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REVIEW

Ectomycorrhizal symbiosis of tropical African trees

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Abstract The diversity, ecology and function of ectomycorrhizal (EM) fungi and ectomycorrhizas (ECMs) on tropical African tree species are reviewed here. While ECMs are the most frequent mycorrhizal type in temperate and boreal forests, they concern an economically and ecologically important minority of plants in African tropical forests. In these African tropical forests, ECMs are found mainly on caesalpionioid legumes, Sarcolaenaceae, Dipterocarpaceae, Asterpeiaceae, Phyllantaceae, Sapotaceae, Papilionoideae, Gnetaceae and Proteaceae, and distributed in open, gallery and rainforests of the Guineo-Congolian basin, Zambezian Miombo woodlands of East and South-Central Africa and Sudanian savannah woodlands of the sub-sahara. Overall, EM status was confirmed in 93 (26%) among 354 tree species belonging to EM genera. In addition, 195 fungal taxa were identified using morphological descriptions and sequencing of the ML5/ML6 fragment of sporocarps and ECMs from West Africa. Analyses of the belowground EM fungal communities mostly based on fungal internal transcribed spacer sequences of ECMs from Continental Africa, Madagascar and the Seychelles also revealed more than 350 putative species of EM fungi belonging mainly to 18 phylogenetic lineages. As in temperate forests, the /russula–lactarius and /tomentella–thelephora lineages dominated EM fungal flora in tropical Africa. A low level of host preference and dominance of multi-host fungal taxa on different African adult tree species and their seedlings were revealed, suggesting a potential for the formation of common ectomycorrhizal networks. Moreover, the EM inoculum potential in terms of types and density of propagules (spores, sclerotia, EM root fragments and fragments of mycelia strands) in the soil allowed opportunistic root colonisation as well as long-term survival in the soil during the dry season. These are important characteristics when choosing an EM fungus for field application. In this respect, Thelephoroid fungal sp. XM002, an efficient and competitive broad host range EM fungus, possessed these characteristics and appeared to be a good candidate for artificial inoculation of Caesalps and Phyllanthaceae seedlings in nurseries. However, further efforts should be made to assess the genetic and functional diversity of African EM fungi as well as the EM status of unstudied plant species and to strengthen the use of efficient and competitive EM fungi to improve production of ecologically and economically important African multipurpose trees in plantations.

Keywords Ectomycorrhizal African trees · Ectomycorrhizal fungal communities · Common ectomycorrhizal networks · Ectomycorrhizal sucession · Growth response

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Introduction

Mycorrhizal symbiosis is a mutualistic plant–fungus association that plays a major role in function, maintenance and evolution of biodiversity and ecosystems stability and productivity (Smith and Read 2008). It plays a key role in the biology and ecology of forest trees, affecting growth, water and nutrient absorption and protection against pathogens. Mycorrhizas are the most widespread symbiosis in forest and cultivated ecosystems (Brundrett 2009). At least 80% of surveyed land plant species and families are mycorrhizal (Wang and Qiu 2006). Mycorrhizas are classified into two major types: endomycorrhizas and ectomycorrhizas (ECMs). Within endomycorrhizas, arbuscular mycorrhizas (AMs) are the predominant and ancestral type of mycorrhizal (Pirozynski and Malloch 1975; Schüßler et al. 2001). ECMs are clearly younger than the ancient AMs and are the most widespread mycorrhizal type in the forests of cool-temperate and boreal latitudes (Smith and Read 2008). Many important tree species of these areas, such as those in the Pinaceae, Fagaceae, Salicaceae and Betulaceae, are associated with a high diversity of ectomycorrhizal (EM) fungi (Molina et al. 1992). ECMs also occur in an ecologically and economically important minority of tropical tree species belonging to the families and sub-families of Fagaceae, Caesalpinioideae, Betulaceae, Dipterocarpaceae, Leptospermoideae in the Myrtaceae, Phyllanthaceae, Gnetaceae, Sapotaceae, Papilionoideae, Proteaceae, Casuarinaceae and Acacieae (Watling and Lee 1995; Béreau et al. 1997; Moyersoen et al. 2001; Henkel et al. 2002; Haug et al. 2004; Nataranjan et al. 2005; Peay et al. 2010). Some of these families and sub-families, such as Caesalpinioideae, Dipterocarpaceae, Phyllanthaceae, Gnetaceae, Sapotaceae, Papilionoideae and Proteaceae, are naturally present in tropical Africa. Furthermore, two families (Sarcolaenaceae and Asteropeiaceae) are endemic to Madagascar. The occurrence of ECMs on Sarcolaenaceae, a family sister to Dipterocarpaceae, suggests that the origin of ECMs on Dipterocarpaceae is from supercontinent Gondwana (Ducousso et al. 2004). Recent discovery of *Pakaraimaea dipterocarpacea* EM status (Moyersoen 2006), an ancestral Neotropical Dipterocarpaceae, raises important questions about the evolution of EM symbiosis. A possible hypothesis is that ECMs evolved in Dipterocarpaceae ancestors before splitting of South America from Africa, ca. 135 million years ago (Moyersoen 2006). Alternative hypothesis for the EM status of Neotropical Dipterocarpaceae have been proposed such as long distance dispersal and/or independent acquisition of EM status (Alexander 2006).

Most previous reviews on the ecology and importance of ECMs have been focussed on boreal and temperate regions (Read and Perez-Moreno 2004; Brundrett 2009; Tedersoo et al. 2010a). One recent review has discussed the management of EM trees to improve reforestation performances in tropical Africa, but this review has focussed primarily on exotic tree species (Bâ et al. 2010). The present review will concentrate on the diversity, ecology and function of EM fungi that colonise roots of tropical African tree species producing timber of high value and fodder in agroforestry systems (Thiès 1995). First, the EM status of African tree species and the diversity of their associated fungi were considered. Then, the different EM propagules were described to reveal which fungal species involved during the early-seral of EM succession on *Afzelia africana* seedlings. We also examined the importance of EM propagules of mature trees as sources of inoculum for survival of seedlings and the variation of EM host specificity during the life cycle of different tree species that can be linked by common ectomycorhizal networks (CENs). Seeds of African caesalpinioid legumes and Phyllanthaceae tree species exhibit a considerable range of seed mass. In this respect, we discuss how tree species having smaller seeds would show greater EM dependency than those with large seeds. To conclude, we discuss what are research priorities and new challenges about EM symbioses in tropical Africa.

