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Phosphorus nutrition of ectomycorrhizal and arbuscular mycorrhizal tree seedlings from a lowland tropical rain forest in Korup National Park, Cameroon

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ABSTRACT. The relationship between mycorrhizal colonisation and phosphorus acquired by seedlings of the arbuscular mycorrhizal tree *Oubanguia alata* Bak f. (Scytopetalaceae) and the ectomycorrhizal tree *Tetraberlinia moreliana* Aubr. (Caesalpinioideae) was evaluated at low and high inorganic phosphorus availability. AM colonisation was positively correlated with phosphorus uptake by *O. alata* at low, but not at high phosphorus availability. Seedlings growth was positively related to arbuscular mycorrhizal colonisation at both low and high phosphorus availability, suggesting that growth promotion by arbuscular mycorrhizas is not simply related to an increase of phosphorus uptake. In contrast, phosphorus uptake by *T. moreliana* was correlated with EM colonisation at both low and high phosphorus availability, but there was no relationship between growth and ectomycorrhizal colonisation. Promotion of phosphorus uptake by arbuscular mycorrhizas and ectomycorrhizas at low phosphorus availability is consistent with the co-occurrence of the two types of mycorrhiza in tropical rain forests where available soil phosphorus is low. However, ectomycorrhizal colonisation may also be of advantage where inputs of phosphorus rich litter raise the phosphorus status of the soil, as seen in the groves of ectomycorrhizal trees in Korup National Park, and may be one of the factors reinforcing local dominance by these trees.

KEY WORDS: arbuscular mycorrhiza, Caesalpinioideae, co-occurrence, ectomycorrhiza, phosphorus, rain forest, Scytopetalaceae, tropics.

INTRODUCTION

It is well documented that mycorrhizal fungi can transfer phosphorus (P) to the host in both ectomycorrhizas (EM) (e.g. Melin & Nilsson 1958) and arbuscular

mycorrhizas (AM) (e.g. Cox *et al.* 1975), and that this can result in an increase of P uptake by plants colonised by EM (Jones *et al.* 1990, 1991) or AM (Sanders & Tinker 1971, 1973; Smith 1982). However, most of the work has been performed using temperate species. In tropical rain forests, almost all tree species are mycotrophic (Alexander 1989), but while nutrient supply (particularly P) is generally regarded as a critical factor in tropical tree growth (Proctor 1989, Vitousek 1984), the role that mycorrhizal fungi play rests largely on inference rather than experimental data.

In most experiments with tropical rain forest tree species, the influence of AM fungi on P nutrition has been evaluated indirectly by measuring the growth response of inoculated and non-inoculated plants cultivated in soils with controlled levels of P (e.g. Alexander *et al.* 1992, McHargue 1981; Janos 1977, 1980; Redhead 1975). Only a few experiments have evaluated plant P uptake in relation to AM colonisation and these were either on *Citrus* spp. seedlings (Kleinschmidt & Gerdemann 1972) or on a pioneer shrub (*Clusia minor* L.) in Venezuela (Cáceres & Cuenca 1996). Growth promotion by indigenous EM has been observed in four woody genera from tropical rain forests (Alexander *et al.* 1992, Lee & Alexander 1994, Janos 1985, Lee 1994, Redhead 1980), but only Lee & Alexander (1994) evaluated the influence of EM on the acquisition of P by native plants from tropical rain forests.

Evidence is accumulating which supports the hypothesis first substantiated by Sanders & Tinker (1971) for AM fungi and Melin & Nilsson (1950) for EM fungi that absorption of P by external hyphae of these types of mycorrhiza is more efficient than by the fine roots of their host. The resulting stimulation of P uptake typically decreases as soil P becomes less limiting for both AM (Sanders & Tinker 1971, 1973) and EM (Bougher *et al.* 1990, Jones *et al.* 1990, MacFall *et al.* 1991). Other structures present only in EM may also influence the uptake of P by their host. The fungal sheath covering the roots acts as an organ for P storage (Harley & Smith 1983). Skinner & Bowen (1974) demonstrated transport of P over distances of 12 cm in rhizomorphs, although the importance of this mechanism for P uptake by the plant still has to be demonstrated (Timonen *et al.* 1996). Excised EM (e.g. Alexander & Hardy 1981, Bartlett & Lewis 1973, Dighton 1991, Williamson & Alexander 1975) and EM mycelium from litter (Colpaert & Van Laere 1996) can produce phosphatases suggesting the ability to access organic forms of P, although this has not yet been confirmed.

