

Management of ectomycorrhizal symbionts associated to useful exotic tree species to improve reforestation performances in tropical Africa

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Abstract

- The objective of this review was to summarize scientific data on the symbiotic status of exotic tree species useful in tropical Africa, and to update reports about their growth improvement through microbial inoculations, especially ectomycorrhizal symbionts.
- The studies reviewed microbial symbionts associated to exotic tree species belonging to *Myrtaceae*, *Pinaceae*, *Casuarinaceae* and *Leguminosae*. In their native areas, these trees are associated either with ectomycorrhizal (ECM) fungi (e.g. *Pinaceae*) or both ECM and arbuscular mycorrhizal (AM) fungi (e.g. *Eucalyptus*), or sometimes as in *Casuarina* and *Acacia* with three coexisting symbionts (nitrogen fixing bacteria, ECM and AM fungi). In their new habitats, using highly efficient mycorrhizal fungi, controlled mycorrhization experiments have pointed out the importance of root symbionts in establishment and growth of exotic tree species such exotic pines or Australian acacias.
- Since the challenge in silviculture and reforestation was to determine the best compromise between symbiotic compatibility and efficiency of both partners under local soil constraints, further researches have to be encouraged to elucidate the complexity of these tree symbioses in terms of diversity, interaction and effectiveness of their symbiotic partners for their better exploitation in reforestation programmes.

Résumé – Valorisation des symbiotes ectomycorhiziens associés aux essences forestières exotiques d'intérêt économique pour améliorer les performances des programmes de reboisement en Afrique tropicale.

- L'objectif de cet article de synthèse est de résumer les connaissances scientifiques acquises sur le statut symbiotique des essences forestières exotiques utilisées en Afrique tropicale et d'actualiser les principaux résultats concernant l'impact de l'inoculation microbienne (plus particulièrement l'inoculation ectomycorhizienne) sur le développement de ces espèces ligneuses.
- Les résultats présentés concernent les symbiotes microbiens associés aux arbres exotiques appartenant aux familles des *Myrtaceae*, *Pinaceae*, *Casuarinaceae* et *Leguminosae*. Dans leur région d'origine, ces arbres sont associés aussi bien à des champignons ectomycorhiziens (ECM) (Ex : *Pinaceae*) et/ou des champignons à arbuscules (CMA) (Ex : *Eucalyptus* spp.), ou parfois, comme chez les *Casuarina* et les *Acacia*, à trois types de symbiose (symbiose fixatrice d'azote, champignons ECM et MA). Dans leur zone d'introduction et en utilisant des symbiotes fongiques performant, les expériences de mycorrhization contrôlée montrent l'importance des ces symbiotes racinaires dans l'établissement et la croissance des essences forestières exotiques comme les pins ou les acacias australiens.
- La principale difficulté dans ces opérations de mycorrhization contrôlée est d'identifier le meilleur compromis entre la compatibilité de la souche fongique inoculée avec l'espèce forestière utilisée et un effet optimal sur la croissance de la plante hôte. Des études doivent être réalisées afin de comprendre les bases biologiques du fonctionnement de la symbiose mycorrhizienne (diversité des composantes de la symbiose, mécanismes régissant les interactions plante hôte/symbiotes fongiques, etc.) afin de valoriser de manière optimale la symbiose mycorrhizienne dans les programmes de reboisement.

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1. INTRODUCTION

In tropical Africa, two pedoclimatic zones can be distinguished: humid tropics with dense rainforests or gallery forests, and dry tropics with open bush woodlands, savannas, arid steppes (Garbaye et al., 1988; Le Tacon et al., 1989). In the first ecological zone, where water resources are not a limiting factor for tree growth, forestry is often turned to promote high productivity of timber species by genetic selection, clonal propagation, and use of fast growing exotic species (Khasa and Bousquet, 1995). Therefore high value industrial plantations (e.g. pines, acacias and eucalypts) have been implanted in many humid tropical African areas. In the second ecological zone, where dryness naturally keeps down timber productivity, reforestation is a vital need as the forests are at the basis of population survival, through firewood, non-timber products, soil stabilization. However, the success of reforestation programs required a selection of locally adapted plant species (e.g. fast growing, tolerant of dryness, salinity, heavy metal toxicity) able to face drastic conditions and thus to provide improved environmental situation (Smith and Read, 2008). In this context, exotic tree species belonging to *Myrtaceae*, *Pinaceae*, *Casuarinaceae* and *Leguminosae* were often used.