EM status of tropical African tree species

Approximately 6,000 plant species are involved in EM symbiosis (Brundrett 2009), although EM tree species inventories are far from complete in tropical areas (Bâ et al. 2011). The majority of known EM tree species is located in temperate and boreal zones (Smith and Read 2008). In tropical Africa, ECMs are mainly distributed in open, gallery and rainforests of the Guineo-Congolian basin, Zambezian Miombo woodlands of East and South-Central Africa, and Sudanian savannah woodlands of the sub-Sahara (Fig. 1) (Newbery et al. 1988; Thoen and Bâ 1989; Sanon et al. 1997; Onguene and Kuyper 2001; Ducousso et al. 2004; Rivière et al. 2007; Ducousso et al. 2008). ECMs are found mainly on caesalpinioid legumes (16 genera in the Amherstieae and *Afzelia* in the Detarieae), Sarcolaenaceae (four genera), Dipterocarpaceae (three genera), and one genus in the Asteropeiaceae, Phyllantaceae, Sapotaceae, Papilionoideae, Gnetaceae and Proteaceae (Table 1). EM legumes and Phyllanthaceae can form groves or extensive monodominant stands (Newbery et al. 2000; Diédhiou et al. 2010). Bâ et al. (2011) determined that only 26% of the EM tree species belonging to known EM genera in tropical Africa have been examined and confirmed to form ECMs (Table 2). In the tropical African forests with high plant diversity, tree species are generally associated with AMs, and when ECMs are present, they usually co-occur with AMs (Moyersoen et al. 1998a, b). In Nigeria,

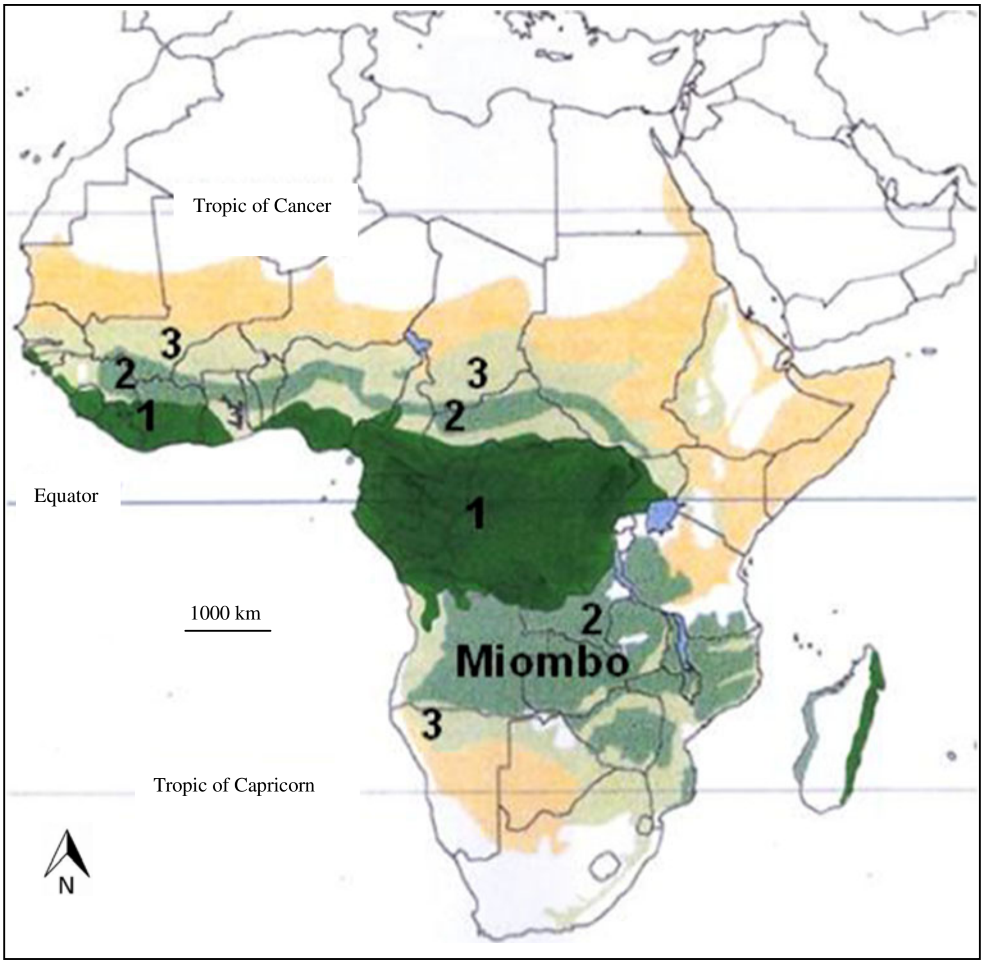

Fig. 1 Distribution of EM trees in tropical Africa (from Bâ et al. 2011): *1* Rainforests in the Guinea-Congo region, *2* open forests in the Sudano-zambezian region, *3* Savanna woodlands in the Sudano-zambezian region

Redhead (1968a, b) reported of the 51 plant species recorded, only three formed ECMs, the remaining ones being associated with AMs. Rambelli (1973) also observed a low frequency of EM species in Ivory Coast. In Tanzania, Högberg and Nylund (1981) noted of the 47 native species recorded, 40 formed AMs, six were with ECMs and one showed ECMs and AMs. In Cameroon, Newbery et al. (1988) indicated of the 55 examined plant species, 32 were with AMs and 23 were with ECMs. Onguene and Kuyper (2002) also confirmed this trend in Cameroon. In Senegal, Thoen and Bâ (1989) recorded only two EM native tree species. This scarcity of EM trees was also observed in open and gallery forests of Burkina Faso (Sanon et al. 1997) and in rainforests of Guinea (Thoen and Ducousso 1989; Rivière et al. 2007; Diédhiou et al. 2010). Although they are not as extensive as mostly AM forests, some tropical forests can be dominated by ECMs, i.e. the open forests *Brachystegia*, *Isoberlinia* and *Julbernardia* of the Miombo in East Africa (Högberg and Nylund 1981), and the rainforests *Gilbertiodendron dewevrei* in the basin of Congo (Torti et al. 2001). Similar situations occurred on Dipterocarpaceae in Southeast Asia (de Alwis and Abeynayake 1980) and *Dicymbe corymbosa* in South America (Henkel et al. 2002; McGuire 2007).

In tropical Africa, most studies indicated that ECMs are mainly found on caesalpinoid legume tree species (Table 2). They include ecologically and economically important multipurpose trees (e.g. *Brachystegia*, *Isoberlinia* and *Afzelia*) that play a major role in forestry and agroforestry (Thiès 1995). Caesalpionioid legumes with ECMs were traditionally placed in the tribes Amherstieae (14 genera from tropical Africa) and Detarieae (two genera, *Afzelia* and *Intsia* from tropical Africa and Asia, respectively) (Alexander 1989; Bâ et al. 2011). Following recent phylogenetic studies (Bruneau et al. 2001; Herendeen et al. 2003), caesalpionioid legumes with ECMs are placed in two separate clades within Amherstieae sensu Bruneau et al. (2001): the "Macrolobiae" clade and an isolated clade within "Amherstieae" clade (*Afzelia*). The same phylogenetic relationship has been observed in South America with the EM caesalpinioid *Dicymbe* (Henkel et al. 2002) belonging to "Macrolobiae" clade and in SE Asia with the EM caesalpinioid *Intsia* (Chalermpongse 1987) belonging to isolated clade within "Amherstieae" clade.

