Phosphorus response of three native Brazilian trees to inoculation with four arbuscular mycorrhizal fungi

M.C. Pagano[1], M.N. Cabello[2*] and M.R. Scotti[1]

[1]Institute of Biological Sciences, Federal University of Minas Gerais, Av. Antônio Carlos, 6627, Pampulha, CEP: 31270-901, Belo Horizonte, MG, Brazil
[2]Instituto Spegazzini, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Aven 53 No 477, B1900AVJ, La Plata, Argentina

Pagano, M.C., Cabello, M.N. and Scotti, M.R. (2007). Phosphorus response of three native Brazilian trees to inoculation with four arbuscular mycorrhizal fungi. Journal of Agricultural Technology 3(2): 231-240.

The effects of arbuscular mycorrhizal fungi (AMF), phosphorus addition and their interaction, on the growth and phosphorus uptake of three facultative mycotrophic legume trees (*Anadenanthera peregrina, Enterolobium contortisiliquum* and *Plathymenia reticulata*) were investigated. The experimental design was factorial, with five treatments of inoculation (a- control; b- *Acaulospora* spp.; c- *Gigaspora margarita*; d- *Glomus* sp. 1; e-*Scutellospora heterogama*) × three levels of soil P (32.5, 50 and 136 $mgdm^{-3}$), each with three replicates. Plants were grown in pots for 5 months. Plant weight and shoot phosphorus concentration were measured at harvest. Phosphorus fertilization improved growth of all species. Phosphorus increased to enhance the positive effects of AMF on the three studied species. Tissue nutrient concentrations showed slight variation among species and were influenced by both AMF inoculation and Phosphorus. Plants inoculated, with higher doses of KH_2PO_4 showed more vigorous seedlings. Results suggest that in low fertility soils *A. peregrina, E. contortisiliquum* and *P. reticulata* seedlings should be inoculated with AMF to enhance plant growth.

Key words: arbuscular mycorrhizal fungi, brazilian pioneer species growth, dry forest, phosphorus fertilization, phosphorus shoot concentration

Introduction

AMF (arbuscular mycorrhizal fungi) are members of the phylum Glomeromycota (Schüßler *et al*., 2001) and the number of species of mycorrhizal plants will certainly increase as research progresses. Mycorrhizal colonization increases the uptake of phosphorus and other nutrients from soil by means of the external mycelium. In the tropics, the majority of species form AM due to their role in these Phosphorus deficient soils (Smith and Read, 1997). Mycorrhizal plants in low-P soil can be highly dependent on the symbiosis, but

* Corresponding author: M. N. Cabello; e-mail: mcabello@netverk.com.ar

the responsiveness of plants to AMF colonization varies with species, genotype, and with environmental conditions (Smith and Read, 1997). Also, glasshouse experiments showed that AMF taxa differ in their capacity to supply plants with phosphorus (P) (Jakobsen *et al*., 1992; van der Heijden *et al*., 2003).

By far, most research has been devoted to the role of AMF in host mineral nutrient acquisition (mostly phosphate) (Rillig, 2004). Inorganic phosphorus often occurs in low concentrations in soil and primarily moves to roots by diffusion. As phosphorus is absorbed rapidly, phosphorus depletion zones can form around roots and hyphae (Vance *et al*., 2003) which provided that root density is low, extraradical AM fungus hyphae can extend beyond root phosphorus depletion zones, thereby improving phosphorus uptake by mycorrhizal plants. Positive growth effects of AMF occur when the benefits of mycorrhizas exceed their carbon cost (Fitter, 1991).

The need to develop sustainable agroforest systems in natural undisturbed ecosystems, with reduced external inputs of pesticides and manufactured fertilizers has encouraged soil microbiologists to seek other microorganisms that can likewise benefit crop production. AMF can directly take up inorganic nitrogen from the soil and transfer it to the host plant; this biochemical pathway was recently elucidated by Govindarajulu *et al*. (2005). There are two ways in which AMF may conceivably enhance legume performance. Firstly, AMF may promote plant vigor and hence biomass production and N uptake, and secondly AMF may affect symbiotic dependence, i.e., the proportional dependence of the legume on atmospheric N_2 (P_{atm}). The response of legume species to AMF inoculation can be markedly different depending on AMF inoculation, differences in root architecture and AMF dependency.