In their native areas, these exotic tree species are associated with symbiotic microorganisms (mycorrhizal fungi and nitrogen fixing bacteria) which play a significant role in survival and growth of trees. Therefore, the success of tree establishment in a new area involves the availability of functional compatible symbiotic partners. This was convincingly illustrated by the unsuccessful attempts to introduce exotic pines in the tropics until the necessary symbiotic ECM fungi were introduced (Mikola, 1970). Subsequently, seedling inoculation with natural inoculants (soil, crushed fruitbodies or excised ECM roots) has been applied in many tropical African countries to introduce exotic tree species (Garbaye, 1991). However, this practice did not always give best results in growth improvement of exotic tree species in their new habitats, due to the competition between the introduced symbiotic partners and local soil microorganisms (Kabre, 1982; Marx et al., 1985). Hence, to optimize the growth of exotic tree species, use of competitive and effective symbiotic microbial strains was required (Garbaye, 1991; Lamhamedi and Fortin, 1991; Rincón et al., 2007). In this context, the challenge in silviculture and reforestation was to determine the best compromise between symbiotic compatibility and efficiency of both partners under local soil constraints. This however involves a knowing of symbiotic partners of exotic tree species both in their introduction and native areas.

In this respect, we propose here to review the symbiotic status of exotic tree species useful in reforestation in tropical Africa, and to update reports about their growth improvement through microbial inoculations, specially including ectomycorrhizal ones.

2. PINACEAE

In West Africa, the tropical pine species native of Southeast Asia (e.g. *Pinus kesiya*), Caribbean archipelago (e.g.

P. caribaea var. *caribaea*), Central America (e.g. *P. strobus*) and North America (e.g. *P. radiata*) are far the most planted species. These pines are obligate ectotrophs unable to survive or to have a normal growth without symbiotic ECM partners (Delwaulle et al., 1987; Marx et al., 1985; Zhu et al., 2008). Most of their fungal symbionts (*Rhizopogon* spp., *Suillus* spp.) are highly host specific, even though some others such as those belonging to the genus *Pisolithus* may have a broad range of hosts (Bruns et al., 2002; Martin et al., 2002; Marx, 1977; Molina and Trappe, 1994).

P. radiata was the first pine species introduced in Kenya in 1902. However, its seedlings were scrubby and had hardly survived the nursery stage. This failure was only solved in 1910 when the Royal Botanical garden in Kew suggested importing some soil, bearing fungal propagules, harvested under ancient pine plantations from South Africa. Successfully used in Kenya this practice was then generalized in several other countries such as Tanzania, Uganda, Zimbabwe, Zambia and Malawi (Mikola, 1970). In West Africa, the first successful pine (*P. kesiya*) plantations were obtained in Dalaba (Guinea) in 1914. Their associated ECM fungus was identified as a *Rhizopogon*, which thought to be pine-specific (Delwaulle et al., 1987; Molina and Trappe, 1994). Later, the soil inoculation practice was applied to successfully introduce pines in Cameroon, Congo, Nigeria, Liberia, Ivory Coast and Ghana (Delwaulle et al., 1987; Marx, 1980; Momoh and Gbadegesin, 1980). It is still unclear how the original nursery saplings were first inoculated. Three hypotheses, non exclusive, were proposed to explain the inoculum origin: (i) planted pines would have been introduced as ornamentals, by migrants coming from European countries; (ii) pine seeds would have harboured fungal spores; and (iii) planted pines fungi would have contracted symbiotic relationships with local ECM fungi. However, due to the symbiotic incompatibility between introduced pines and some indigenous ECM fungi (Bâ, 1990), the third hypothesis seems unlikely. This could be supported by the failure to introduce *P. caribaea* in Casamance (South Senegal) where the environmental conditions seemed to be cost attractive to the development of this pine species (Delwaulle, 1978; Kabre, 1982).