Table 1 Symbiotic status and geographic distribution of some tropical African tree, shrub, herbaceous and liana species (from Bâ et al. 2011)

Taxonomic group	Nodule	AM	ECM	Countries and references
Asteropeiaceae				
Asteropeia amblyocarpa Tul.[a]	−	nd	+	Madagascar (anonymous)
A. densiflora Baker[a]	−	+	+	Madagascar (anonymous)
A. micraster Hallier f.[a]	−	+	+	Madagascar (32)
A. multifolia Thou[a]	−	+	+	Madagascar (32)
A. rhopaloïdes (Baker) Baill.[a]	−	nd	+	Madagascar anonymous
Dipterocarpaceae				
Marquesia macroura Gilg.[a]	−	−	+	Zambia (13)
M. acuminata (Gilg) R.E.Fr.[a]	−	+	+	Zambia (13)
Monotes africana (Welw.) Adc.[a]	−	−	+	Zambia (11)
M. elegans Gilg.[a]	−	−	+	Zambia (11)
“	−	−	+	Tanzania (14)
M. kerstingii Gilg.[a]	−	−	+	Burkina Faso (5)
Vateriopsis seychellarum (Dyer) Heim[a]	nd	nd	+	The Seychelles (34)
Fabacea				
Caesalpinioideae				
Detarieae				
Afzelia africana Sm.[a]	−	−	+	Ghana (1)
	−	−	+	Nigeria (2)
	−	−	+	Senegal (3)
	−	+	+	Guinea (4)
	−	−	+	Burkina Faso (5)
A. bella Harms[a]	−	−	+	DR of Congo (6)
	−	−	+	Nigeria (2)
	−	−	+	Guinea (16)
	−	+	+	Cameroon (22)
A. bipendensis Harms[a]	−	−	+	Cameroon (7)
	−	+	+	Cameroon (8)
	−	+	+	Cameroon (20)
A. bracteata T. Vogel.[a]	−	−	+	Guinea (4)
A. pachyloba Harms[a]	−	−	+	Cameroon (7, 8)
A. quanzensis Welw.[a]	+	−	+	Tanzania (9)
	−	−		Tanzania (10)
	+	−		Zimbabwe (26)
	−	−		Kenya (20)
Amherstieae				
Anthonotha cladantha (Harms) Léon.[a]	−	−	+	Cameroon (7)
A. crassifolia (Baill.) Léon.[a]	−	−	+	Guinea (4)
A. fragans (Bak.f.) Exell & Hillc.[a]	−	−	+	Cameroon (7, 8)
	−	+	+	Cameroon (20)
A. lamprophylla (Harms) Léon.[a]	−	−	+	Cameroon (7)
A. macrophylla P. Beauv.[a]	−	−	+	Cameroon (7, 8)
	−	−	+	Cameroon (20)
Aphanocalyx margininervatus Léon.[a]	−	−	+	Cameroon (7)
A. cynometroides Oliver[a]	−	−	+	Cameroon (20)
Berlinia bracteosa Benth.[a]	−	−	+	Cameroon (7)
B. confusa Hoyle[a]	−	−	+	Cameroon (26)
B. crabiana Bak. f.[a]	−	−	+	Cameroon (7)
B. grandiflora (Vahl) Hutch. & Dalziel[a]	−	nd	+	Burkina Faso (31)

Table 1 (continued)

Taxonomic group	Nodule	AM	ECM	Countries and references
Berlinia sp.[a]	−	−	+	Cameroon (7)
	−	+	+	Cameroun (20)
Brachystegia allenii Burtt Davy & Hutch.[a]	−	−	+	Zambia (13)
Brachystegia bohemi Taub.[a]	−	−	+	Tanzania (11)
	−	−	+	Zambia (13)
B. bussei Harms.[a]	−	−	+	Tanzania (11)
	−	−	+	Zambia (13)
B. cynometroides Harms[a]	−	+	+	Cameroon (8, 25)
B. eurycoma Harms.[a]	−	−	+	Tanzania (12)
	−	−	+	Cameroon (8)
	−	−	+	Nigeria (2)
B. floribunda Benth.[a]	−	−	+	Zambia (11)
	−	−	+	Zambia (13)
B. glaberrima R.E.Fr.[a]	−	−	+	Zambia (12)
	−	−	+	Zambia (13)
B. laurentii (De Wild.) Louis & Hoyle[a]	−	−	+	DR of Congo (6)
B. longifolia Benth.[a]	−	−	+	Zambia (11)
	−	−	+	Tanzania (14)
	−	−	+	Zambia (13)
B. manga De Wild.[a]	−	−	+	Zambia (13)
B. microphylla Harms[a]	−	−	+	Tanzania (11, 14)
	−	−	+	Zambia (13)
B. nigerica Hoyle & A.Jones[a]	−	−	+	Nigeria (27)
B. spiciformis Benth.[a]	−	−	+	Zambia (11)
	−	−	+	Tanzania (9)
	−	−	+	Zambia (13)
B. taxifolia Harms[a]	−	−	+	Zambia (13)
B. utilis Burtt Davy & Hatch[a]	−	−	+	Zambia (13)
B. wangermeeana De Wild.[a]	−	−	+	Zambia (13)
B. zenzeri Harms[a]	−	−	+	Cameroon (8)
Cryptosepalum tetraphyllum (Hook. f) Benth.[a]	−	nd	+	Guinea (16)
Didelotia africana Baill.[a]	−	−	+	Cameroun (7, 8)
	−	+	+	Cameroun (20)
D. letouzeyi Pellegr.[a]	−	−	+	Cameroun (8)
	−	−	+	Cameroun (20)
Gilbertiodendron brachystegioides (Harms) J.Leonard[a]	−	−	+	Cameroun (7, 8)
G. demontrans (Baill.) Léon.[a]	−	−	+	Cameroun (7)
G. dewevrei (De Wild.)[a]	−	−	+	DR of Congo (15)
	−	−	+	Cameroun (7, 8)
	−	+	+	DR of Congo 19)
G. limba (Scott Elliot) J. Leonard[a]	−	−	+	Guinea (16)
G. ogoonense (Pell.)[a]	−	−	+	Cameroon (7)
G. preussi (Harms) J. Leonard	−	−	+	Sierra Leone (33)
Gilbertiodendron sp.[a]	−	−	+	Cameroon (7)
Gilbertiodendron sp 1[a]	−	−	+	Cameroon (20)
Gilbertiodendron sp 2[a]	−	+	+	Cameroon (20)
Isoberlinia angolensis (Benth. Hogle et Brenan)[a]	−	−	+	Zambia (7)
	−	−	+	Zambia (13)
I. dalziellii Craib. & Stapf.[a]	−	−	+	Burkina Faso (5)

Table 1 (continued)

