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Contrasting responses to ectomycorrhizal inoculation in seedlings of six tropical African tree species

Abstract Five caesalpinioid legumes, *Afzelia africana*, *Afzelia bella*, *Anthonotha macrophylla*, *Cryptosepalum tetraphylum* and *Paramacrolobium coeruleum*, and one Euphorbiaceae species, *Uapaca somon*, with a considerable range in seed sizes, exhibited different responses to inoculation by four species of ectomycorrhizal (ECM) fungi, *Scleroderma dictyosporum*, *S. verrucosum*, *Pisolithus* sp. and one thelephoroid sp. in greenhouse conditions. Thelephoroid sp. efficiently colonized seedlings of all of the five caesalpinioid legumes except *U. somon*, but provided no more growth benefit than the other fungi. Thelephoroid sp. and *S. dictyosporum* colonized seedlings of *U. somon* poorly, but stimulated plant growth more than the other fungi. The relative mycorrhizal dependency (RMD) values of the caesalpinioid legumes were never higher than 50%, whilst *U. somon* had RMD values ranging from 84.6 to 88.6%, irrespective of the fungal species. The RMD values were negatively related to seed mass for all plant species. Potassium concentrations in leaves were more closely related than phosphorus to the stimulation of seedling biomass production by the ECM fungi. Our data support the hypothesis that African caesalpinioid legumes and euphorbe tree species with smaller seeds show higher RMD values than those with the larger seeds.

Keywords Caesalpinioid legumes · *Uapaca somon* · Seed mass · Relative mycorrhizal dependency · Mineral nutrition

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Introduction

Ectomycorrhizal tree species in tropical Africa include many caesalpinioid legumes (12 genera in the Amherstieae and one genus, *Afzelia*, in the Detarieae) and some members of the Dipterocarpaceae (*Marquesia* and *Monotes*), Euphorbiaceae (*Uapaca*), Fabaceae (*Pericopsis*), Proteaceae (*Faurea*), Gnetaceae (*Gnetum*) and Sapotaceae (*Manilkara*) (Newbery et al. 1988; Thoen and Bâ 1989; Thoen and Ducousso 1989; Sanon et al. 1997; Torti and Coley 1999; Onguene and Kuyper 2001). Two new genera belonging to the caesalpinioid tribe Amherstieae, *Cryptosepalum tetraphyllum* and *Pelligriodendron diphyllum* (Bâ et al. 2000a), and one new family, Sarcolaenaceae (*Sarcolaena*, *Leptolaena* and *Schizolaena*) (Ducousso et al. 2004), have also been found to be colonized by ECM fungi in the Guinean and Malagasy rain forests, respectively. These ECM tree species are encountered in rain forests and dry woodlands (Buyck et al. 1996), and in the Miombo of Central Africa, the coastal woodland is dominated by ECM (Högberg and Nylund 1981). A similar situation occurs in West African woodlands and rain forests, where ectomycorrhizal trees in caesalpinioid legumes and Euphorbiaceae species are locally dominant (Thoen and Bâ 1989; Thoen and Ducousso 1989; Sanon et al. 1997).

Phosphorus (P) deficiency in soil is one of the limiting factors for tropical African tree growth (Duponnois and Bâ 1999; Bâ et al. 2000b), and it could be a critical key factor for the establishment of seedlings particularly when P content in seeds is low (Allsopp and Stock 1992; Zangaro et al. 2000). In this respect, seed size and P

content may be important factors affecting initial mycorrhizal colonization and plant growth (Allsopp and Stock 1992; Zangaro et al. 2000, 2003). In the case of arbuscular mycorrhizas, Allsopp and Stock (1992) showed that South African perennial fynbos plants with small seeds of low P contents tend to be more reliant on the mycorrhizal habit than large-seeded plants for growth in P-deficient soils.

Seeds of African caesalpinioid legumes and Euphorbiaceae species exhibit a considerable range in seed mass. We tested the hypothesis that plants having smaller seeds show greater ECM dependency than those with large seeds. For this, we assessed the effects of four ECM fungi, *Scleroderma dictyosporum* IR408, *S. verrucosum* IR500, *Pisolithus* sp. IR100 and one thelephoroid sp. ORSXM002, on growth and mineral nutrition in seedlings of five caesalpinioid legumes, *Afzelia africana*, *Afzelia bella*, *Anthonotha macrophylla*, *C. tetraphyllum* and *Paramacrolobium coeruleum*, and one Euphorbiaceae species, *Uapaca somon*, in greenhouse conditions.