In a revision paper, Rillig (2004) showed that positive responses to AMF inoculation can occur in unfertilized soil, but they are more likely to occur in soils where low available P status has been corrected by superphosphate application. The use of different extractants for available P in the studies reviewed did not allow for an assessment of the relationship between available P status of soils and response to AMF inoculation, but this is one area in which further research needs to be carried out.

Plants species differ in their nutritional demand due to their ecophysiological characteristics, such as successional group (Gonçalves *et al*., 1992) and their capacity to form symbioses with soil microorganisms, especially with mycorrhizal fungi. For artificial revegetation it is necessary to know the nutrient requirements of the plants species and the mycorrhizal dependency. Greenhouse experiments aid to optimize seedlings production.

Three nodulate legume species were used which occur in the dry Forest of the Brazilian Southeastern region (Rizzini, 1997) to test the principal question we addressed: what species and available phosphorus maximize plant growth or phosphorus uptake benefits from AMF. *Anadenanthera peregrina* Speg. ("Angico") is a pioneer leguminous tree with low growth and potential use in recuperation of degraded lands that have been used for agroforestry in Brazil (Scotti and Correa, 2004; Pagano, 2007). Their nutritional requirements are scarcely known and the AMF symbioses have been showed (Pereira *et al*., 1996; Carneiro *et al*., 1998; Pagano, 2007). *Enterolobium contortisiliquum* (Vell.) Morong ("Tamboril") is a secondary N_2-fixing tree (Lorenzi, 2000) which has showed AMF symbioses (Carneiro *et al*., 1998; Patreze, 2003; Pagano, 2007) and also occurs in the Brazilian riparian forest (Duringan and Silveira, 1999). *Plathymenia reticulata* Benth. ("Guanambira") also known as ''vinhático do campo'' is a secondary species that can attain 15 m high. *P. reticulata* occurs mainly in the Cerrado region (a savanna vegetation) (Rizzini, 1997), a Brazilian biome classified as hotspot for conservation priorities (Myers *et al*., 2000).

The aims of this study were to evaluate the effects of AM fungus inoculation on the growth of *Anadenanthera peregrina*, *Enterolobium contortisiliquum* and *Plathymenia reticulata*, native species which present ecological and environmental interest for southern Brazil, and to establish the potential inoculants for these species.

Materials and methods

Greenhouse test

The experiment was conducted as a randomized block design with a factorial array of 5 treatments and 3 replicates, and comprised a total of 39 plants of each vegetal species, since no inoculated seedlings were tested only with 100% P fertilization.

The factors were as follows:- control without inoculation and four inoculation treatments × three levels of P addition (32.5, 50 and 136 mg dm-3), each with three replicates. The levels of P in the soil were tested based on reports for native trees (Pereira et al., 1996; Paron et al., 1996; Burity et al., 2000).

Fungal isolates

The inoculum supplied consisted of spores of each AMF type. The AMF strains used were from the Biological Science Institute (ICB) Belo Horizonte (BH) culture collection.

Three isolates of AMF from pot cultures with *Brachiaria decumbens* Stapf were used as follows:- *Glomus* sp1 culture N° BHICB-J-Glo1, isolated from Jaíba locality (Brazil) (Pagano, 2007), *Gigaspora margarita* Becker & Hall culture N° BHICB-B-1, and *Scutellospora heterogama* (Nicolson and Gerdemann) Walker & Sanders culture N° BHICB-B-2, from the Brucutu mine (Brazil).

Three treatments were inoculated with an arbuscular mycorrhizal fungus except treatment 4, in which an equal mixture of two *Acaulospora* species was used. The mixed species used were *Acaulospora scrobiculata* Trappe culture N° BHICB-J-AcS, isolated from Jaíba (Brazil) and *Acaulospora spinosa* Walker & Trappe culture N° BHICB-B-AcSP from the Brucutu mine (Brazil).
Plant species and mycorrhizal inoculation.

Seeds of *Anadenanthera peregrina*, *Enterolobium contortisiliquum* and *Plathymenia reticulata*, native plant species, were collected from mature plants located in the Forest Reserve at Jaíba (15o 09'S 43o56' W) – state of Minas Gerais, Brazil. After sterilization (with Na hypochlorite 10% for 1 min) the seeds were placed in sterilized cotton in Petri dishes. Seeds of *E. contortisiliquum* were scarified before with the same sterilization process.

After germination, seedlings of the three native species were transferred to pots (2L) containing sterilized sand and vermiculite substrate mixture (1:1) and inoculated with AMF. All inoculated treatments received 100 spores from either one of the species (*G. margarita* or *S. heterogama* or *Glomus* sp. 1) or from two species (*Acaulospora spinosa* and *Acaulospora scrobiculata*), in this case, 50 spores from each species. Seedlings were cultivated in pots for 5 months.