Garbaye (1991) reviewed the advantages and disadvantages of the use of natural inoculants (e.g. soil from old plantations, fruitbodies, spores). Indeed, if they are costly attractive compared to the pure strain inoculants, natural inoculants are also a way of parasite dissemination. Therefore, use of pure cultures of selected ECM fungi remains the best practice to optimize the efficiency of inoculums for improvement of tree growth (Lamhamedi and Fortin, 1991; Rincón et al., 2007). This was repeatedly illustrated in pine nurseries and plantations in a range of situations (Tab. I). As an example Momoh and Gbadegesin (1980) and later Delwaulle et al. (1982) reported a better growth response of *P. caribaea* inoculated with a pure *Pisolithus tinctorius* strain than those with a soil from pine plantations. Nevertheless, this case did not always occur as instanced by Kabre (1982) and Marx et al. (1985). These authors showed that selected fungal strains were less efficient than natural soil inoculants. According to Kabre (1982), the higher efficiency of natural soil inoculants may

Table I. Controlled ectomycorrhization of *Pinus caribaea* introduced in Central and West Africa.

Localities	Measured parameter	Fungal inoculant	Inoculation effect (compared to the uninoculated treatment)	References
Nigeria	Height (after 30 month plantation)	<i>Pisolithus tinctorius</i>	×1.2 to 2.8	Momoh and Gbadegesin (1980)
Ghana	Height (after 18 month plantation)	<i>Pisolithus tinctorius</i>	×0.6 to 1	Ofosu-Asiedu (1980)
		<i>Rhizopogon luteolus</i>	×1	
		<i>Thelephora terrestris</i>	×0.8 to 1.2	
DRC ^a	Height (after 20 month plantation)	<i>Pisolithus tinctorius</i>	×1.2 to 1.5	Delwaulle et al. (1982)
		<i>Suillus bovinus</i>	×1.1	
		<i>Suillus bevisi</i>	×1	
Senegal	Aerial biomass after 8 month plantation	<i>Pisolithus tinctorius</i>	×1.4 to 13.5	Kabre (1982)
Liberia	Aerial volume after 3 y plantation	<i>Pisolithus tinctorius</i>	×1.5	Marx et al. (1985)
		<i>Thelephora terrestris</i>	×1	
DRC	Height (after 12 month plantation)	<i>Pisolithus tinctorius</i>	×1.2	Delwaulle et al. (1987)

^a Democratic Republic of Congo.

result from the presence of antagonistic soil actinomycetes against the introduced *Pisolithus* strains. However, in many cases *Pisolithus* was shown as the most efficient genus for tropical pines (Le Tacon et al., 1989).

3. MYRTACEAE

This family comprises 3 000 species gathered in 130 genera. Several genera are known as ectomycorrhizal among which *Eucalyptus*, *Melaleuca* and *Syzygium*. African native species all belong to the genus *Syzygium* (Aubréville, 1950). *Eucalyptus* and *Melaleuca* genera are native from Australia, Indonesia and Papua New Guinea but have been introduced in the whole tropics, particularly in Africa. *Eucalyptus* which is the most planted tree genus in the world includes five subgenera: *Monocalyptus*, *Symphomyrtus*, *Corymbia*, *Eudesmia* and *Idiogenes* (Chilvers, 1972). In their native areas, eucalypts contract both arbuscular and ectomycorrhizal symbioses. Among the different subgenera, *Monocalyptus* (including *E. fastigata* and *E. radiata*) and *Symphomyrtus* (including *E. camaldulensis* and *E. grandis*) contain the most ectotrophic species (Chilvers, 1972). According to Chilvers (1972), the diversity of associated ECM fungi would be greater within the *Monocalyptus* subgenus than within *Symphomyrtus*. This higher ECM diversity could explain the ability of *Monocalyptus* to colonize relatively poorer soils than *Symphomyrtus* (Pryor and Johnson, 1971).