Materials and methods

Soil preparation and inoculation

The soil used was a sandy top soil (0–20 cm) collected in a stand of *A. africana* Sm at Kolda in a southern Sudanese zone of Senegal (Diédhiou et al. 2004a). The soil was crushed, passed through a 2-mm sieve and autoclaved for 1 h at 120°C to eliminate native microflora. After autoclaving, the soil was stored 1 month. Soil analysis after sterilization gave 7.7% clay, 13.7% silt, 76.5% sand, 0.5% total carbon, 0.04% total nitrogen, C/N ratio 12.5, K 0.1 mEq 100 g^{-1} soil, Ca 2.6 mEq 100 g^{-1} soil, Mg 0.7 mEq 100 g^{-1} soil, 13.6 ppm P-Olsen, pH (H_2O) 7.0 and pH (KCl) 6.0. According to regional standards, this is NPK-deficient.

Four ECM fungi were used. *S. dictyosporum* Pat. IR408 and *S. verrucosum* Pers. IR500 were isolated from sporocarps collected from under *Uapaca guineensis* and *U. somon* stands, respectively, in southern Burkina Faso (Sanon et al. 1997). A thelephoroid sp. ORSXM002 was isolated from dark-brown ectomycorrhizas collected on *A. africana* seedlings grown in the Bayottes forest soil collected in southern Senegal (Bâ and Thoen 1990). A *Pisolithus* species IR100 was isolated from sporocarps collected from under a monospecific forest plantation of *Acacia mangium* in the Cassankil forest in southern Senegal. Cultures used are deposited in the culture collection of IRD-Dakar in Senegal and LSTM-Montpellier in France. Fungal cultures were kept at 30°C on MMN medium (Marx 1969). Glass jars (1 l) were half-filled with a mixture of vermiculite and peat moss (4:1; v/v) and autoclaved (120°C, 20 min). This substrate was moistened with 300-ml liquid MMN medium, autoclaved again and ten plugs of cultures were inoculated per jar. The substrate was colonized by ECM fungi after 2–3 months of growth at 30°C. The resulting fungal inoculum was mixed with

soil (1:10; v/v). Portions of 2 kg of the mixture were transferred into plastic bags (24×7.5 cm). Uninoculated controls received a mixture of moistened vermiculite-peat moss with nutrient solution and no fungal culture.

Plant culture

Seeds of *A. bella*, *A. macrophylla*, *C. tetraphyllum*, *P. coeruleum* and *U. somon* were provided by the Institut de Recherche Agronomique in Conakry, Guinea. Seeds of *A. africana* were obtained from Institut Sénégalais de Recherches Agricoles in Dakar, Senegal. Seeds of *A. africana*, *A. bella*, *A. macrophylla* and *P. coeruleum* were scarified in 95% sulfuric acid for 2 h, and seeds of *U. somon* and *C. tetraphyllum* were surface sterilized by treating them with 95% sulfuric acid for 5 min. They were rinsed with tap water and planted as two per plastic bag. After emergence, the seedlings were thinned to one plant per plastic bag. Plants were screened from rain and grown in a greenhouse (mean temperature 35°C day and 25°C night, relative humidity varying from 16 to 89%, day length approximately 12 h, maximum light intensity 196 W m^{-2}). Plants were watered to near field capacity twice per week with tap water pH 6.8 without nutrient solution. For each plant species, the experiment was set up as a 1×5 factorial design consisting of one plant species and four ECM fungi plus a non-inoculated control which were arranged in a completely randomized design with ten replicates per treatment combination.

Quantitative evaluation

Seed fresh weight and period of cotyledon fall were determined for each tree species. Plants were harvested after 7 months growth. Shoot height and dry weight of shoots and roots (plant material was dried at 70°C for 5 days) were measured. For each inoculated and non-inoculated treatment, a sample of ten lateral roots was washed gently and dispersed in a dish of water. Numbers of root tips of mycorrhizal roots and non-colonized roots were counted under a stereomicroscope at ×100 magnification for each lateral root to determine the percentage of mycorrhizal colonization (number of mycorrhizal roots/total number of roots ×100). Mycorrhizal colonization was evaluated according to the grid-line intersection method modified by Brundrett et al. (1996) and was confirmed by microscopic (×400) examination of root tips to determine the presence of a mantle and a Hartig net. The relative mycorrhizal dependency (RMD) was calculated as follows: (biomass of ECM plants−biomass of non-ECM plants/biomass of ECM plants) ×100 (Plenchette et al. 1983).