The experiment was performed in a greenhouse in natural conditions of temperature, light, and humidity. The maximum and minimum averages for temperature and humidity were 38.6°C and 19.6°C, 90% and 33%, respectively. Contamination was avoided as follows: each pot stood on a 2-cm deep plate in an indoor greenhouse. Plants were harvested at 5 months, and the height was measured. Plants were dried at 65^{o}C to constant weight and weighed. Leaves and steams were used to determine aerial plant biomass. The root system was also weighed.

Phosphorus and base nutrient addition

Pots were watered as needed and fertilized once per week as follows:Phosphorus treatments were applied as 150 ml per pot of soluble KH_2PO_4 in three different concentrations each week beginning 1 week after planting with modified Hoagland's nutrient solution (Hoagland and Arnon, 1951) using three phosphorus concentrations: 136 mg P dm-3 (100 % P fertilization), 65 mg P dm-3 (50% P fertilization) and 32.5 mg P dm-3 (25% P fertilization).

Base nutrients were as follows:- 0.61g KNO_3, 0.95g $Ca(NO_3)_2{\cdot}4H_2O$, 0.43g $MgSO_4{\cdot}7H_2O$, 0.049 g ferric citrate, 0.0034g $MnSO_4{\cdot}7H_2O$, 0.0005g $CuSO_4{\cdot}5H_2O$, 0.0006 g $ZnSO_4{\cdot}7H_2O$, 0.0037 g H_3BO_3, and 0.0001g $(NH_4)6Mo_7O_{24}{\cdot}4H_2O$. Plants received N supply by means of application of 10 ml of KNO_3 solution each month.

Determination of phosphorus (P) on shoots

After harvest, the shoots were separated from the roots, dried at 65°C, ground and processed for determining concentration of phosphorus by nitroperchloric digestion and spectrophotometric reading at 880 nm. P content in leaves was estimated according to Sarruge and Haag (1974) using the Vanado-Molybdate Method.

Data analysis

One-way ANOVA with Tukey's honestly significant difference contrast was performed to study differences ($P<0.05\%$) among AM treatments.

Results

No parameters evaluated in *A. peregrina* showed significant differences with the exception of height of plants inoculated with *Glomus* sp. 1 and *Acaulospora* spp. fertilized with 65 mg P dm-3 (50%). The highest P concentration in leaves was obtain when plants were inoculated with *Scutellospora heterogama* whereas not differ significantly when compared to no inoculated control plants (Table 1).

The growth parameters evaluated for *E. contortisiliquum* and P content in plant tissues. The values of plant height and aerial biomass were significantly higher in treatment with 100% P, which was inoculated with *Glomus* sp. 1 and *Gigaspora margarita*. The highest root dry weight was observed in 100% P in

inoculated treatment using *Glomus* sp. 1, showing significant differences in relation with treatments of inoculation with the others AMF species, whereas at 50% P level the inoculation with *G. margarita* showed the highest root dry weight (Table 2). Values of P content in aerial biomass from treatment with 100% P and inoculated with *Glomus* sp. 1 were significantly different from those in which plants were inoculated with *S. heterogama*, *Acaulospora* spp. and no inoculated control.

Table 1. Influence of AMF inoculation and phosphorus fertilization on *Anadenanthera peregrina* seedlings after 5 months growth.

Fertilization		Fungi				
		***Glomus* sp.1**	***Gigaspora margarita***	***Scutellospora heterogama***	***Acaulospora* spp.**	**Control [α]**
Height (cm)	25 (32.5mgPdm^{-3})	16.50 a	16.50 a	13.53 a	12.33 a	
	50 (65 mgPdm^{-3})	24.0 b	14.33 a	14.53 a	20.90 b	
	100(136mgPdm^{-3})	17.16 a	28.16 ab	33.63 b	25.66 ab	32.16 ab
Shoot dry weight (g)	25%	0.236 a	0.296 a	0.216 a	0.176 a	
	50%	0.530 a	0.293 a	0.233 a	0.440 a	
	100%	0.336 a	0.850 ab	1.266 b	0.526 ab	0.903 ab
Root dry weight (g)	25%	0.88 a	1.23 a	0.67 a	0.68 a	
	50%	1.19 a	1.31 a	1.08 a	0.8 a	
	100%	1.01 a	1.50 a	1.53 a	1.02 a	1.2a
Phosphorus concentration[β]	25%	1.151 a	1.362 a	1.147 a	0.997 a	
	50%	1.825 a	1.637 a	1.330 a	2.293 a	
	100%	1.927 a	2.847 ab	4.004 b	1.984 a	2.739 ab

Values are means for three separated harvest. Values followed by the same letter do not differ significantly by one-way ANOVA and Tukey's HSD test ($P \leq 0.05$).

