58	57	Very highly dependent?	0.347
S. saponaria	0	36	24	Very highly dependent?	0.395
T. serratifolia	59	89	80	Very highly dependent	0.406
A. parvifolium	0	68	0	Highly dependent	0.464
C. langsdorffii	0	50	38	Very highly dependent?	>0.464

[a] Not perfectly fit

levels, respectively), but not with the root characteristics presented in this paper (Table 4).

Discussion

Considering the basic biology of plant–fungus interactions, it is to be expected that the extent of mycorrhizal colonization of the root system and related plant responses will vary in different plant–fungus combinations (Hetrick et al. 1996; Smith and Read 1997). Nevertheless, study of host response to inoculation with a single fungus isolate can provide useful information. This is particularly true where the inoculating fungus exhibits a broad host range, as is the case for the *Glomus etunicatum* isolate used in this study. We found wide variation in root colonization and host mycorrhiza responsiveness and dependency among the 29 woody species grown in a low-fertility soil with ambient or increased P in the soil solution. Considering that there is little or no evidence for host–fungus specificity in AM, difference in plant susceptibility to mycorrhiza formation and responsiveness can be attributed mostly to the host genome rather than to that of the fungus. In fact, the woody species *Liquidambar styraciflua* L. exhibits high dependence and responds positively to several fungus species (Kormanik et al. 1981). As AM fungi all have a similar strategy for host growth enhancement in low-fertility soils, by increasing nutrient acquisition, the results and their interpretation obtained with a single isolate could change, though not to a great extent, when a different effective isolate is used to colonize the plants.

Although the extent of AM colonization varies markedly with different host genotypes, as reported here, the biochemical and physiological mechanisms and the genetic control of these interactions have not been elucidated. Thus, our findings can not be explained with the current state of knowledge. The variation may represent an evolutionary process of this mutualistic association which is expressed differently in different hosts from similar plant communities. Because fungus and growing conditions were standardized, our results suggest that differences in AM susceptibility and degree of colonization are determined by plant intrinsic characteristics, as suggested also by Koide and Schreiner (1992). In contrast, host responsiveness is determined by fungal efficiency (Saggin-Júnior and Siqueira 1995) and by the environment (Janos 1996). We found variation in colonization parameters even within species with high colonization and responsiveness. These may be determined by differences in plant–fungus relationships at the chemical or anatomical levels (Brundrett et al. 1990; Gianinazzi-Pearson 1992). However, with an adequate P supply for plant growth, AM colonization may be determined by specific plant factors related to mycorrhizal dependence. High P is known to depress mycorrhiza formation (Amijee et al. 1989), but in the present study such an effect was not uniform among species, in agreement with

results of Habte and Manjunath (1991). Sensitivity to AM colonization by a given fungus at an excess of P may be controlled by differences in host dependence on mycorrhizae for P uptake (Manjunath and Habte 1991), with these characteristics being inversely related. In fact, *Solanum granuloso-leprosum* and *Trema micrantha*, which are not very dependent, showed a drastic reduction (up to 90%) in AM colonization after an increase in solution P from 0.02 to 0.2 mg l^{-1}. Controlling mechanisms for such effects are very complex (Brundrett 1991) and are still unresolved. Colonization appears to be under the control of both partners, but the plant may have an overriding role considering the evidence that the regulation is nutritionally mediated. As indicated by Siqueira et al. (1984) and the data shown here, plant nutrient requirements and their fulfillment in the absence of AM are the major factors determining P effects on root colonization.

In our study, several species were non- or poorly mycorrhizal and, thus, considered to be non-mycotrophic or mycorrhiza independent. Most of these species also exhibited a low response to P in contrast to mycotrophic species, which generally had high colonization and responsiveness to both AM and P. Colonization was more closely related to the Plenchette et al. index at 0.02 and 0.2 mg l^{-1} P than at 0.002 mg l^{-1}. Therefore, mycorrhiza formation, response to added P, host nutrient requirement, and mycorrhiza responsiveness are all interrelated and, as stated by Janos (1996), host independence of AM is a consequence of low nutrient requirement or the ability of roots alone to take up all required mineral nutrients.