Taxonomic group	Nodule	AM	ECM	Countries and references
I. doka Craib. & Stapf.[a]	−	−	+	Burkina Faso (5)
Julbernardia globiflora (Benth.) Troupin[a]	−	−	+	Tanzania (14)
	−	−	+	Zambia (13)
J. paniculata (Benth.) Troupin[a]	−	−	+	Zambia (11)
	−	−	+	Zambia (13)
J. seretii (De Wild.) Troupin[a]	−	−	+	DR of Congo (17, 18)
	−	−	+	Cameroon (7, 8)
	−	+	+	DR of Congo (19)
Microberlina bisulcata A. Chev[a]	−	−	+	Cameroon (7)
	−	−	+	Cameroon (20)
Monopetalanthus microphyllus Harms[a]	−	−	+	Cameroon (7, 8)
M. letestui Pellegr[a]	−	−	+	Cameroon (8)
Monopetalanthus sp.[a]	−	−	+	DR of Congo (6)
Monopetalanthus sp. nov.[a]	−	−	+	Cameroon (7)
Monopetalanthus sp.[a]	−	+	+	Cameroon (20)
Paraberlinia bifoliolata Pellegr.[a]	−	−	+	Cameroon (8)
Paramacrolobium coeruleum (Taub.) Léon[a]	−	−	+	DR of Congo (6)
	−	−	+	Guinea (16)
P. flagrans (Bak.) Out.[a]	−	−	+	DR of Congo (6)
Pelligriniodendron diphylum (Harms) J. Léonard[a]	−	−	+	Guinea (16)
Tetraberlinia bifoliolata (Harms.) Hauman[a]	−	−	+	Cameroon (7, 8)
	−	+	+	Cameroon (20)
T. moreliana Aubr.[a]	−	−	+	Cameroon (7)
	−	−	+	Cameroon (20)
Toubaouate brevipaniculata (J. Léonard) Aubrév. & Pellegr.[a]	−	−	+	Cameroon (8)
Papilionoideae				
Sophoraceae				
Pericopsis angolensis (Bak.) van Meeuween[a]	−	−	+	Zambia (13)
	−	−	+	Zambia (11)
	+	−	−	Zimbabwe (26)
	+	+	−	Tanzania (14)
Phyllanthaceae				
Uapaca acuminata (Hutch.) Pax & K. Hoffn[a]	−	−	+	Cameroon (25)
U. benguelensis Müll. Arg.[a]	−	−	+	Zambia (13)
U. bojeri Baillon[a]	−	+	+	Madagascar (29)
U. chevalieri Beille[a]	−	−	+	Guinea (4)
U. ferruginea Baill.[a]	−	+	+	Madagascar (32)
U. guineensis Müll. Arg.[a]	−	+	+	Senegal (3)
	−	+	+	Guinea
	−	+	+	Burkina Faso (5)
	−	−	+	Cameroon (8)
U. kirkinia Muell.Arg.[a]	−	−	+	Tanzania (11)
	−	+	+	Zambia (14)
	−	−	+	Zambia (13)
U. littoralis Denis[a]	−	+	+	Madagascar (32)
U. nitida Muell.Arg.[a]	−	−	+	Zambia (11)
	−	−	+	Zambia (13)
U. pilosa Hutch.[a]	−	−	+	Zambia (13)
U. robynsii De Wild.[a]	−	−	+	Zambia (13)

Table 1 (continued)

Taxonomic group	Nodule	AM	ECM	Countries and references
U. sansibarica Pax.[a]	−	−	+	Zambia (13)
U. somon Aub. Linn.[a]	−	+	+	Burkina Faso (5)
U. staudtii Pax.[a]	−	+	+	Cameroon (7)
	−	+	+	Cameroon (20)
U. thouarsii Baill. & Denis[a]	−	+	+	Madagascar (32)
U. togoensis Pax.[a]	−	−	+	Nigeria (28)
U. vanhouttei De Wild.[a]	−	−	+	Cameroon (25)
Gnetaceae				
Gnetum africanum Welw.[b]	−	−	+	DR of Congo (23)
	−	−	+	Cameroon (24)
G. buchholzianum Engl.[b]	−	−	+	Cameroon (25)
Gnetum sp[b]	−	+	+	Cameroon (25)
Proteaceae				
Faurea saligna Harv.[c]	−	−	+	Zambia (13)
Sapotaceae				
Manilkara sp[a]	−	+	+	DR of Congo (19)
Sarcolaenaceae				
Leptolaena paucifolia Thouars[a]	−	+	+	Madagascar (32)
L. multiflora Thouars[a]	−	+	+	Madagascar (32)
Leptolaena sp1[a]	−	+	+	Madagascar (32)
Leptolaena sp2[a]	−	+	+	Madagascar (32)
Sarcolaena eriophora Thou.[a]	−	+	+	Madagascar (32)
S. grandifolia Thou.[a]	−	+	+	Madagascar (32)
S. multiflora Thouars[a]	−	+	+	Madagascar (32)
S. oblongifolia F. Gérard[a]	−	nd	+	Madagascar anonymous)
Schizolaena elongata Lowry[a]	−	+	+	Madagascar (32)
S. exinvolucrata Lowry[a]	−	+	+	Madagascar (32)
Schizolaena sp[a]	−	+	+	Madagascar (32)
S. microphylla H. Perrier[a]	−	nd	+	Madagascar (anonymous)
Xyloolaena humbertii Cavaco[a]	−	nd	+	Madagascar (anonymous)

AM arbuscular mycorrhiza, *ECM* ectomycorrhiza, *nd* not determined, + presence, − absence, *1* Jenik and Mensah 1967, *2* Redhead 1968a, *3* Thoen and Bâ 1989, *4* Thoen and Ducousso 1989a, *5* Sanon et al. 1997, *6* Fassi and Fontana 1962, *7* Newbery et al. 1988, *8* Onguene and Kuyper 2001, *9* Högberg and Nylund 1981, *10* Munyanziza and Kuyper 1995, *11* Alexander and Högber 1986, *12* Redhead 1979, *13* Högberg and Piearce 1986, *14* Högberg 1982, *15* Peyronnel and Fassi 1957, *16* Rivière et al. 2007, *17* Fassi and Fontana 1961, *18* Peyronel and Fassi 1960, *19* Torti and Coley 1999, *20* Moyersoen and Fitter 1999, *21* Ducousso et al. 2004, *22* Alexander 1989, *23* Fassi 1957, *24* Bechem and Alexander 2011, *25* Onguene 2000, *26* Corby 1974, *27* Redhead 1968b, *28* Redhead 1974, *29* Ramanankierana et al. 2007, *30* Martin et al. 1998, *31* Sanon et al. 2009, *32* Ducousso et al. 2008, *33* Bakarr and Janos 1996, *34* Tedersoo et al. 2007

[a] Tree

[b] Liana

[c] Shrub

By contrast, in the tribes Caesalpinieae, Cercidieae and Cassieae, only three tree species, *Erythrophleum succirubrum* (Caesalpinieae), *Cassia garrettiana* (Cassieae) and *Bauhinia malabarica* (Cercidieae) endemic to Thailand, have been found to be colonised by EM fungi (Chalermpongse 1987). African EM tree species can also form AMs. For instance, some Amherstieae (e.g. *G. dewevrei*, *Anthonotha fragrans* and *Tetraberlinia bifoliolata*) and Detarieae (e.g. *Afzelia bipendensis* and *Afzelia pachyloba*) form both mycorrhizal types (ECMs and AMs). However, the majority of caesalpinioid legumes is colonised by arbuscular mycorrhizal fungi only (Newbery et al. 1988; Onguene and Kuyper 2001). Nodulation of Caesalpinioideae concerns approximately 23% of examined legume species (Allen and Allen 1981; de Faria et al. 1989, 2010). It is virtually absent in species belonging to Amherstieae, Detarieae and Cercidieae