The ECM fungal partners of eucalypts are highly diversified, including both epigeous fungi (e.g. *Laccaria laccata*, *Scleroderma laeve*, *P. tinctorius*) with a wide host spectrum and hypogeous fungi (e.g. *Hymenogaster albellus*, *Hydnangium carneum*) with a narrower host spectrum (Castellano and Bougher, 1994; Chen et al., 2007; Malajczuk et al., 1982; Tedersoo et al., 2007). The ECM fungi associated to eucalypts include numerous taxa native from African hardwoods or from

American conifers (Chen et al., 2007; Malajczuk et al., 1982; Tedersoo et al., 2007). However, eucalypts would not be compatible with some fungal genera such as *Rhizopogon* and *Suillus* generally specific to pines (Malajczuk et al., 1982; Molina and Trappe, 1994). One of the best known eucalypt-associated fungal genera is *Pisolithus* and its infra-specific diversity was assessed to identify the most efficient isolates promoting eucalypt growth (Aggangan et al., 1996a; Burgess et al., 1994b). Burgess et al. (1994a) and then Martin et al. (2002) reported a large genotypic diversity among *Pisolithus*. This genotypic diversity was also established at the functional level through eucalypt growth responses to inoculation with *Pisolithus* isolates from various geographical origins (Aggangan et al., 1996b; Burgess et al., 1994b). The largest plant growth responses were generally recorded with *Pisolithus* isolates native from Australia (Burgess et al., 1994b).

Eucalypt AM symbioses are much less studied than its ECM symbioses. After Asai (1934) and Maeda (1954), it was only in the 1980s that they were really investigated (Malajczuk et al., 1981). Numerous works (Boudarga et al., 1990; Chen et al., 2000a; 2000b; Chilvers et al., 1987; Lapeyrie and Chilvers, 1985) showed that AM and ECM fungi could coexist not only on the same root system but even in the same root apex. The relative implication of each mycorrhizal type in the plant growth response is not clearly established (Chen et al., 2000a; 2000b; 2007; Lapeyrie and Chilvers, 1985). Nevertheless, a distinct plant response to both types of symbioses was observed along the plant development stage: arbuscular mycorrhizae generally are predominant on young saplings and ectomycorrhizae on older trees (de Mendonça Bellei et al., 1992; Oliveira et al., 1997). The biological processes leading to this mycorrhizal succession remain unknown (van der Heijden, 2001).

Outside their native areas, eucalypts are most commonly associated with ECM fungi belonging to the genera *Pisolithus* and *Scleroderma* (Bakshi, 1966; Garbaye et al., 1988; Mikola,

1970; Thapar et al., 1967; Thoen and Ducouso, 1989). The question of the origin (indigenous or introduced) of these fungal genera is still under debate (Garbaye et al., 1988; Le Tacon et al., 1989). Hence, when using eucalypts as exotic tree species in a new plantation two strategies are eligible: either introducing selected ECM fungal strain that shared the same evolutionary history with their natural host, from Australia, or selecting efficient fungal strains among the indigenous fungi (Bâ, 1990; Garbaye et al., 1988). In a field trial in Congo, tree productivity of *E. urophylla* × *E. kirtoniana* hybrid trees inoculated with a North-American pine-compatible *Pisolithus* strain was 30% over the uninoculated controls (Garbaye et al., 1988). However, after one year of plantation, the inoculated strain was rapidly replaced by a local *Scleroderma* species, revealing the low compatibility of this North-American *Pisolithus* strain to eucalypts under local pedoclimatic conditions. Furthermore, in vitro experiments evidenced that an Australian *Pisolithus*, isolated from its natural *E. urophylla* host was much more aggressive in terms of root colonization than the North-American strain used in Congo (Lei et al., 1990; Malajczuk et al., 1990). This result shows the need of preliminary compatibility and efficiency tests with fungal strains isolated from the native area of the host tree, before field inoculations in a new area. For instance, field trials in China and Philippines (where indigenous fungi had poor compatibility with eucalypts) showed that 2 y after inoculation with selected Australian *Pisolithus* and *Scleroderma* strains, the growth of eucalypts was improved 2.5 times over the uninoculated trees (Dell and Malajczuk, 1997). Moreover, local *Pisolithus* and *Scleroderma* strains were much less efficient than Australian strains, both in nursery and field experiments in China (Chen et al., 2006; Dell et al., 2002). Molecular tracing of Australian *Pisolithus* strains revealed that they survived and even fructified in the Chinese plantation soils over 3 y plantation (Dell et al., 2002).