Ideas on the ecological role of AM and EM in tropical rain forests are principally based on the occurrence and distribution of the two types of mycorrhiza and what we know of their role in temperate ecosystems. Indigenous tropical tree species are commonly associated with AM (e.g. Béreau & Garbaye 1994, De Alwis & Abeynayake 1980, Janse 1896, Lodge 1987, Moyersoen 1993, Newbery *et al.* 1988). Since it has been hypothesised that P is the limiting element in most tropical rain forests (Vitousek 1984, Vitousek & Sanford 1986), AM

might be expected to play an important role in P nutrition. However, recent findings show that P does not always limit the growth of tropical rain forest seedlings (Burslem *et al*. 1995, Raaimackers & Lambers 1996). The occurrence of EM in the tropics on extremely poor soil (Högberg & Piearce 1986, Moyersoen 1993, Newbery *et al*. 1988, Singer & Araujo 1979, 1986) suggests that EM are particularly beneficial in these habitats. Morphological and physiological differences between EM and AM might determine their success in different habitats as hypothesised by Read (1991) at a global scale and by Janos (1985) for the tropical areas. Some tropical tree taxa might have evolved the ability to associate with EM as a response to habitat specialisation, as suggested at a global scale by Fitter & Moyersoen (1996).

In this study we compare P uptake by one AM and one EM tree species from tropical rain forest to test the hypothesis that they differ in their ability to acquire inorganic phosphorus (Pi) from soil. We used seedlings of species from an Atlantic rain forest in Korup National Park, SW Cameroon (Gartlan *et al*. 1986): *Oubanguia alata* Bak f. (Scytopetalaceae), an understorey/canopy species, is AM and is abundant and widely distributed in the southern part of the Park (Gartlan *et al*. 1986). *Tetraberlinia moreliana* Aubr. (Caesalpinioideae) in contrast, is a large emergent which forms EM and contributes a high proportion of the basal area in localised clumps of EM trees (Newbery *et al*. 1997). Previous field studies in Korup have shown that Pi availability in the mineral soil is low and may influence the distribution of tree species (Gartlan *et al*. 1986, Newbery *et al*. 1988, 1997). The study reported here is part of a wider investigation into the growth and nutrition of ectomycorrhizal legumes in Korup.

METHODS

Experimental material and growth conditions

In November 1995, 20-wk old *T. moreliana* seedlings and 15-wk old *O. alata* seedlings were lifted from a nursery established at Mana Bridge (by J. J. Green) on the edge of Korup National Park. The seedlings had been grown in a mixture of mineral soil from a palm plantation with organic matter and litter collected underneath adult trees of the same species in the forest in order to promote a natural mycorrhizal colonisation. The plants were transported, bare-rooted in insulated boxes, by air to Aberdeen and potted in 3-l containers (16 cm diameter, 19 cm deep) containing a 1:1 mixture of coarse acid river sand and soil from the B horizon of an iron podzol from Glen Dye, Aberdeenshire (see Sanger *et al*. 1994 for the description of main chemical characteristics). The resulting texture was a coarse loamy sand. The intention was to simulate the soil of the natural forest (i.e. oxisol/ultisol with high levels of Fe-oxides and hydroxides and high free-Al). All pots received 10 g m^{-2} of slow release N fertiliser as urea (Gold N, Canadian Industries Limited) and full strength Rorison (-N, -P) solution (Hendry & Grime 1993). Rorison solution (-N, -P) was applied a second time 2 mo after the start of the experiment.

The main chemical characteristics of the soil samples at the end of the experiment were (n = 6): pH(H_2O) 4.8, pH($CaCl_2$) 4.2, Ca (in 1 M ammonium acetate) 0.13 mg g^{-1}, Mg (in 1 M ammonium acetate) 0.02 mg g^{-1}, total N (Kjeldhal) 0.01%.