AM-independent species also show a low response to raised P in the soil solution, while responsive species may not necessarily have a high degree of dependence. To cope with a low nutrient situation, non- or low-responsive species may have other strategies such as a low growth rate or high seed reserves of nutrients (Chapin 1980). Our data show that mycotrophic species exhibit varied responsiveness to AM and to added P and that these responses may not be related to the mycorrhiza dependence of a particular host. For example, *Trema micrantha* and *Solanum granuloso-leprosum* exhibited high responsiveness (Plenchette et al. index) but not high T′, *Cedrella fissilis* and *Tabebuia serratifolia* high responsiveness and high T′, while *Tabebuia impetiginosa* and *Sapindus saponaria* had a low response and high T′. Even though concepts for host dependence and responsiveness to AM have been controversial (Habte and Manjunath 1991), our results show that these characteristics can be distinguished in some tropical woody species. Responsiveness is best expressed at intermediate P levels, where responsive species show large differences after inoculation with AM fungus. In contrast, dependency as measured by T′ is expressed at a P level sufficient for plant growth. This reflects the continued requirement for AM at high P and not the extent of the mycorrhiza effect and is a measure of the host requirement for mycorrhiza relative to the contribution of roots alone in nutrient acquisition. Mycorrhizal dependence is an inherent characteristic for which plant nutrient requirement and uptake efficiency are important parameters and not fungal effectiveness or environmental conditions.

It has been widely accepted from research in temperate regions (usually soils with high P) that plants with highly branched and fine roots have sparse mycorrhizae and derive little benefit from AM. They, thus, show little dependence on AM according to the proposition by Baylis (1975). Our results do not support this hypothesis in that some AM-independent species, such as *Platyciamus regnellii* and *Ormosia arborea*, have coarse roots and few root hairs. Furthermore, other species with finer roots and abundant root hairs, such *Tabebuia serratifolia*, were dependent. Overall, no relationship was found between root characteristics and any of the mycorrhiza-dependence indicators. Similarly, Manjunath and Habte (1991) showed that plants with similar root morphological characteristics could differ in degree of mycorrhiza dependence. At low-available P, as found in most tropical soils, even finely branched roots may not ensure adequate nutrition for fast-growing species, making them very responsive to and dependent on AM, as demonstrated here for some of the species we studied. That some plants with coarse roots are able to grow well without mycorrhizae in low-P soils indicates additional nutrient acquisition mechanisms (Chapin 1980) or high use efficiency (Manjunath and Habte 1991) acquired along with long-term adaptation to such environments.

Considering the importance of mycorrhiza dependence for seedling survival (Janos 1980a), it is of great interest to categorize species according to this characteristic. Although the results also reflected the Plenchette et al. index (=responsiveness), Habte and Manjunath (1991) were able to separate plants according to their degree of mycorrhiza dependence. However, this procedure was not adequate for separating the species we studied because they fitted into only three categories and some could not be categorized. It may well be that the species selected for this study presented low diversity in this respect. In contrast, T′ values were effective for separating the mycotrophic species as a continuous trait. All species with T′≥0.198 mg l^{-1} P could be considered to have high dependence. All 19 mycotrophic species fitted into this group, but exhibited different degrees of dependence. Species with T′≥0.346 mg l^{-1} P could be considered as obligatory mycotrophic because they only responded to P in the presence of AM. In addition, most species in the latter group exhibited low AM responsiveness. Therefore, this variation in T′ values indicates diversity of this feature among species, and the degree of mycorrhizal dependency of a given host is not necessarily related to its responsiveness to a fungus or to added P. Usually, high P responders were mycotrophic, but these species were not amongst those with a high degree of dependency (T′). Moreover, maximal T′ values were found in the mycotrophic species least responsive to P when they are non-mycorrhizal. Thus, the degree of AM responsiveness can be experimentally distinguished from the degree of AM dependence by estimating T′.

At the initial growth stage, the woody species studied here were either non-mycotrophic (independent) or had a high degree of mycotrophy, the latter being the most common. With some AM-independent and P-responsive species, P fertilizer should be applied in order to guarantee adequate seedling development. Dependent species can be either non-responsive or responsive to different degrees to increased available soil P. Even species responsive to P should be inoculated with effective AM in order to enhance outplant survival and initial growth in the field.

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