Mineral analyses were performed by CIRAD-AMIS-Montpellier in France, according to ISO 9002 certification. After mineralization of ground leaf samples through heating at 500°C and digestion in fluorhydric acid, total phosphorus, potassium and calcium contents were determined

through ICP spectrometry using a Varian Vista spectrometer equipped with a CCD detector. Total nitrogen determinations were made by catharometry after mineralization of ground leaf samples at 850°C.

Statistical analysis

All data were subjected to one- or two-way analysis of variance, and mean values were compared using Newman–Keuls multiple range test (Gagnon et al. 1989). Data of mycorrhizal colonization were transformed by arc sin (square root) before analysis.

Results

Root colonization and plant growth

The extent of ECM colonization by the four fungal species varied from 24.5 to 86.7% depending on the tree species (Table 1). For example, thelephoroid sp. ORSXM002 colonized the five caesalpinioid legumes well but did not appear to colonize roots of *U. somon* extensively. In contrast, percentage root colonization by *S. verrucosum* and *Pisolithus* sp. in *U. somon* was significantly higher when compared to other fungi (Table 1). There was little difference in the ability of the three Gasteromycetes to colonize roots of the five caesalpinioid legumes.

Table 1 Effect of inoculation with four ectomycorrhizal (ECM) fungi on growth variables and ECM colonization in seedlings of six tropical African tree species at 7 months

Seedlings with or without ECM fungi	Height (cm)	Shoot dry weight (g)	Root dry weight (g)	Total dry weight (g)	Root colonization (%)
A. africana					
S. dictyosporum IR408	63.04 a	6.84 a	4.06 b	10.91 b	49.30 b
S. verrucosum IR500	56.90 a	5.98 a	3.62 b	9.60 ab	69.90 c
Pisolithus sp. IR100	61.35 a	6.99 a	3.76 b	10.75 b	52.30 b
Thelephoroid ORSXM002	64.25 a	6.83 a	3.83 b	10.67 b	70.40 c
Control	56.15 a	5.95 a	2.11 a	8.06 a	0.00 a
A. bella					
S. dictyosporum IR408	42.80 a	3.19 b	1.90 b	5.10 c	34.60 b
S. verrucosum IR500	41.10 a	3.31 b	1.91 b	5.22 c	54.30 c
Pisolithus sp. IR100	37.4 a	2.38 a	1.74 b	4.13 b	59.90 c
Thelephoroid ORSXM002	39.20 a	2.58 a	1.53 b	4.12 b	86.70 d
Control	39.35 a	2.35 a	0.52 a	2.88 a	0.00 a
A. macrophylla					
S. dictyosporum IR408	26.55 ab	2.53 a	5.02 a	7.55 b	42.90 bc
S. verrucosum IR500	23.10 a	2.36 a	4.53 a	6.89 a	45.00 bc
Pisolithus sp. IR100	21.90 a	2.36 a	6.13 a	8.49 a	37.30 b
Thelephoroid ORSXM002	29.20 b	2.91 a	5.47 a	8.38 a	54.70 c
Control	24.00 ab	2.06 a	4.90 a	6.96 a	0.00 a
C. tetraphyllum					
S. dictyosporum IR408	29.70 a	1.66 b	0.90 cd	2.56 c	25.70 b
S. verrucosum IR500	23.45 a	1.02 a	0.62 b	1.65 ab	27.20 b
Pisolithus sp. IR100	26.00 a	1.22 a	0.73 bc	1.96 bc	45.30 c
Thelephoroid ORSXM002	23.90 a	0.96 a	1.02 d	1.99 bc	67.55 d
Control	23.85 a	0.89 a	0.32 a	1.22 a	0.00 a
P. coeruleum					
S. dictyosporum IR408	33.05 a	2.78 a	0.96 b	3.74 b	49.10 c
S. verrucosum IR500	32.20 a	2.68 a	0.94 b	3.63 b	24.50 b
Pisolithus sp. IR100	31.40 a	2.48 a	0.96 b	3.45 b	55.60 c
Thelephoroid ORSXM002	33.10 a	2.44 a	0.94 b	3.39 b	85.40 d
Control	34.35 a	2.00 a	0.36 a	2.37 a	0.00 a
U. somon					
S. dictyosporum IR408	25.30 c	3.37 c	2.37 c	5.74 b	33.70 b
S. verrucosum IR500	20.80 b	3.16 bc	1.66 b	4.82 b	52.80 c
Pisolithus sp. IR100	21.80 bc	3.60 c	2.32 c	5.93 b	58.60 c
Thelephoroid ORSXM002	23.20 bc	2.73 b	1.45 b	4.58 b	30.20 b
Control	11.13 a	0.47 a	0.16 a	0.63 a	0.00 a