The plants were arranged on the greenhouse bench under six polythene cloches to maintain high temperature and high relative humidity, and watered to field capacity every 2 d during the experiment with tap water at room temperature. The bench was covered by a wet capillary matting and the plants were misted three times a day with warm water. The temperature in the cloches was maintained between 20 and 35 °C (exceptionally up to 38 °C) and the relative humidity between 60 and 98% (exceptionally down to 35%). Supplementary lighting was provided to give a minimum day length of 12 h. The range of PAR (400–700 nm) measured with a light sensor (Skye Instruments, Wales) in the six cloches in contrasting situations was between 140 to 320 μmol m^{-2} s^{-1} (after dusk) and 330 to 640 μmol m^{-2} s^{-1} (bright day at midday).

Experimental design

There were six P treatments, obtained by applying 0, 3, 15, 30, 150 or 300 mg P kg^{-1} dry soil as sparingly soluble rock phosphate (Scotphos Limited) to each pot. P fertiliser was ground to pass a 250-μm mesh, suspended in 200 ml water and applied onto the soil once at the start of the experiment (2 December 1995). Eight holes with a diameter of 5 mm each, to 3/4 depth of the pot were made at equal distance from the base of the stems to allow for a deeper penetration of the P fertiliser.

The pots were arranged in randomised block design, each of the six cloches on the greenhouse bench representing a block. Due to the difference in sizes between the plants of each species at the start of the experiment, the seedlings were ranked by size and an equal number of each size category allocated to each P treatment. There were three plants of each species and of each P treatment in each block. The pots were re-randomised three times in each block during the course of the experiment. Harvests were made after 9, 14 and 19 wk (*O. alata*) or 11, 17, 23 wk (*T. moreliana*). Because of differences in seedling mortality between blocks, between four and six replicates of each species (maximum one per block) in each P treatment were harvested. The plants were planted on 2 December 1995 and the final harvest was on 16 April 1996 (*O. alata*) and 13 May 1996 (*T. moreliana*).

Harvesting

Height (the maximum distance between the soil and the apex of the plant) and the total number of leaves (including cotyledons) were recorded at the start of the experiment and at each harvest. The plants were severed at ground level, and stem and foliage were dried at 60 °C for at least 5 d before dry weight measurement. Intact root systems were carefully separated from the

soil. The soil was then sieved (0.5-mm mesh) to recover any broken roots. The root system was spread on a A3-size glass and photocopied for root length measurement (see also below). A sub-sample of fine roots was taken at random for assessment of mycorrhizal colonisation (see also below). The dry weight of the remaining fine roots and coarse roots was obtained as above, after recording their fresh weight. The fresh to dry weight ratio of the fine roots was used to estimate the dry weight of the sub-sample used for mycorrhizal assessment.

The total root length of each sample was measured using the line intercept method (Tennant 1975) on the photocopies of the root system. The fractional colonisation of *T. moreliana* by EM was scored with a dissecting microscope using Hatch's method (1937). EM characteristics were easily recognisable, and no staining was necessary for their scoring, but their colonisation was confirmed by observing a Hartig net in selected squashed roots cleared and stained using a phenol-free modification of Philips & Hayman's (1970) method. Between 39 and 306 tips were scored per sample, and the total amount of tips colonised by EM was estimated multiplying the total root length by the fraction of tips colonised.

Roots of *O. alata* were cleared and stained in the same way and the fractional colonisation by AM was scored with a compound microscope (magnification, ×200) using the method of McGonigle *et al.* (1990). Between 22 and 73 microscope fields were scored per slide, and three slides were screened for most of the samples. Arbuscules were frequently observed, but coils and vesicles were also scored as AM. The total root length colonised by AM was estimated by multiplying the total root length by the fractional colonisation. Roots from randomly selected plants were screened to confirm the presence of AM and EM at the start of the experiment.

Chemical analysis

A sub-sample of soil from the pot of each harvested plant was air-dried at room temperature and soil inorganic P was extracted using an anion resin (Allen 1989). Pi concentration in the extract was determined by flow injection colorimetry using the phosphomolybdenum-blue reaction. After dry weight measurement, roots, stem and foliage of each plant were ground in a stainless steel ball-mill. P concentration was determined as before after digesting the material using H_2SO_4-H_2O_2 (Allen 1989).