It has been shown in axenic conditions that some scleroderma strains (e.g. *S. dictyosporum* and *S. verrucosum*) isolated from African native trees were not compatible with *E. camaldulensis* that is the most planted species in Senegal (Bâ, 1990) whereas fruitbodies of *S. verrucosum* and *S. capense* spontaneously occurred in *E. camaldulensis* plantations (Thoen and Ducouso, 1989). Nevertheless, regarding the intra-specific variation and distribution of African eucalypt-compatible scleroderms (Sanon et al., 1997), it is unclear whether these *S. verrucosum* constituted the same strain.

4. CASUARINACEAE

Members of *Casuarinaceae* family are actinorrhizal trees. They comprise 96 species including 59 *Allocasuarina*, 17 *Casuarina*, 2 *Ceuthostoma* and 18 *Gymnostoma* (Maggia and Bousquet, 1994). Their native areas range from Australia to South East Asia. Some species of *Casuarina* and *Allocasuarina* have been exported to the whole inter-tropical zone mainly as windbreaks or fuelwood; *Casuarina equisetifolia*, *C. cunninghamiana* and *C. glauca*, being dominant in plantations. In Senegal, thousands of hectares were planted

with *Casuarinaceae* in the Niayes area and all along the littoral between Dakar and Saint-Louis to stabilize sand dunes (Dommergues et al., 1999). Within native area, *Casuarinaceae* are associated to a wide diversity of ECM fungi, some being common with Eucalypts (Reddell et al., 1991). *Allocasuarina* is the most ectotrophic genus with a wide diversity of fungal partners: about 20 fungal genera (e.g. *Amanita*, *Elaphomyces*, *Pisolithus*) were registered, while only few species (*Scleroderma* sp. and *Thelephora* sp.) were identified below *Casuarina* trees (Dell et al., 1994; Duponnois et al., 2003; Reddell et al., 1986; Thoen et al., 1990). Moreover, *Casuarina* does not systematically form ectomycorrhizae (Duponnois et al., 2003; Reddell et al., 1986). Nowadays, few data are available about the AM symbioses among *Casuarinaceae*, despite that these types of symbioses would be more common in the genus *Casuarina* (Duponnois et al., 2003; Reddell et al., 1986). A very particular feature of mycorrhizal symbioses has been described within some Neocaledonian species of *Gymnostoma* as “myconodules” hosting AM fungi belonging to the genus *Glomus* (Duhoux et al., 2001).

Casuarinaceae are also naturally associated with the nitrogen-fixing actinomycetous *Frankia*, which has been successfully inoculated to promote the growth of species used for the stabilisation of sand dunes in Senegal (Dommergues et al., 1999). This particular type of symbiosis may be responsible for the success of *Casuarinaceae* as exotics trees in the forest plantations in many countries. The three types of symbioses (ECM, AM and actinorrhizal symbiosis) have been shown to coexist on the same *C. equisetifolia* root system (Bâ et al., 1987), but their functional relevance remains unclear. Diem and Gauthier (1982) demonstrated that mycorrhization of *C. equisetifolia* saplings with *Glomus mosseae* improved the plant growth, *Frankia* nodulation and nitrogen fixation. Nevertheless, there is likely no report on mycorrhization of *Casuarinaceae* species beyond the nursery stage, despite its potential promoting effect on nitrogen fixation and plant growth.