Table 2 Presumed ectomycorrhizal host genera of tropical African tree, shrub and liana species, and number and percentage of species examined for ectomycorrhizal symbioses (from Bâ et al. 2011)

Taxonomic group	Genera	Total number of species	Number of examined species	Examined species (%)
Asteropeiaceae	*Asteropeia*	8	4	50
Dipterocarpaceae	*Marquesia*	4	2	50
	Monotes[a]	36	3	8
	Vateriopsis	1	1	100
Fabaceae				
Caesalpinioideae				
Detarieae	*Afzelia*[a]	7	6	86
Amherstieae	*Anthonota*[a]	30	5	16
	Aphanocalyx	3	1	33
	Berlinia[a]	18	3	17
	Brachystegia	36	13	36
	Cryptosepalum[a]	11	1	9
	Didelotia	12	1	8
	Gilbertiodendron[a]	28	7	25
	Isoberlinia[a]	5	3	60
	Julbernardia	11	3	27
	Microberlinia	2	2	100
	Monopetalanthus	20	5	25
	Paramacrolobium[a]	2	2	100
	Pelligriniodendron[a]	1	1	100
	Tetraberlinia	3	3	100
	Toubaouate	1	1	100
Papilionoideae	*Pericopsis*	3	1	33
Phyllanthaceae	*Uapaca*[a]	50	11	22
Gnetaceae	*Gnetum*	3	3	100
Proteaceae	*Faurea*	18	1	5.5
Sapotaceae	*Manilkara*	20	2	10
Sarcolaenaceae	*Leptolaena*	6	2	33
	Sarcolaena	3	2	66
	Schizolaena	7	3	42.8
	Xyloolaena	5	1	20
Total	29	354	93	26.27

Summary of Table 1; Thoen 1993

[a] Genera with at least one EM species in West Africa

and seems more common in Caesalpinieae and Cassieae where AMs predominate. Overall, in Caesalpinioideae, nodulation often coexists with AM symbiosis. On the other hand, different symbiotic statuses of the Papilionoideae, *Pericopsis angolensis*, have been documented following the sampling sites: ECMs being reported on *P. angolensis* in Zambia (Alexander and Högber 1986; Högberg and Piearce 1986), nodules in Zimbabwe (Corby 1974), and AMs and nodules in Tanzania (Högberg 1982). Nevertheless, Tedersoo et al. (2011) found that *P. angolensis* and *Faurea* spp. are incapable of forming ECMs. Furthermore, the three types of symbiosis (nodules, AMs and ECMs) did not seem to coexist on *P. angolensis* as in some Mimosoideae (e.g. *Acacia holosericea*) and Casuarinaceae (e.g. *Casuarina equisetifolia*) introduced in tropical Africa (Warcup 1980; Reddell et al. 1986; Bâ et al. 1987, 1994c; Le Tacon et al. 1989). The coexistence of both AMs and ECMs seems to prevail in Asteropeiaceae, Phyllanthaceae, Sapotaceae and Sarcolaenaceae (Table 1). The mechanisms by which AM and ECM coexist in the same roots or ECM succeed to AM during the growth of dual ECM/AM plants are not yet completely elucidated (Thoen and Bâ 1989; Moyersoen and Fitter 1999; Ramanankierana et al. 2007).

Overall, EM status was confirmed in 93 (26%) among 354 tree species belonging to EM genera (Tables 1 and 2). This is a small proportion of tree species in tropical regions, but it is high compared to the number of EM species in temperate and boreal regions. Inventories are probably not exhaustive and new EM genera might remain to be discovered. Indeed, the discovery of two new families of trees (Sarcolaenaceae and Asteropeiaceae) and two genera in the family of EM Caesalpinioideae (*Cryptosepalum* and *Pelligriniodendron*), respectively, in Madagascar and Guinea forest, may lead to reconsider a widespread view that the EM tropical trees are scarce both in species number and phylogenetic groups (Bâ et al. 2000; Rivière et al. 2007; Ducousso et al. 2008). Not only the status of EM trees remains poorly known in African tropical forests where plant species diversity is much higher than in temperate forests, but also the EM fungi associated with tropical trees could be very diverse and similar to that observed in temperate forests.

Morphological and genetic diversity of EM fungi and ECMs

The first discovery of EM fungi in tropical Africa dates from Hennings's studies (1895) (Buyck et al. 1996). Later, ECMs have been described on *G. dewevrei*, a timber tree, and *Gnetum africanum*, a lianescent species of great interest for food (Fassi 1957; Peyronel and Fassi 1957; Bechem and Alexander 2011). A formal link has been established for the first time in tropical Africa between bright yellow ECMs of *G. africanum* and the EM fungus *Scleroderma* sp. (Fassi 1957). Ingleby et al. (1998) gave a detailed description of ECMs formed between *G. africanum* and *Scleroderma sinnamariense* and recently Bechem and Alexander (2009) confirmed this symbiotic association by EM synthesis. The diversity of ECMs of this plant was unusually low for an EM plant (Bechem and Alexander 2011). In Central Africa, most of the EM fungi were collected in the vicinity of *Gilbertiodendron* spp., *Brachystegia* spp. and *Julbernardia* spp. (Buyck 1993). So far, only two fungal flora of tropical Africa entilted "Flore iconographique des champignons du Congo (fascicules no.1 à 14)" and "Flore illustrée des champignons d'Afrique Centrale (fascicules no. 15 à 17)" have been published. In these fungal flora, some EM fungi such as *Amanita* spp. were described by Beeli (1935), *Boletus* spp., *Cantharellus* spp. and *Tricholoma* spp. by Heinemann (1954, 1959, 1966), *Thelephora* spp. and *Clavaria* spp. by Corner and Heinemann (1967), *Lactarius* spp. by Heim (1955), *Scleroderma* spp. by Dissing and Lange (1963, 1964) and *Russula* spp. by Buyck (1993).

EM fungi from West Africa have received much less attention than those from Central Africa, although some reports on mycological surveys are available (Heim 1955). There is no reference book on fungal flora from West Africa equivalent to those from central Africa. Since 1985, mycological surveys were conducted on EM trees in forests from Senegal, Guinea, Benin and Burkina Faso (Bâ 1986; Thoen and Bâ 1987, 1989; Thoen and Ducousso 1989; Sanon et al. 1997; Bâ et al. 2000; Rivière et al. 2007; Yorou et al. 2007; Sanon et al. 2009; Diédhiou et al. 2010). Furthermore, a book was recently published on diversity, ecology, study methods, use and edibility of EM fungi in West Africa (Bâ et al. 2011).