Statistical analysis

To allow for the analyses of an unbalanced design, the General Linear Model of ANOVA (MINITAB v.10) was used to test for the effect of P treatments on P content and for the comparison of root characteristics between species and harvests. The relationship between plants characteristics (height and number of leaves increase, dry weight, P concentration in tissues, P content, root length), mycorrhizal colonisation and extractable P was tested using a correlation analysis (Pearson's coefficient). Data on fractional colonisation were

arcsin-transformed in order to meet assumptions of a normal distribution. For clarity, only data from the third harvest are presented in detail.

RESULTS

Only high P application rates increased soil P availability (Figure 1). The lowest three rates (0, 3 and 15 mg P kg^{-1}) did not raise the extractable Pi

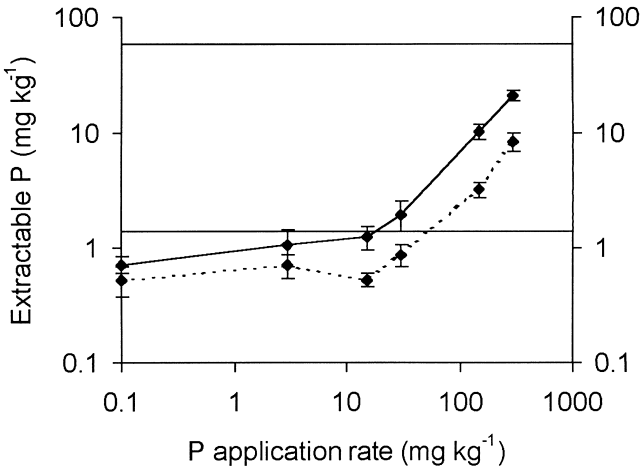

Figure 1. Mean resin extractable P in relation to rock P application over harvest one (——) and three (- - -). For comparison, concentrations of P extracted by anion exchange resin from field soils were 45–73 mg kg^{-1} in the litter layer and 1.1–1.7 mg kg^{-1} in the mineral soil (Newbery *et al.* 1997); horizontal lines represent mean values for these two layers.

concentration, even at the first harvest, but the highest three rates (30, 150 and 300 mg P kg^{-1}) all raised Pi concentration significantly. At the three highest rates, Pi concentrations were initially higher than those found in the mineral soil at the field site in Korup National Park by Newbery *et al.* (1997), but lower than the concentration in the litter.

There was no significant relationship ($P > 0.05$) between the increase in either height or total number of leaves of the seedlings between the start of the experiment and the third harvest and extractable P (*T. moreliana*, height increase: $t_{30} = 1.189$; number-of-leaves increase; $t_{30} = 1.236$; *O. alata*, height increase: $t_{25} = -1.062$; number-of-leaves increase: $t_{25} = -1.026$). Mean dry weights (± SE) of the seedlings at the first and the third harvest were 2.58 (± 0.12) g and 4.48 (± 0.26) g for *O. alata* and 3.17 (± 0.11) g and 5.38 (± 0.17) g for *T. moreliana*, respectively. No significant relationship ($P > 0.05$) was found between seedling dry weight and extractable P at the three harvests for either species. (*T. moreliana*, harvest 1: $t_{33} = 0.538$; harvest 2: $t_{33} = 0.806$; harvest 3: $t_{30} = 0.632$; *O. alata*, harvest 1: $t_{33} = 0.524$; harvest 2: $t_{26} = -0.029$; harvest 3: $t_{25} = -0.831$).

No significant relationship ($P > 0.05$) was also found between P concentration in foliage, stem and roots and extractable P concentration at the third harvest for either species (*T. moreliana*, foliage: $t_{30} = 1.786$; stem: $t_{30} = 1.639$; roots: $t_{30} = 2.028$; *O. alata*, foliage: $t_{25} = 0.713$; stem: $t_{25} = 0.072$; roots: $t_{25} =$