Mean values were compared in each tree species (ten replicates per treatment). Different letters within a column indicate significantly different values at *P*<0.05. Control, non-inoculated plants

Average seed weight was 0.20±0.03, 0.77±0.13, 1.84± 0.29, 2.18±0.52, 3.21±0.64 and 15.15±3.64 g (*n*=20) for *U. somon*, *C. tetraphyllum*, *P. coeruleum*, *A. bella*, *A. africana* and *A. macrophylla*, respectively. The length of time that cotyledons remain attached in inoculated and non-inoculated seedlings was similar for each tree species. It was approximately 5, 6, 6, 10, 9 and 14 weeks for *U. somon*, *C. tetraphyllum*, *P. coeruleum*, *A. bella*, *A. africana* and *A. macrophylla*, respectively.

Effects on plant growth after inoculation with ECM fungi varied with the tree species. Inoculation with any one of the ECM fungi significantly improved total dry weight of *U. somon*, *A. bella* and *P. coeruleum* seedlings, as compared with non-inoculated controls (Table 1). Total dry weight of *A. africana* and *C. tetraphyllum* increased when inoculated with all the ECM fungi except *S. verrucosum*, whilst there was no significant difference between inoculated *A. macrophylla* and controls for total dry weight. The height and shoot dry weight of colonized and non-colonized caesalpinioid legumes were similar, but they significantly increased in *U. somon* whatever the ECM fungi used. Root dry weight increased in all the inoculated plants except for *A. macrophylla*.

The RMD clearly differed between plant species and the ECM fungi (Fig. 1). For example, *P. coeruleum*, *A. bella* and *C. tetraphyllum* inoculated with *S. dictyosporum* had comparable RMD values which never exceeded 50%, whilst *U. somon* had RMD values ranging from 84.6 to 88.6%, irrespective of the species of fungi. *A. macrophylla* and *A. africana* showed the lowest RMD values, reaching no more than 30% whatever the ECM fungi used. Seed mass was negatively correlated with RMD (r^2=0.30, $P<$ 0.01, *n*=24; Fig. 2). No evident relation was found between increased growth and extent of mycorrhization.