[α] Control = 100% Phosphorus (136 mg dm^{-3})

[β] Phosphorus concentration in leaves (mg g^{-1})

The growth parameters evaluated for *P. reticulata* and P content in plant tissues. The values of aerial biomass and plant height were significantly higher in treatment with 100% P, which was inoculated with *Glomus* sp. 1 and *S. heterogama* or in control plants. Values of P content in aerial biomass from treatment with 100% P and inoculated with *Glomus* sp. 1 were significantly different from those in which plants were inoculated with *Gigaspora margarita*, *Acaulospora* spp. and no inoculated control (Table 3).

Comparing the species of *E. contortisiliquum* and *P. reticulata* presented the higher P tissue concentrations when inoculated with *Glomus* sp. 1.

Table 2. Influence of AMF inoculation and phosphorus fertilization on *Enterolobium contortisiliquum* seedlings after 5 months growth.

Fertilization		Fungi				
		***Glomus* sp.1**	***Gigaspora margarita***	***Scutellospora heterogama***	***Acaulospora* spp.**	**Control [α]**
Height (cm)	25 (32.5 mgPdm^{-3})	29 a	23.25a	17.33 a	30 a	
	50 (65 mgPdm^{-3})	21.67a	38 b	13.67 a	22.5 a	
	100 (136mgPdm^{-3})	39.67 b	46 b	21.33 a	15.5 a	26.33 a
Shoot dry weight (g)	25%	0.7667 a	1.16a	0.46 a	0.9633a	
	50%	0.7367 a	1.1667a	0.5133 a	1.1733a	
	100%	1.9167 b	1.515 b	0.5967a	0.6033a	0.8367 a
Root dry weight (g)	25%	1.147b	2.325b	0.39 a	0.677a	
	50%	0.6 a	3.765c	0.42 a	1.887b	
	100%	3.91 b	1.325a	1.19 a	1.79a	1.01a
Phosphorus concentration[β]	25%	1.094 a	1.528 a	0.738 a	1.809a	
	50%	2.166 a	1.52 a	0.936 a	1.05 a	
	100%	5.722 b	3.288 ab	1.046 a	0.941 a	0.935 a

Values are means for three separated harvest. Values followed by the same letter do not differ significantly by one-way ANOVA and Tukey's HSD test ($P \leq 0.05$).
[α] Control = 100% Phosphorus (136 mg dm^{-3})
[β] Phosphorus concentration in leaves (mg g^{-1})

Table 3. Influence of AMF inoculation and phosphorus fertilization on *Plathymenia reticulata* seedlings after 5 months growth.

Fertilization		Fungus				
		***Glomus* sp. 1**	***Gigaspora margarita***	***Scutellospora heterogama***	***Acaulospora* spp.**	**Control[α]**
Height (cm)	25 (32.5 mgPdm^{-3})	4.75 a	6.0 a	8.233 a	11.53 a	
	50 (65 mgPdm^{-3})	8.25 a	6.7 a	10.0 a	8.667 a	
	100 (136mgPdm^{-3})	13.567 b	7.033 a	17.0 b	11.167 ab	15.167 b
Shoot dry weight (g)	25 %	0.145 a	0.045 a	0.35 a	0.3467 a	
	50 %	0.445 a	0.19 a	0.30 a	0.5033 a	
	100 %	1.0867 b	0.2733 a	0.6867 ab	0.3433 a	0.676 ab
Root dry weight (g)	25 %	0.17a	0.07a	0.40 a	0.25a	
	50 %	0.31 a	0.21 a	0.33 a	0.36 a	
	100 %	0.8 a	0.17 a	0.37 a	0.24 a	0.38 a
Phosphorus concentration[β]	25 %	0.1703 a	----------	0.1637 a	0.332 a	
	50 %	0.5755 a	0.0971 a	0.6245 a	0.2907 a	
	100 %	1.5288 c	0.3356 a	1.0305 bc	0.4201 ab	0.8405 b