5. DIPTEROCARPACEAE

Members of the *Dipterocarpaceae* are found in the tropics and predominantly in the rain forests of South East Asia. Their economic importance as timber is considerable. In Malaysia, they represent 70% of the timber production (Langenberger, 2006; Maruyama, 1997). *Dipterocarpaceae* often constitute pure forest stands in South East Asia, where the most common genera are *Dipterocarpus*, *Hopea* and *Shorea*. Some species, belonging to the genera *Monotes* and *Marquesia*, are naturally present in African forests, one genus (*Pakaraimaeae*) in South America, and one genus in the Seychelles (*Vateriopsis*). Their mycorrhizal status is generally ectotrophic (Moyerso, 2006; Nataranjan et al., 2005; Rivière et al., 2007; Singh, 1966; Smits, 1992; Tedersoo et al., 2007) and more rarely endotrophic (Aniwat, 1987). Their associated ECM fungi are highly diversified (Hong, 1979; Nataranjan et al., 2005; Watling and Lee, 1995). Six hundred and thirteen fungal species are known to fructify under dipterocarps:

255 of which presumably are ECM fungi (e.g. *S. verrucosum*, *Amanita hemibapha*, *Lactarius virescens*) and 187 constitute new taxa (Watling and Lee, 1995). The genera *Amanita*, *Russula* and *Phylloporus* are among the most frequent both in natural stands and artificial plantations (Nataranjan et al., 2005), while scleroderms are the most represented fruiting taxa in *Hopea* spp. and *Shorea* spp. nurseries (Yazid et al., 1996). Recently, Sirikantaramas et al. (2003) using molecular tools evidenced that *Thelephoraceae* was one of the most common and abundant fungal families found on roots of *Dipterocarpaceae*.

So far, there is no pure cultivated strain from dipterocarp associated ECM fungi available in the literature (Yazid et al., 1994). This seriously limits the ECM synthesis experiments and controlled ectomycorrhization in nurseries and plantations. However, several features plead for a strong dependency of dipterocarp saplings to ECM fungi. Dipterocarp saplings exhibit a very poor growth without ECM partner, as it has been classically observed with pines (Smits et al., 1988). In addition, inoculations with crushed fruitbodies, excised ECM tips or spores contribute to a significant growth promotion of dipterocarp saplings (Lee, 1991; Lee and Alexander, 1994; Turjaman et al., 2005). Pure ECM fungal cultures would probably be much more beneficial and safer for sapling growth as the crushed fruitbodies and excised ECM tips may also be sources of contaminants (Garbaye, 1991). Furthermore, inoculation experiments in Malaysia using a pure allochthonous strain of *P. tinctorius* revealed a significant growth response with several *Hopea* species, but this *Pisolithus* strain was less competitive than native ECM fungi in plantation (Yazid et al., 1995).

The African dipterocarps are much less diversified than their Asian homologs. *Monotes kerstingii* is the only Western African dipterocarp which is encountered in association with *Isoperlinia* forming mixed stands (Aubreville, 1959; Sanon et al., 1997). *M. kerstingii* forms both AM and ECM symbioses (Sanon et al., 1997). Numerous ECM fruitbodies are detected under this tree species, some of them (e.g. *S. verrucosum*, *Lactarius gymnocarpus*) being also associated to *Caesalpinioideae* (Sanon et al., 1997). In East Africa, dipterocarps are represented in both *Monotes* and *Marquesia* genera with several ECM species, such as *Monotes elegans*, *M. africanus* and *Marquesia macroura* (Alexander and Högberg, 1986; Högberg, 1982). Regarding the economic importance of dipterocarps, more works should be developed to elucidate their mycorrhizal dependency and potential benefits of nursery inoculation practices.

6. LEGUMINOSAE

Three subfamilies (Caesalpinioideae, Mimosoideae and Papilionoideae), some containing ECM tree species, constitute the *Leguminosae* family. In tropical Africa, the most exploited exotic leguminous tree species for their considerable economic interest as multipurpose in traditional agroforestry systems were gathered in Mimosoideae. This subfamily comprises about 2 800 species mainly ligneous in semi-arid, subtropical or tropical zones of Africa, America and Australia. The *Acacia*