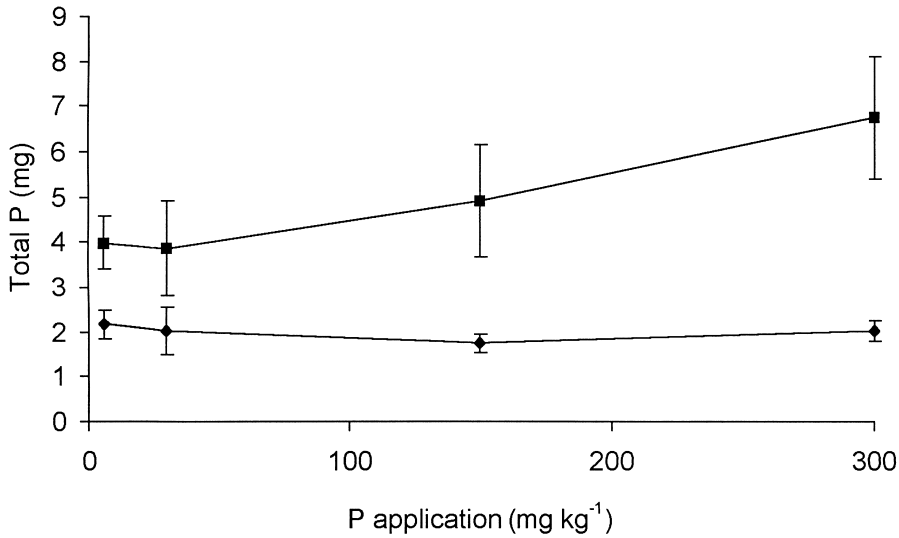

Figure 2. Mean total P content of *O. alata* (◆) and *T. moreliana* (■) in relation to P application treatments at harvest three. The replicates of 0, 3, 15 mg kg^{-1} rock P applied are combined within a '6 mg kg^{-1}' rock P applied treatment.

-0.023). Figure 2 shows the total P content of *O. alata* and *T. moreliana* seedlings at different P application treatments at the third harvest. Because the three lower P application treatments (0, 3, 15 mg kg^{-1} added) did not affect extractable P values in the soil, these treatments have been plotted as a single P application treatment, presented in Figure 2 as '6 mg kg^{-1}' (i.e. the average of the three lower -P application rates). There were no significant differences ($P > 0.05$) in total P content of *T. moreliana* and *O. alata* seedlings due to P application (*T. moreliana*, $F_{3,28} = 1.77$; *O. alata*, $F_{3,23} = 0.15$). In both species, the total P content varied widely among replicates, as shown by the standard errors (Figure 2). The extent of both AM and EM fractional colonisation varied greatly among plants but was unaffected by extractable P concentration (Figure 3) and did not vary between harvests.

Taking into account the wide variation in P content between replicates and the absence of any significant relationship between plant dry weight or P concentration in plant tissues and extractable P concentration in the soil, we tested whether plant P concentration was affected by the degree of mycorrhizal colonisation. Highly significant relationships were found between P concentration in plant tissues of both species and fractional mycorrhizal colonisation at the third harvest (Table 1). Because there was no relationship (Table 1)

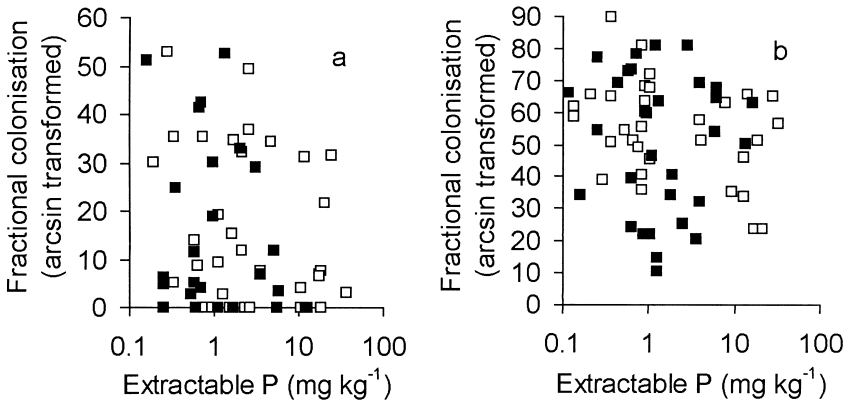

Figure 3. Mycorrhizal fractional colonisation of (a), *O. alata* and (b) *T. moreliana* in relation to extractable P at harvests one (□) and three (■).