Nutrient concentrations in leaves

There was a large variation in N, P, K and Ca concentrations in leaves of plant species, depending on the ECM fungi used (Table 2). Comparisons of the concentrations of mineral nutrients in leaves of inoculated plants with non-inoculated controls showed K nutrition to be most enhanced by inoculation in *A. africana* and *U. somon*. Three different types of plant response were observed: increase in K concentration in leaves associated with growth stimulation in terms of biomass production (*A. africana* and *U. somon* with all fungi, *C. tetraphyllum*/*Pisolithus* sp.), increase in K concentration without growth stimulation (*A. macrophylla*/*Scleroderma* spp., *A. macrophylla*/thelephoroid, *P. coeruleum*/*S. verrucosum* and *P. coeruleum*/ *Pisolithus* sp.) and no increase in either K concentration in leaves or plant growth in the remains of plant/fungus combinations. Increase in P concentration in leaves did not always associate with plant growth stimulation by the ECM fungi. In contrast, the N concentration in leaves of inoculated plants, irrespective of the species of ECM
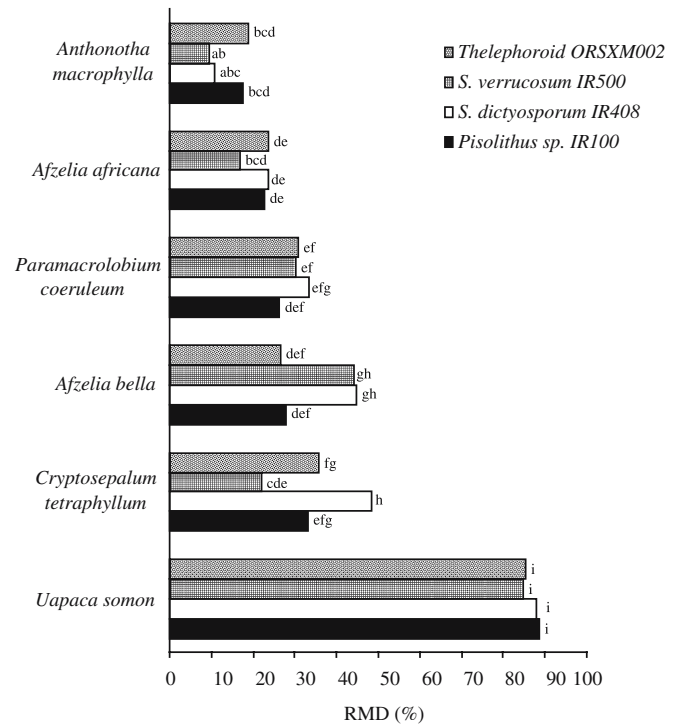

Fig. 1 Relative mycorrhizal dependency (RMD) in seedlings of six African tree species. *Columns* with the same letter do not differ significantly (*P*<0.05)

fungi, hardly differed from those of the control plants (Table 2). Increase in Ca concentrations in leaves was associated only with growth stimulation of *P. coeruleum* in symbiosis with *S. verrucosum* or *Pisolithus* sp.
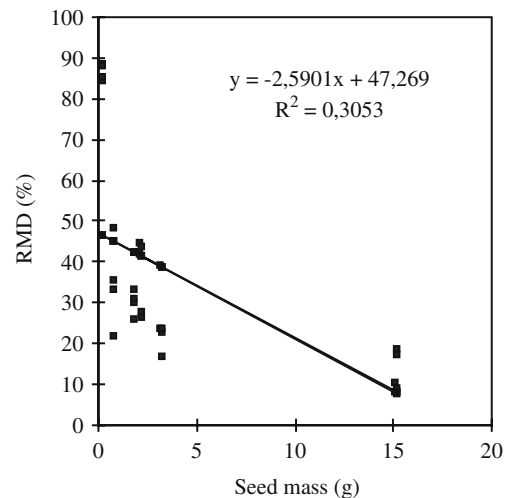

Fig. 2 Relationship between relative mycorrhizal dependency (RMD) and seed mass for seedlings of caesalpinioid legumes and *U. somon*. Statistics are shown in the text

Table 2 Changes in nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) concentrations in leaves of seedlings of six tropical African tree species in response to colonization by four ECM fungi at 7 months