Diversity of EM fungi

EM fungi are relatively well known in the temperate and boreal forests (Smith and Read 2008). By contrast, there is much less information on EM fungi in tropical forests. Furthermore, one study based on a comparison of four temperate and four tropical rainforests, suggested that the diversity of EM fungi in tropical forests was lower than that in temperate forests (Tedersoo and Nara 2010). This study should be considered with caution because African tropical forests are still undersampled relative to temperate forests and further surveys are clearly needed to confirm Tedersoo and Nara's (2010) hypothesis. In some studies made in West Africa (Thoen and Bâ 1989; Thoen and Ducousso 1989; Rivière et al. 2007), it appeared that the number of harvested EM fungi was quite remarkable and typical genera (e.g. *Russula*, *Lactarius*, *Amanita*, *Boletus*, *Cantharellus* and *Scleroderma*) formed ECMs like in temperate and other tropical regions (Trappe 1962; Watling and Lee 1995; Yokota et al. 1996; Sirikantaramas et al. 2003; Tedersoo et al. 2007, 2011; Peay et al. 2010). In West Africa, a total of 161 species of sporocarps fruiting in the vicinity of 18 putative host plant species was identified in eight orders and 25 genera (Tables 3 and 4) (Thoen and Bâ 1989; Thoen and Ducousso 1989; Rivière et al. 2007). Majority of sporocarps were harvested in Guinean tropical rainforests (Rivière et al. 2007). These authors indicated that the maximum likelihood method for inferring phylogenetic trees from a small (≈400 bp) fragment of the mitochondrial large subunit rRNA gene displayed well-supported phylogenetic relationships among sporocarps at the family level. Hence, the phylogenetic placement of all these collected sporocarps was in agreement with the morphological description at the family or genus level. Three genera *Russula* (33 species), *Amanita* (30 species) and *Lactarius* (21 species), including several putative new species, displayed a great diversity. These three genera together accounted for over half of all species harvested under EM tree species. As in the temperate region, Russulales (*Russula* and *Lactarius*) showed the largest number of described species in West Africa. Some of the species of *Russula* harvested from West African have also been described in East and Central Africa (Buyck et al. 1996) (Table 5), whereas African *Russula* are different from European *Russula* (Buyck 1993). Considering the number of described species in tropical Africa and the primitive features of a large number of them, Buyck (1993) suggested that *Russula* has an African origin.

Table 3 Diversity of ectomycorrhizal fungi identified from sporocarps and ECMs collected from native tree species in West Africa (Burkina Faso, Guinea and Senegal) (from Bâ et al. 2011)

Orders, species[g]	Number of voucher material	GenBank Accession no.	BF	FG	FDG	SE
Amanitales						
Amanita annulatovaginata Beeli	C72[f]	AM117709[f]	−	+	−	−
A. cf. *annulatovaginata* Beeli	C7659[c]	−	−	−	+	−
A. baccata (Fr.) Gillet	C7956[c]	−	−	−	+	−
A. crassiconus Bas	C7976[c]	−	−	−	+	+
A. cf. *crassiconus* Bas	C7664[d]	−	+	−	−	−
A. cf. *fulvopulverulenta* Beeli	C7957[c]	−	−	−	+	−
A. aff. *griseofloccosa*	C19[f]	−	−	+	−	−
A. hemibapha (Berk. & Br.) Sacc.	CIR25[d],C7658[b]	−	+	−	−	+
A. cf. *lanosa* Bas	C49[f]	AM117686[f]	−	+	−	−
A. cf. *lanosula* Bas	C7905[c]	−	−	−	+	−
A. aff. *rubescens* (Pers : Fr.) S. Gray	C7487[f],C112[b]	−	−	+	−	+
Amanita sp 1	CIR67[d]	−	+	−	−	−
Amanita sp 2	CIR26[d]	−	+	−	−	−
Amanita sp 3	C601=E19[f]	AM117697[f]	−	+	−	−
Amanita sp 4	C342[f]	AM117668[f]	−	+	−	−
Amanita sp 5	C294[f]	AM117651[f]	−	+	−	−
Amanita sp 6	C314[f]	AM117657[f]	−	+	−	−
Amanita sp 7	C322[f]	AM117659[f]	−	+	−	−
Amanita sp 8	C352[f]	AM117669[f]	−	+	−	−
Amanita sp 9	C378[f]	AM117682[f]	−	+	−	−
Amanita sp 10	C288[f]	AM117647[f]	−	+	−	−
Amanita sp 11	C315[f]	AM117658[f]	−	+	−	−
Amanita sp 12	C291[f]	AM117648[f]	−	+	−	−
Amanita sp 13	C173[f]	AM117636[f]	−	+	−	−
Amanita sp 14	C7907[c]	−	−	−	+	−
Amanita sp 15	C7897[c]	−	−	−	+	−
Amanita sp 16	C7644[b]	−	−	−	−	+
Amanita sp 17	C7648[b]	−	−	−	−	+
Amanita sp 18	C7672[b]	−	−	−	−	+
Amanita sp 19	C7674[b]	−	−	−	−	+
Boletales						
Austrogautiera sp.[a]	CIR29[d],C7700[b]	−	+	−	−	+
Boletellus cf. *lepidospora* Gilb	C7989[c]	−	−	−	+	−
Boletellus sp 1	CIR19[d]	−	+	−	−	−
Boletellus sp 2	CIR48[d]	−	+	−	−	−
Boletellus sp 3	CIR52[d]	−	+	−	−	−
Boletellus sp 4	CIR53[d]	−	+	−	−	−
Boletellus sp 5	CIR65[d]	−	+	−	−	−
Boletellus sp 6	C7518[b]	−	−	−	−	+
Boletus sp 1	C39[f]	AM117683[f]	−	+	−	−
Boletus sp 2	C364[f]	AM117675[f]	−	+	−	−
Boletus sp 3	C661[f]	AM117701[f]	−	+	−	−
Boletus sp 4	C510[f]	AM117689[f]	−	+	−	−
Boletus sp 5	C332[f]	AM117635[f]	−	+	−	−
Boletus sp 6	C170[f]	AM117625[f]	−	+	−	−
Boletoid fungal species	E160[f]	AM117622[f]	−	+	−	−
Boletoid fungal species	E2[f]	AM117627[f]	−	+	−	−
Boletoid fungal species	E319[f]	AM117628[f]	−	+	−	−

Table 3 (continued)