genus is the most represented with about 1 500 species, including three subgenera (*Acacia*, *Aculeiferum*, and *Phyllodinae*) that are distinguished on the molecular phylogeny of the chloroplast DNA sequences (Luckow et al., 2003). Subgenus *Acacia* contains several important and often emblematic African species (e.g. *Acacia nilotica* and *A. tortilis*). As *Acacia*, the subgenus *Aculeiferum* includes some important African species such as *A. senegal*. The third subgenus *Phyllodinae* contains Australian species of major economical importance as *A. mangium*, *A. auriculiformis* and *A. crassicarpa*. *A. mangium* is being extensively planted in South East Asia for pulp production (Cossalter, 1986). They are also appreciated in wet African countries as fuel or multipurpose woods (Galiana et al., 1996). In general, all species within *Acacia* are nodulated with nitrogen – fixing bacteria (Ducousso, 1991; Le Tacon et al., 1989), and are AM mycorrhized (Bâ and Guissou, 1996; Colonna et al., 1991; Duponnois et al., 2002). Generally, species that fit within the subgenus *Phyllodinae* are also ectomycorrhizal (Ducousso, 1991; Le Tacon et al., 1989). These different types of symbioses are often synergistic, the nitrogen-fixing symbioses having their highest efficiency only after inoculation with AM fungi (Cornet and Diem, 1982). In their native area, Australian acacias are spontaneously associated to the three symbionts (Warcup, 1980), but contrarily to eucalypts there is very few information about the diversity of their associated ECM fungi.

In Africa, the spontaneous ECM partners of Australian acacias would be restricted to the genus *Pisolithus* (Ducousso, 1990; Duponnois and Bâ, 1999). The origin of these compatible *Pisolithus* is still unclear, maybe fortuitously introduced. Nonetheless, several authors (Bâ, 1990; Bâ et al., 1994; Duponnois and Plenchette, 2003) detected true ectomycorrhizas between Australian acacias and native African ECM fungi in axenic conditions. For instance, ectomycorrhizal syntheses were obtained between *A. holosericea* and *Scleroderma dictyosporum* in axenic and glasshouse conditions (Bâ, 1990; Duponnois and Plenchette, 2003). Duponnois et al. (2005, 2007) observed in several experimental sites in Senegal, through inoculation trials with *Pisolithus albus* (strain IR100) (Tab. II), a significant growth promotion of *A. holosericea* and a reduction of negative effects during field transfer. *P. albus* was even able to develop its full life cycle as fruitbodies within the stand, 2 y after inoculation. In addition, *P. albus* was found to promote the efficiency of *Bradyrhizobium* inoculation and therefore growth response of *A. holosericea* (André et al., 2005). Some temperate ECM fungi such as *Boletus* and *Suillus* were also reported to colonize and promote the growth of *A. auriculiformis*, in Nigeria (Osonubi et al., 1991). In Madagascar, *P. microcarpus* strain 441 was found to persist on the roots of *A. crassicarpa*, another Australian species locally appreciated by farmers, while *P. albus* strain COI 007 was no longer detected after 19 months in the field (Ducousso et al., 2004).

Outside its native area, *A. mangium* inoculated with native Australian *Bradyrhizobium* strains generally gave excellent growth responses compared to the local spontaneous bacterial strains (Galiana et al., 1991; 1996). This was observed in African (Galiana et al., 1998; Prin et al., 2003)

Table II. Field measurements of *Acacia holosericea* growth parameters in controlled ectomycorrhization trials conducted in Senegal. From Duponnois et al. (2007).

Plantations	Duration (months)	Growth parameters						
		SD ^a	H	H _{est}	LB	SBB	WB	TB
EC7	30							
Control		9.9 a ^b	4.39 a	4.49 a	13.2 a	11.8 a	17.9 a	42.6 a
<i>P. albus</i> IR100		13.8 b	4.93 b	5.16 b	27.4 b	24.7 b	42.5 b	91.6 b
EC8	18							
Control		2.7 a	2.49 a	2.9 a	0.77 a	0.64 a	0.60 a	2.11 a
<i>P. albus</i> IR100		3.3 b	2.82 b	2.82 a	1.20 b	1.00 b	1.02 b	3.37 b
EC9	18							
Control		2.6 a	2.43 a	2.55 a	0.71 a	0.59 a	0.55 a	1.94 a
<i>P. albus</i> IR100		3.5 b	2.87 b	2.89 b	1.36 b	1.15 b	1.19 b	3.86 b
EC10	18							
Control		2.5 a	2.37 a	2.51 a	0.65 a	0.54 a	0.49 a	1.77 a
<i>P. albus</i> IR100		4.3 b	3.15 b	3.16 b	2.14 b	1.82 b	2.03 b	6.21 b
EC11	18							
Control		5.7 a	3.63 a	3.55 a	3.96 a	3.42 a	4.24 a	11.89 a
<i>P. albus</i> IR100		6.5 b	3.81 b	3.76 b	5.28 b	4.59 b	5.97 b	16.11 b
EC13	18							
Control		3.1 a	2.60 a	2.75 a	1.04 a	0.88 a	0.86 a	2.91 a
<i>P. albus</i> IR100		6.6 b	3.81 b	3.78 b	5.46 b	4.75 b	6.21 b	16.68 b