Table 1. Correlations of total root length, P concentration in foliage, stem and roots of O. *alata* and *T. moreliana* and mycorrhizal fractional colonisation and plant dry weight at the third harvest.

Species		Fractional colonisation	Total dry weight
O. alata (n = 28)	Total root length	–0.009	0.740***
	P concentration: foliage	0.635***	–0.052
	stem	0.405*	–0.038
	roots	0.416*	–0.102
T. moreliana (n = 33)	Total root length	0.572***	0.571***
	P concentration: foliage	0.797***	0.044
	stem	0.826***	0.128
	roots	0.800***	0.302

* $P \leq 0.05$, *** $P \leq 0.001$.

between dry weight and P concentration in either species, or between root length and fractional colonisation in *O. alata* we conclude that the relationship between P concentration in plant tissues and mycorrhizal fractional colonisation is not due to the size of the plants. Although there was a positive relationship between *T. moreliana* root length and fractional colonisation at the third harvest (Table 1), the correlations between P concentration in plant tissues and root length (foliage: $r_{31} = 0.317$, $P > 0.05$; stem: $r_{31} = 0.567$, $P < 0.01$; roots; $r_{31} = 0.602$, $P < 0.001$) were weaker than those with fractional colonisation (Table 1).

Since fractional mycorrhizal colonisation influenced P concentration in plant tissues, we evaluated the effect of mycorrhizal colonisation on P acquisition of the two species at different levels of P availability in the soil (Table 2). Because only the three higher P application rates (30, 150, 300 mg kg^{-1}) raised the concentration of extractable P, these three treatments were grouped as a single high P application rate treatment, whereas the three lowest P application rates were grouped in a single low P application treatment. Total P content of both *O. alata* and *T. moreliana* seedlings was a function of mycorrhizal colonisation

Table 2. Correlations of total P content and estimated root length colonised by AM and number of root tips colonised by EM, and of total P content per unit root length and mycorrhizal fractional colonisation of *O. alata* and *T. moreliana*, at low (0, 3, 15 mg kg^{-1}) and high (30, 150, 300 mg kg^{-1}) P application treatments at the third harvest.

Species	P application treatment (n)	P total and total colonisation		P total per root length and fractional colonisation	
		r	P	r	P
O. alata	Low (15)	0.843	<0.001	0.842	0.001
	High (12)	0.588	0.045	0.145	0.652
T. moreliana	Low (18)	0.892	<0.001	0.730	0.002
	High (16)	0.808	<0.001	0.694	0.002

at both low and high P application rate at the third harvest. A similar result was obtained when the 30 mg P kg^{-1} treatment was grouped with the low P treatment.

Furthermore, as mycorrhizal colonisation acts by increasing P inflow (uptake per unit root length), we calculated the correlation coefficient between the total P accumulated by the plants per unit root length (as a surrogate for inflow) and fractional colonisation (Table 2). In *O. alata*, colonisation was related to P content per unit root length at low, but not at high P application rates, whereas in *T. moreliana* EM fractional colonisation was related to P content per unit root length at both low and high P availability at the third harvest. Similar results were obtained if the 30 mg P kg^{-1} treatment was grouped with the low P treatment.

Height increase of *O. alata* at the third harvest was positively related to root length colonised by AM (Table 3). The increase in the total number of leaves showed the same response (data not shown). In contrast, no clear relationship was found between either the height increase (Table 3) or the increase in total number of leaves (data not given) of *T. moreliana* in relation to the estimated amount of tips colonised by EM. The relationship between the total dry weight and mycorrhizal colonisation was statistically significant for *O. alata* only for the third harvest at high P application ($r_{10} = 0.609$, $P = 0.036$), whereas no relationship ($P > 0.05$) was found for *T. moreliana* at the third harvest (low P application treatment: $t_{13} = 1.789$; high P application treatment: $t_{15} = 1.853$).

Specific root length (i.e. length per unit root weight) and root fraction (i.e. root weight as a proportion of total dry weight) were measured at harvests one

Table 3. Correlations of height increase of *O. alata* and *T. moreliana* between start of the experiment and the third harvest against estimated root length colonised by AM and number of root tips colonised by EM at low (0, 3, 15 m kg^{-1}) and high (30, 150, 300 mg kg^{-1}) P application treatments.