Seedlings with or without ECM fungi	N (%)	P (%)	K (%)	Ca (%)
A. africana				
S. dictyosporum IR408	1.378 a	0.076 a	1.297 b	1.157 a
S. verrucosum IR500	2.143 b	0.108 b	1.392 b	1.646 ab
Pisolithus sp. IR100	1.693 a	0.096 ab	1.302 b	1.346 a
Thelephoroid ORSXM002	1.855 ab	0.102 b	1.360 b	1.388 a
Control	1.610 a	0.078 a	0.553 a	1.920 b
A. bella				
S. dictyosporum IR408	1.735 a	0.112 a	1.088 a	1.361 a
S. verrucosum IR500	1.734 a	0.108 a	0.766 a	1.483 a
Pisolithus sp. IR100	1.853 ab	0.163 b	1.303 a	1.316 a
Thelephoroid ORSXM002	2.068 ab	0.151 ab	0.963 a	1.152 a
Control	2.119 b	0.118 a	1.055 a	1.268 a
A. macrophylla				
S. dictyosporum IR408	2.265 b	0.138 a	1.295 b	1.133 b
S. verrucosum IR500	2.227 a	0.151 a	1.359 b	0.983 b
Pisolithus sp. IR100	1.836 a	0.140 a	1.025 a	0.634 a
Thelephoroid ORSXM002	2.212 b	0.147 a	1.329 b	0.897 b
Control	2.083 b	0.137 a	1.089 a	0.921 b
C. tetraphyllum				
S. dictyosporum IR408	1.714 a	0.082 a	1.011 a	1.736 b
S. verrucosum IR500	1.978 b	0.087 ab	1.101 ab	1.446 ab
Pisolithus sp. IR100	1.976 b	0.104 b	1.332 b	1.490 ab
Thelephoroid ORSXM002	1.996 b	0.124 c	1.273 ab	1.288 a
Control	1.884 b	0.076 a	1.012 a	1.536 ab
P. coeruleum				
S. dictyosporum IR408	1.697 a	0.091 a	0.986 a	0.851 a
S. verrucosum IR500	1.593 a	0.069 a	1.158 b	1.054 b
Pisolithus sp. IR100	1.465 a	0.079 a	1.115 b	1.076 b
Thelephoroid ORSXM002	1.340 a	0.099 a	0.945 a	0.894 a
Control	1.587 a	0.063 a	0.958 a	0.882 a
U. somon				
S. dictyosporum IR408	1.254 ab	0.066 b	2.993 b	1.042 a
S. verrucosum IR500	1.209 ab	0.051 a	2.634 b	1.068 a
Pisolithus sp. IR100	1.304 b	0.074 b	2.608 b	1.045 a
Thelephoroid ORSXM002	1.076 a	0.048 a	2.761 b	1.173 a
Control	1.626 c	0.044 a	1.821 a	1.139 a

Mean values were compared in each tree species (five replicates per treatment). Different letters within a column indicate significantly different values at $P<0.05$. Control, non-inoculated plants

Discussion

Although the ECM status of trees in tropical Africa has been reported, the role of ECM fungi in tree growth remains an open question (Newbery et al. 1988; Sanon et al. 1997; Onguene and Kuyper 2001). Only studies of *A. africana* and *A. quanzensis* have shown the ability of the selected ECM fungi to stimulate plant growth and mineral nutrition (Bâ et al. 1999, 2002; Diédhiou et al. 2004a,b). Our results demonstrate for the first time that ECM fungi have positive effects on *A. bella*, *C. tetraphyllum*, *P. coeruleum* and *U. somon* seedlings and no effect on *A. macrophylla* seedlings. They confirm the previously observed positive but varied response of

A. africana to inoculation with different ECM fungi (Bâ et al. 1999; Diédhiou et al. 2004a,b). In these latter studies, the same ECM fungi as tested here, thelephoroid sp. ORSXM002 and *S. dictyosporum* IR408, were identified as the most appropriate fungi for improving initial *A. africana* growth. Furthermore, the thelephoroid sp. ORSXM002 proved to be competitive and effective in both ECM propagule-free savanna soil and unsterilized forest soil (Diédhiou et al. 2004a,b). Thelephoroid sp. ORSXM002 employs different survival strategies in the soil, namely, sclerotia, ECM root fragments and fragments of mycelial strands (Bâ et al. 1991), and these propagules allow opportunistic root colonization as well as long-term survival in the soil during the dry season,

which is an important characteristic when choosing an ECM fungus for field application in semi-arid climates in West Africa (Bâ et al. 1991). Therefore, thelephoroid sp. ORSXM002 appears to be a good candidate for artificial inoculation of caesalps and *U. somon* seedlings in forest nurseries and plantations.

ECM colonization in seedlings of the legume and euphorbe tree species differed greatly from one fungus to another. For example, thelephoroid sp. ORSXM002 colonized caesalpinioid legumes quite well, but colonized *U. somon* only poorly. Nevertheless, all ECM fungi stimulated the root system of caesalpinioid legumes (except *A. macrophylla*) and *U. somon*, suggesting that there is no clear relationship between the degree to which a plant is colonized by ECM fungi and the potential for the plant to benefit from this. To a very large extent, positive mycorrhizal effects on the legume trees were manifested belowground rather than aboveground. Such shifts in root-to-shoot ratio following ECM formation have already been reported in African tropical trees (Guissou et al. 1998; Bâ et al. 1999, 2002). Several works have shown that the development of root systems can be a key factor in tree seedling growth improvement after outplanting (Garbaye and Wilhem 1984; Al-Abras et al. 1988; Villeneuve et al. 1991). The RMD of the caesalpinioid legumes appeared moderate (<50%) to low (9.3%) depending on the fungi used, whilst the euphorbe, *U. somon*, showed high RMD values (84.6–88.6%) irrespective of the ECM fungi used. These values for ECM dependency in *U. somon* seedlings are also high when compared with values reported for highly dependent tropical tree species introduced in western Africa such as *Pinus* spp., hybrid eucalyptus (*Eucalyptus urophylla* × *E. kirtoniana*) and *A. mangium* (Marx et al. 1985; Garbaye et al. 1988; Duponnois and Bâ 1999).