Values are means for three separated harvest. Values followed by the same letter do not differ significantly by one-way ANOVA and Tukey's HSD test ($P \leq 0.05$).
[α] Control = 100% Phosphorus (136 mg dm^{-3})
[β] Phosphorus concentration in leaves (mg g^{-1})

Discussion

Individual tree species can be considered as the basic unit for forest regeneration, either through natural succession or through reforestation (Siqueira et al., 1998). Although their major features related to successional habit have been identified (Budowski, 1965), fundamental physiological aspects of seedling growth requirements still remain as a great gap in our knowledge (Gomez Pompa and Burley, 1991). Our results showed aleatory responses to either inoculation with different AM fungal species or phosphorus addition.

Nevertheless A. peregrina did not show significantly differences in growth parameters and phosphorus concentration in leaves, it can be noted that *Scutellospora heterogama* improve those parameters. This fact could be taken in consideration because physiological characters of pioneers plants such as tolerance, high nutrient absorption and accumulation capacity, high photosynthetic rate and abundant small seeds (Bazzaz, 1991) which contributed to the partnership of the host plant with an obligatory mutualistic AMF symbiont (Siqueira et al., 1985).

E. contortisiliquum and *P. reticulata* were significantly beneficed when were inoculated with *Glomus* sp. 1-*Gigaspora margarita* or *Glomus* sp.1-*Scutellospora heterogama*, respectively.

Considering the basic biology of plant-fungus interactions, it is to be expected that the AMF root length colonization and related plant responses vary in different plant-fungus combinations (Smith and Read, 1997). This study of three trees species from Brazil inoculated with a single fungus isolate provides useful information. This is particularly true in the case of *Glomus* sp. 1 isolate used in this study. We found wide variation in host mycorrhiza responsiveness among *A. peregrina* fertilized with 65 mg P dm-3, and *Glomus* sp. 1-*G. margarita* or *Glomus* sp. 1-*S. heterogama* in *E. contortisiliquum* and *P. reticulate*, respectively. Considering that there is little or no evidence for host-fungus specificity in AMF, differences in plant susceptibility to mycorrhiza formation and responsiveness can be attributed mostly to the host genome rather than that of the fungus (Siqueira and Saggin-Júnior, 2001).

It is important to know the response to fertilization and inoculation with AMF species. In our study we provide information on the trees species initial growth, suggesting that the pioneer plant *A. peregrina* is non-mycotrophic and secondary species like *E. contortisiliquum* and *P. reticulata* showed a certain degree of mycotrophy. In this way, P fertilizer should be applied in order to guarantee adequate seedling development of these AMF-independent and P-responsive species. Nevertheless, more studies are necessary in order to found

the most appropriate host-fungus combination and to adjust the level of fertilizer applied.

Acknowledgements

The authors are grateful to CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for a scholarship granted to Marcela C. Pagano. We thank Alexander Diego da Silva and Gustavo Assis for helpful in the experimental work. M. N. Cabello is a researcher from CIC, Argentina.

References

Bazzaz, F. A. (1991). Regeneration of tropical forests: physiological responses of pioneer and secondary Species. In: Rain Forest Regeneration and Management (eds. A. Gomez-Pompa, T. C. Whitmore and M. Hadley). The Parthenon Publishing Group, Paris: 91–118.

Budowski, A. (1965). Distribution of tropical American rain forest species in the light of succession progress. Turrialba 15: 40-42.

Burity, H. A., Lyra, M. C. C. P., Souza, E. S., Mergulhão, A. C. E. S. and Silva, M. L. R. B. (2000). Efetividade da inoculação com rizóbio e fungos micorrízicos arbusculares em mudas de sabiá submetidas a diferentes níveis de fósforo. Pesquisa Agropecuária Brasileira 35: 801-807.

Carneiro, M. A. C., Siqueira, J. O., Moreira, F. M. S., Carvalho, D., Botelho, S. A. and Saggin-Junior, O. J. (1998). Micorriza arbuscular em espécies arbóreas e arbustivas nativas de ocorrência no Sudeste do Brasil. CERNE 4: 129-145.

Durigan, G. and Silveira, E. R. da (1999). Riparian forest restoration in cerrado, Assis, SP, Brazil. Scientia Forestalis 56: 135-144.

Fitter, A. (1991). Costs and benefits of mycorrhizas: implications for functioning under natural conditions. Experientia 47:350-355.