Species	P application treatments (n)	r	P
O. alata	Low (15)	0.659	0.008
	High (12)	0.900	0.001
T. moreliana	Low (15)	0.015	0.958
	High (17)	0.376	0.137

Table 4. Root fraction and specific root length of *O. alata* and *T. moreliana* at harvests one and three.

		Root fraction		Specific root length (m g^{-1})	
Harvest	Species (n)	Mean	SE	Mean	SE
1	*O. alata* (35)	0.36*	0.010	7.46†	0.205
	T. moreliana (34)	0.31*†	0.007	8.25	0.576
3	*O. alata* (27)	0.39	0.012	4.99*†	0.225
	T. moreliana (32)	0.37†	0.009	8.15*	0.414

*: Statistically significant difference ($P \leq 0.001$) between the two species, within the same harvest: †: statistically significant differences between the two harvests, within the same species ($P \leq 0.001$).

and three (Table 4). The two species had a similar root fraction, although *O. alata* allocated 5% more biomass to the root system at harvest one ($F_{1,63} = 17.87$, $P < 0.001$). The specific root length was lower in *O. alata* than *T. moreliana* and declined with age, confirming the visual impression that *O. alata* has a less finely-divided root system than *T. moreliana*.

DISCUSSION

The clear relationship between P uptake and mycorrhizal colonisation in *T. moreliana* observed in this study gives further support to the existence of a functional relationship between EM colonisation and P acquisition by tree species from lowland tropical rain forests. The relationship between AM colonisation and P acquired by *O. alata* at lower soil P availability is consistent with the previous reports concerning the positive influence of AM on the P acquisition of tropical rain forest indigenous woody species (Cáceres & Cuenca 1996, Kleinschmidt & Gerdemann 1972).

The comparison of the role of EM and AM is confounded in this study because we used two different tree species with different growth and nutritional physiology. *O. alata* and *T. moreliana* were selected because they co-occur in the same forest (Gartlan *et al.* 1986), and must therefore share some ecological requirements. Ideally, the effect of EM and AM colonisation should be compared on the same host species, but tree species with dual mycorrhizal colonisation are uncommon in the forest we studied (Newbery *et al.* 1988; B. Moyersoen *et al.*, unpubl. data). Conclusions about comparative mycorrhizal functioning must therefore be drawn with caution.

The differences in the relationship between P content of the plant and total root length (or tips) colonised, and the P acquired expressed per unit root length and fractional colonisation, show how difficult it is to isolate mycorrhizal colonisation from root length as a factor influencing P uptake by the plant. In this study, P application rate was varied, but had little direct effect on plant growth or P uptake. However, there was wide variation in colonisation intensity. This was not caused by P application treatment and presumably resulted from natural variation in inoculum in the nursery. We therefore considered the relationship between mycorrhizal colonisation and P content under high

and low P applications to separate its effect from those of P application rate. We also expressed P uptake as a function of root length (by analogy with calculations of inflow) in order to allow for variation in plant size. The relationship between P uptake of *O. alata* and mycorrhizal colonisation only at low P availability suggests that this species is partially dependent on AM for the absorption of P. In contrast, EM increased P uptake by *T. moreliana* at both low and high P availability. A possible explanation for this difference of P acquisition between AM and EM species could be that *O. alata* has a more effective root system for the absorption of P. This is unlikely because *T. moreliana* has a higher specific root length than *O. alata*, and fine roots are normally regarded as more effective in P uptake. A more plausible explanation is that EM are more effective than AM in increasing P uptake, so that their effect is additive to the effect of an increase of P availability. Consequently, the P acquired by *T. moreliana* is a function of an interaction between the EM colonisation and the P available in the soil.

The significant positive relationship between AM colonisation and both P acquisition and height increase at low P availability demonstrates that AM can improve the growth of indigenous tropical tree seedlings through an increase of P uptake. This supports the conclusion of previous studies where the positive growth response to AM was attributed indirectly to an increase of P uptake (e.g. Janos 1975, 1977, 1980; McHargue 1981, Redhead 1975). However, growth promotion by AM was also observed at high P availability in the soil. Because AM did not promote P acquisition per unit root length at high P availability, these results suggest that the promotion of plant growth by AM is not simply related to an increase of P uptake by the plant and support the hypothesis of a broader functional role of AM (Fitter *et al.* 1996).