Orders, species[g]	Number of voucher material	GenBank Accession no.	BF	FG	FDG	SE
Chalciporus sp.	C365[f]	AM117676[f]	−	+	−	−
Gyrodon cupreus Heinem	C365[b]	−	−	−	−	+
G. intermedius (Pat.) Sing.	C7460[b]	−	−	−	−	+
Gyroporus microsporus (Sing.) & (Grinl.) Heinem. & Rammeloo var. *congolensis* (Heinem.) Heinem. & Rammeloo	C7613[b]	−	−	−	−	+
Leccinum sp 1	C573=E223[f]	AM117726[f]	−	+	−	−
Leccinum sp 2	C32=E32[f]	AM117665[f]	−	+	−	−
Leccinum sp 3	C570[f]	AM117693[f]	−	+	−	−
Leccinum sp 4	C59[f]	AM117696[f]	−	+	−	−
Leccinum sp 5	C7990[c]	−	−	−	+	−
Mucilopus sp.	C7964[c]	−	−	−	+	−
Porphyrellus niger Heinem. & Gooss	C7875[b]	−	−	−	−	+
Porphyrellus sp.	C7969[c]	−	−	−	+	−
Pulveroboletus aff. *tritinensis* Heinem.	C7461[b]	−	−	−	−	+
P. ravenelii (Berk. & Curt.) Murr.	C7977[c]	−	−	−	+	−
Scleroderma dictyosporum Pat	CIR215[d],C7906[e] ,C7510[c]	AJ509787[e]	+	−	+	+
S. verrucosum Pers	CIR501[d], C7921[e],C7508[c]	AJ509788[e]	+	−	+	+
Scleroderma sp 1	CIR406[d]	−	+	−	−	−
Scleroderma sp 2	CIR100[d]	−	+	−	−	−
Scleroderma sp 3	C156=E119[f]	AM117611[f]	−	+	−	−
Scleroderma sp 4	C157=E17[f]	AM117612[f]	−	+	−	−
Scleroderma sp 5	C302[f]	AM117653[f]	−	+	−	−
Scleroderma sp 6	C22=E22[f]	AM117643[f]	−	+	−	−
Scleroderma sp 7	C109[f]	AM117605[f]	−	+	−	−
Scleroderma sp 8	C296[f]	AM117634[f]	−	+	−	−
Scleroderma sp 9	C153[f]	AM117610[f]	−	+	−	−
Sclerodermataceae	E9[f]	AM117633[f]	−	+	−	−
Sclerodermataceae	E124[f]	AM117723[f]	−	+	−	−
Sclerodermataceae	E137[f]	AM117618[f]	−	+	−	−
Sclerodermataceae	Eb1[e]	AJ509791[e]	−	−	−	+
Sclerodermataceae	Ea3[e]	AJ509803[e]	−	−	−	+
Sclerodermataceae	Ea1[e]	AJ509799[e]	−	−	−	+
Sclerodermataceae	Eb2[e]	AJ509793[e]	−	−	−	+
Sclerogaster sp 1[a]	CIR34[d]	−	+	−	−	−
Sclerogaster sp 2[a]	C7958[c]	−	−	−	+	−
Sclerogaster sp 3[a]	C7660[b]	−	−	−	−	+
Strobilomyces costatispora (Beeli) Gilb.	C7506[b]	−	−	−	−	+
S. aff. *echinatus*	C61[f]	−	−	+	−	−
S. luteolus Heinem	C7892[c]	−	−	−	+	−
Strobilomyces sp 1	CIR40[d]	−	+	−	−	−
Strobilomyces sp 2	C363=E53[f]	AM117674[f]	−	+	−	−
Strobilomyces sp 3	S7896[c]	−	−	−	+	−
Tubosaeta brunneosetosa (Sing.) Horak †	CIR17a[d],C16[b], C7893[f],C7462[c]	AM117614[f]	+	+	+	+
Tylopilus cf. *tenuis* Heinem.	C7891[c]	−	−	−	+	−
Tylopilus sp.	C7908[c]	−	−	−	+	−
Xerocomus aff. *hypoxanthus* Singer	C24[f],C7491[b]	−	−	+	−	+
X. spinulosus Heinem. & Goos.	C7514[b]	−	−	−	−	+
X. subspinulosus Heinem.	CIR66[d],C7489[c],C7965[b]	−	+	−	+	+
X. aff. *subspinulosus* Heinem.	C40[f]	−	−	+	−	+
Xerocomus sp 1	C358[f]	AM117672[f]	−	+	−	−

Table 3 (continued)

Orders, species[g]	Number of voucher material	GenBank Accession no.	BF	FG	FDG	SE
Xerocomus sp 2	C7895[c]	–	–	–	+	–
Xerocomus sp 3	C7974[c]	–	–	–	+	–
Cantharellales						
Cantharellus congolensis Beeli	C7879[b]	–	–	–	–	+
C. pseudofriesii Heinem.	CIR28[d],C7962[c],C7654[b]	–	+	–	+	+
C. rufopunctatus (Beeli) Heinem.	C7971[c]	–	–	–	+	–
Cortinariales						
Inocybe sp 1	CIR10[d]	–	+	–	–	–
Inocybe sp 2	CIR11[d]	–	+	–	–	–
Inocybe sp 3	C7961[c]	–	–	–	+	–
Inocybe sp 4	C7978[c]	–	–	–	+	–
Inocybe sp 5	C7657[b]	–	–	–	–	+
Inocybe sp 6	C7561[b]	–	–	–	–	+
Cortinarioid fungal species	Ea2[e]	AJ509800[e]	–	–	–	+
Cortinarioid fungal species	Ec4[e]	AJ509797[e]	–	–	–	+
Hymenochaetales						
Coltricia cinnamomea (Pers.) Murr.	C7859[b],CIR41[d]	–	+	–	–	+
Russulales						
Elasmomyces sp.[a]	C7652[b]	–	–	–	–	+
Lactarius annulatoangustifolius (Beeli) Buyck	C360[f]	AM117673[f]	–	+	–	–
L. cf. *brunnescens*	C63[f]	AM117699[f]	–	+	–	–
L. cf. *caperatus* Heim & Goos.	C8065[c]	–	–	–	+	–
Lactarius gymnocarpus Heinem.	CIR23[d],C842[b], C7966[c],C7605[f]	AM117717[f]	+	+	+	+
L. aff. *gymnocarpus*	C329[f]	AM117664[f]	–	+	–	–
L. goossensiae Beeli	C320[f]	–	–	+	–	–
L. hispidus	C151[f]	–	–	+	–	–
L. aff. *medusa*	C841[f]	AM117716[f]	–	+	–	–
L. melanogalus Heim	C350[f]	–	–	+	–	–
L. pelliculatus (Beeli) Buyck	C62[f]	–	–	+	–	–
L. sp. nov. sect. *Plinthogali*	C13=E13[f]	AM117608[f]	–	+	–	+
L. aff. *pulchrispermus*	C158[f]	AM117613[f]	–	+	–	–
L. ruvubuensis Verbeken	C305[f]	AM117654[f]	–	+	–	+
L. zenkeri P. Henn	C7618[b]	–	–	–	–	+
Lactarius sp 1	CIR64[d]	–	+	+	–	–
Lactarius sp 2	CIR68[d]	–	+	+	–	–
Lactarius sp 3	C194[f]	AM117640[f]	–	+	–	–
Lactarius sp 4	C703=E25[f]	AM117706[f]	–	+	–	–
Lactarius sp 5	C7968[c]	–	–	–	+	–
Lactarius sp 6	C7662[b]	–	–	–	–	+
Lactarius sp 17	C7606[b]	–	–	–	–	+
Russula annulata Heinem.	CIR46[d]	–	+	–	–	–
R. aff. *annulata* Heinem.	C189[f]	AM117639[f]	–	+	–	–
R. cellulata Buyck	C373[f]	AM117681[f]	–	+	–	–
R. congoana Patouillard var. congoana Patouillard	C14=E20[f]	AM117609[f]	–	+	–	–
R. discopus R. Heim	C293[f]	AM117650[f]	–	+	–	–
R. liberiensis Singer	C183[f]	AM117638[f]	–	+	–	–
R. meleagris Buyck	C292[f]	AM117648[f]	–	+	–	–
R. parasitica (R. Heim) Buyck	C2[f]	AM117652[f]	–	+	–	–
R. aff. *parasitica*	C728[f]	AM117708[f]	–	+	–	–
R. aff. *pruinata*	C312[f]	AM117656[f]	–	+	–	–