Seed mass of the legume and euphorbe tree species was negatively related to their ECM dependency, so that plants with larger seeds (e.g. *A. macrophylla* and *A. africana*) exhibited lower RMD values than those with smaller seeds (e.g. *U. somon*, *C. tetraphyllum* and *A. bella*). According to the proposed importance of cotyledonary reserves for early growth of woody angiosperms (Marshall and Kozlowski 1976; Mulligan and Patrick 1985), large seed reserve is probably important for seedling nutrition and initial growth, and it may explain why complete or partial cotyledon excision significantly affected initial phase of growth of *A. africana* seedlings (Bâ et al. 1994). Moreover, partial or complete cotyledon excision drastically reduced root soluble carbohydrates in *A. africana* seedlings and ectomycorrhiza development (Bâ et al. 1994). Besides seed mass, the length of time that cotyledons remain attached could also be a key factor in influencing the mycorrhizal response of tree species (Zangaro et al. 2003). This parameter varied approximately from 5 to 6 weeks for tree species having the highest RMD values (e.g. *U. somon* and *C. tetraphyllum*) and from 9 to 14 weeks for plants with low RMD values (e.g. *A. macrophylla* and *A. africana*). In the large-seeded species such *A. macrophylla* and *A. africana*, the benefits of the ECM symbiosis may be retarded as long as seed reserves are not exhausted. Conversely, the small-seeded species such as *U. somon*, *C. tetraphyllum* and *A. bella* would be expected to respond more rapidly to an increased access to external resources through ECM development. For arbuscular mycorrhizal plants, this was shown to be related to P content of seeds. This hypothesis can be tested by determining how much P in caesalps and *U. somon* seedlings is derived from seed reserves, and whether the seedlings become dependent on the uptake capacity of their mycorrhizal roots to mobilize P from nutrient-deficient soils with the emptying of the cotyledonary reserves.

Although the major contribution of ECM symbiosis is to improve P uptake by plants in P-deficient soil (Smith and Read 1997), the low soil P level was not a limiting factor for growth and P nutrition of the *U. somon* and caesalps seedlings in most cases during the experimental period of 28 weeks. These results concord with previous data suggesting that soil P deficiency may not limit the growth of some tropical African tree species (Bâ et al. 1999, 2002; Newbery et al. 2002). In contrast, K uptake seems to be more related than P to biomass production of the caesalp and euphorbe. Indeed, in all the tree species except *A. bella*, at least one ECM fungus increased leaf K content. In 11 cases, this was related to increased root biomass, and for six of these, stimulation of total biomass was probably related to increased acquisition of K. Ectomycorrhizas have been seen as an adaptation to a seasonal and stressed environment (Smith and Read 1997). In this respect, K plays an important role in water stress tolerance by regulating stoma and osmotic potential in the vacuoles (Lidhauer 1985). Such a physiological effect of the ECM symbiosis could be of great advantage to the development of African trees during the dry season and merits further investigation under conditions of soil water stress, which are more relevant to the ecological conditions of low rainfall in West Africa.

In conclusion, our data support the hypothesis that African caesalpinioid legumes and euphorbe tree species with smaller seeds show the higher RMD values than those with the larger seeds. *U. somon* seedlings gained more benefits from the ECM symbiosis than seedlings of caesalps in terms of growth and K acquisition. Based on these data and according to RMD categories defined by Habte and Manajunath (1991), *U. somon* can be considered as an obligately mycorrhiza-dependent species, *C. tetraphyllum*, *A. bella* and *P. coeruleum* are moderately mycorrhiza-dependent and *A. africana* and *A. macrophylla* seedlings show little mycorrhiza dependency.

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