Gomez-Pompa, A. and Burley, F. W. (1991). The management of natural tropical forests. In: Rain Forest Regeneration and Management (eds. A. Gomez-Pompa, T. C. Whitmore and M. Hadley). The Parthenon Publishing Group, Paris: 3-17.

Gonçalves, J. L. de M., Kageyama, P. Y., Freixêdas, V. M., Gonçalves, J. C. and Geres, W. L. de A. (1992). Capacidade de absorção e eficiência nutricional de algumas espécies arbóreas tropicais. Anais do Congresso Nacional Sobre Essências Nativas, 2, São Paulo, Instituto Florestal: 463-469.

Govindarajulu, M., Pfeffer, P. E., Jin, H., Abubaker, J., Douds, D. D., Allen, J. W., Bücking, H., Lammers P. J. and Shachar-Hill, Y. (2005). Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature 435: 819-823.

Hoagland, D. R. and Arnon, D. I. (1951). The water culture method for growing plants without soil. University of California, Berkely, CA: 1-32.

Jakobsen, I., Abbott, L. K. and Robson, A. D. (1992). External hyphae of vesicular-arbuscular mycorrhizal fungi associated with Trifolium subterraneum L.: Spread of hyphae and phosphorus inflow into roots. New Phytologist 120: 371-380.

Lorenzi, H. (2000). Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. 3rd ed. Nova Odessa, Instituto Plantarum, São Paulo.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. and Kent, J. (2000). Biodiversity hotsposts for conservation priorities. Nature 403: 853–858.
Pagano, M. C. (2007). Characterization of Glomalean mycorrhizal fungi and its benefits on plant growth in a semi-arid region of Minas Gerais (Jaíba Project), Brazil. PhD thesis. Federal University of Minas Gerais, Belo Horizonte, Brazil.
Paron, M. E., Siqueira, J. O., Curi, N. and Vale, F. R. (1996). Crescimento da Copaíba e Guatambú em resposta a Fungo Micorrízico, Superfosfato, Nitrogênio e Fumigação do solo. Cerne 2, 2.
Patreze, C. M. (2003). Fixação de nitrogênio e micorrização em leguminosas de mata ciliar. M.S. Thesis, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro.
Pereira, E. G., Siqueira, J. O., Curi, N., Moreira, F. M. S. and Purcino, A. A. C. (1996). Efeitos da micorriza e do suprimento de fósforo na atividade enzimática e na resposta de espécies arbóreas ao nitrogênio. Revista Brasileira Fisiologia Vegetal 8:59-65.
Rillig, M. C. (2004). Arbuscular mycorrhizae and terrestrial ecosystem processes. Ecology Letters 7: 740–754.
Rizzini, C. T. (1997). Tratado de fitogeografia do Brasil: aspectos ecológicos, sociológicos e florísticos. Âmbito Cultural Edições Ltda. Rio de Janeiro.
Sarruge, J. R. and Haag, H. P. (1974). Análises químicas em plantas. Piracicaba: ESALQ-USP. São Paulo.
Schüβler, A., Schwarzott, D., Walker, C. (2001). A new fungal phylum, the Glomeromycota: phylogeny and evolution. Mycological Research 105: 1413-1421.
Scotti, M. R. M. and Correa, E. J. A. (2004). Growth and litter decomposition of woody species inoculated with rhizobia and arbuscular mycorrhizal fungi in Semiarid Brazil. Annals of Forest Science 61:87-95.
Siqueira, J. O., Sylvia, D. M., Gibson, J. and Hubbell, D. H. (1985). Spore germination and germ tube growth of vesicular-arbuscular mycorrhizal fungi. Canadian Journal of Microbiology 31: 965-972.
Siqueira, J. O., Carneiro, M. A. C., Curi, N., Silva, S. C. da and Davide, A. C. (1998). Mycorrhizal colonization and mycotrophic growth of native woody species as related to successional groups in Southeastern Brazil. Forest Ecology and Management 107: 241-252.RIGINAL PAPER
Siqueira, J. O. and 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. and Read, D. J. (1997). Mycorrhizal Symbiosis. 2nd edn. Academic Press, London.
van der Heijden, M. G., Wiemken, A. and Sanders, I. R. (2003). Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. New Phytologist 157: 569-578.
Vance, C. P., Uhde-Stone, C. and Allan, D. L. (2003). Phosphorus acquisition and use: critical adaptations by plants for securing a non-renewable resource. New Phytologist 157: 423-447.

(Received 29 August 2007; accepted 27 October 2007)