^a SD: stem diameter (cm); H: height (m); H_{est}: estimated height (m); LB: leaf biomass (kg per tree); SBB: small branches biomass (kg per tree); WB: wood biomass (kg per tree); TB: total aboveground biomass (kg per tree).

^b For each experiment, data in the same column followed by the same letter are not significantly different according to the least significant difference (LSD) multiple range test ($P < 0.05$).

and Asian countries (Frémont et al., 1999; Martin-Laurent et al., 1999). Inoculation of *A. mangium* with AM fungi was less convincing probably due to the presence of native efficient strains (de la Cruz and Yantasath, 1993). Concerning ECM symbioses few data are available on spontaneous fungal associates of *A. mangium*. Only *Thelephora ramarioides* and *Clavaria* spp. were reported on *A. mangium* in Malaysia (Lee, 1990) and Philippines (Anino 1992), respectively. In West Africa, *Pisolithus* was reported in Australian acacias plantations (Ducouso, 1990; Duponnois et al., 2000). Several studies (Duponnois and Bâ, 1999; Duponnois and Plenchette, 2003) showed that the efficiency of the associations between *Acacias* and *Pisolithus* generally depends on soluble P contents in soil.

7. CONCLUSION

The works reported in this review pointed out the importance of root symbionts (mycorrhizal fungi and nitrogen fixing bacteria) in establishment and growth of exotic tree species in tropical Africa. Indeed, it was initially observed that exotic pines were unable to establish in the tropics unless symbiotic compatible ECM fungi were introduced (Hacsakaylo, 1971). These tropical pines are in fact mostly associated with *Rhi-*

zopogon spp., and *Suillus* spp., members of the suilloid group, a monophyletic lineage which includes ECM fungi that exhibit high host specificity (Bruns et al., 2002) and are rarely encountered in tropical Africa (Rivière et al., 2007). Unlike tropical pines, eucalypts are associated with highly diversified ECM fungi. Different growth responses of eucalypts to *Pisolithus* inoculation were obtained depending on the origins of fungal isolates, the best results being generally observed with isolates sharing the same evolutionary history with their host. This illustrates the importance of taking into account the co-evolution of symbiotic partners in the selection of good symbionts for improvement of timber productivity.

The exotic tree species surveyed for their response to inoculation with selected fungal strains displayed significant mycorrhizal dependencies. Nevertheless, in a new habitat, competition may occur between introduced fungal strains and local soil microorganisms and therefore cuts down the beneficial effect of inoculation on growth of these exotic tree species. In this context, it appears difficult to predict the response of exotic tree species to inoculation in a new habitat without testing the efficiency and competitiveness of selected symbiotic partners under local soil constraints.

On the other hand, exclude *Pinaceae* which were colonized by only ECM fungi, all exotic tree species presented here are associated with either both ECM and AM fungi (e.g.

Eucalyptus), or sometimes with three coexisting symbionts (e.g. *Casuarina*, *Acacia*) that are well adapted to the abiotic and biotic factors of their natural habitats. Nevertheless, little is known about the interaction of these different symbionts on their host trees and how they benefit its growth. Hence, the new challenge is to elucidate the relative implication of each symbiont in their host growth promotion for their better exploitation in silviculture and reforestation.

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