In contrast, no clear relationship was found between either P availability in the soil or EM colonisation and the growth of *T. moreliana*. The slow growth rate of the seedlings under our experimental conditions suggest that this tree species has a conservative growth strategy. Consequently, the additional P acquired by *T. moreliana* as a result of increased EM colonisation tends to accumulate in the plant without being used in increased growth. However, growth rate of *T. moreliana* seedlings of the same development stage in nurseries under field conditions can be much greater than achieved in this greenhouse study. Some factor other than P might therefore have limited the growth of *T. moreliana* in our experiment. In addition, EM colonisation may have been high enough to provoke a growth depletion of these young seedlings as a consequence of the carbon drain from the host to the mycorrhizas similar to that reported for *Pinus* spp. (Colpaert *et al.* 1992, Conjeaud *et al.* 1996). Our results demonstrate the complexity of studying P as a limiting factor controlling the growth of tropical tree seedlings and the importance of including a comprehensive study of mycorrhizas for understanding the P nutrition of tropical tree seedlings.

Although this experiment used young tree seedlings and did not permit a comparison of the relative cost of EM and AM, the results do contribute to our understanding of the role of mycorrhizal type in the distribution of their respective partners in different habitats. Studies in Korup National Park forest have shown that EM and AM tree species have different patterns of distribution, related to soil P availability (Gartlan *et al.* 1986; Newbery *et al.* 1988, 1997). Since some EM tree species tend to form clumps in the areas of the forests where P availability in the mineral soil is lower, it was hypothesised that EM are more advantageous there. In contrast AM tree species were more widely distributed. Our data show that both EM and AM improve the P acquisition of seedlings at low P availability. Although the influence of mycorrhizas on *T. moreliana* and *O. alata* P uptake should be compared with other host species and under field conditions, our results suggest that both EM and AM should promote the establishment of seedlings in the least fertile areas of the forest. The frequent occurrence in tropical rain forests on poor soils of AM hosts where EM tree species are an important component (Alexander *et al.* 1992, Högberg & Piearce 1986, Moyersoen 1993, Newbery *et al.* 1988, Reddell *et al.* 1996) is consistent with this hypothesis.

Our results suggest that even at high soil P availability, the P acquired by *T. moreliana* seedlings is closely related to the extent of EM colonisation. In other words, the potential improvement of the nutrient status of the EM seedlings in a P-enriched soil will strongly depend on their mycorrhizal colonisation. A greater litter P concentration and P input to the soil from litter have been observed in patches of the Korup National Park forests where *T. moreliana* is co-dominant with two other species in the Caesalpinioideae (Newbery *et al.* 1997). This, added to our findings, supports the hypothesis that EM trees give rise to soil conditions in which the EM association has a competitive advantage (Gadgil & Gadgil 1971, 1975; Northup *et al.* 1995, Newbery *et al.* 1997). The dependency of the host on EM across a wide range of soil P availability should promote the colonisation of EM seedlings in areas of the forest where EM inoculum is readily available. Alexander *et al.* (1992) demonstrated the importance of living roots as source of inoculum for dipterocarp seedlings. Inoculum distribution could be a factor in the clumping of *T. moreliana* trees in Korup National Park forest.

The range of Pi availability in the soil of our experiment was within the range of available P across the litter and soil horizons of Korup National Park rain forest described by Newbery *et al.* (1997). We cannot ignore the possibility that the effect of EM on P acquisition by *T. moreliana* may decline at higher P availability, as described in other tree species (Bougher *et al.* 1990, Conjeaud *et al.* 1996, Jones *et al.* 1990). The association with AM will be advantageous for P uptake of plants in areas of Korup National Park forest where P availability is low and might become less important to *O. alata* in richer soils. In areas of the forest where the presence of EM trees leads to a soil P enrichment, association with AM may be less advantageous than that with EM. Mycorrhizas

might influence EM trees distribution in local patches in the forest because of the distribution of fungal inoculum (Alexander *et al*. 1992), the relative benefits of EM and AM colonisation in relation to P supply (as shown by our data), or the greater carbon cost of EM associations (Janos 1985).

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