Table 3 (continued)

Orders, species[g]	Number of voucher material	GenBank Accession no.	BF	FG	FDG	SE
R. cf. *radicans*	C51[f]	AM117690[f]	−	+	−	−
Russula sp. nov. *Archaeina*	C53[f]	AM117691[f]	−	+	−	−
Russula sp. nov. aff. *sesenagula*	C366[f]	AM117677[f]	−	+	−	−
Russula sp 1	CIR14[d]	−	+	−	−	−
Russula sp 2	CIR62[d]	−	+	−	−	−
Russula sp 3	C597[f]	AM117695[f]	−	+	−	−
Russula sp 4	C357[f]	AM117671[f]	−	+	−	−
Russula sp 5	C11[f]	AM117606[f]	−	+	−	−
Russula sp 6	C621[f]	AM117698[f]	−	+	−	−
Russula sp 7	C372[f]	AM117680[f]	−	+	−	−
Russula sp 8	C7=E121[f]	AM117713[f]	−	+	−	−
Russula sp 9	C353[f]	AM117670[f]	−	+	−	−
Russula sp 10	C6[f]	AM117704[f]	−	+	−	−
Russula sp 11	C334=E334[f]	AM117667[f]	−	+	−	−
Russula sp 12	C7988[c]	−	−	−	+	−
Russula sp 13	C7970[c]	−	−	−	+	−
Russula sp 14	C7519[b]	−	−	−	−	+
Russula sp 15	C7581[b]	−	−	−	−	+
Russula sp 16	C7633[b]	−	−	−	−	+
Russula sp 17	C7509[b]	−	−	−	−	+
Russula sp 18	C7507[b]	−	−	−	−	+
Russula sp 19	C7580[b]	−	−	−	−	+
Russula sp 20	C7670[b]	−	−	−	−	+
Russuloid fungal species	E18[f]	AM117623[f]	−	+	−	−
Thelephorales						
Thelephoroid fungal species	E21[f]	AM117624[f]	−	+	−	−
Thelephoroid fungal species	E42[f]	AM117629[f]	−	+	−	−
Thelephoroid fungal species	E01[f]	AM117722[f]	−	+	−	−
Thelephoroid fungal species	E128[f]	AM117615[f]	−	+	−	−
Thelephoroid fungal species	E51[f]	AM117630[f]	−	+	−	−
Thelephoroid fungal species	E138[f]	AM117618[f]	−	+	−	−
Thelephoroid fungal species	E130[f]	AM117616[f]	−	+	−	−
Thelephoroid fungal species	E139[f]	AM117620[f]	−	+	−	−
Thelephoroid fungal species	E134[f]	AM117617[f]	−	+	−	−
Thelephoroid fungal species	E148[f]	AM117621[f]	−	+	−	−
Thelephoroid fungal species	E55[f]	AM117631[f]	−	+	−	−
Thelephoroid fungal species	E82[f]	AM117632[f]	−	+	−	−
Tomentella sp	C30[f]	AM117655[f]	−	+	−	−
Thelephoroid fungal species	Ec3[e]	AJ509796[e]	−	−	−	+
Thelephoroid fungal species	Exm[e]	AJ509789[e]	−	−	−	+
Thelephoroid fungal species	Eb5[e]	AJ509790[e]	−	−	−	+
Thelephoroid fungal species	Ec5[e]	AJ509798[e]	−	−	−	+
Thelephoroid fungal species	Eb4[e]	AJ509794[e]	−	−	−	+
Thelephoroid fungal species	Ea5[e]	AJ509802[e]	−	−	−	+
Thelephoroid fungal species	Eb3[e]	AJ509792[e]	−	−	−	+
Thelephoroid fungal species	Ec2[e]	AJ509795[e]	−	−	−	+
Thelephoroid fungal species	Ea4[e]	AJ509801[e]	−	−	−	+
Tricholomatales						
Tricholoma sp 1	C331[f]	AM117666[f]	−	+	−	−
Tricholoma sp 2	C327[f]	AM117662[f]	−	+	−	−

Table 3 (continued)

Orders, species[g]	Number of voucher material	GenBank Accession no.	BF	FG	FDG	SE
Tricholoma sp 3	C572[f]	AM117694[f]	−	+	−	−
Tricholomatoid fungal species	C324[f]	AM117661[f]	−	+	−	−
Tricholomatoid fungal species	C369[f]	AM117678[f]	−	+	−	−
Tricholomatoid fungal species	C323[f]	AM117660[f]	−	+	−	−
Tricholomatoid fungal species	C328[f]	AM117663[f]	−	+	−	−
No. of fungal taxa=195			28	103	32	57

+ presence, − absence, *BF* Burkina Faso, *FG* Forest Guinea, *FDG* Fouta Djalon in Guinea, *SE* Senegal, *C* Sporocarps, *E* Ectomycorhiza

[a] Hypogeous fungi

[b] Thoen and Bâ 1989

[c] Thoen and Ducousso 1989

[d] Sanon et al. 1997

[e] Diédhiou et al. 2004b

[f] Rivière et al. 2007

[g] The identification of sporocarps at the level of genus was based on morphology, and the possibility that some of them could be same species or cryptic species cannot completely rule out

Epigeous sporocarps might not be perfect indicators of belowground species richness for taxa producing inconspicuous or no sporocarps (e.g. members of the thelephoroid, sebacinoid and athelioid clades of basidiomycetes and ascomycetes; Tedersoo et al. 2007). For example, Rivière et al. (2007) found only one sporocarp of *Tomentella* sp. (S30) versus 21 Thelephoroid fungal species from ECMs (Table 3). This discrepancy suggests that thelephoroid sporocarps were much less abundant than their ECMs. In temperate zones, species of the /tomentella–thelephora lineage often prolifically form ECMs from relatively few sporocarps, suggesting a low proportional allocation of resources to reproduction (Lilleskov et al. 2002). Despite the apparent low abundance of thelephoroid sporocarps, more than ten new species of West African resupinate Thelephorales, fruiting on dead trunks that had no contact with the soil, were collected in open forests dominated by Caesalpinioideae, Dipterocarpaceae and Phyllanthaceae (Yorou et al. 2007; Yorou and Agerer 2007, 2008). It is very likely that these Thelephorales species form EM symbiosis with native trees of West Africa. The increase in new species records in the /tomentella–thelephora lineage from West Africa (Yorou et al. 2011a, b, c) suggests that the African tropical forests may harbour numerous new species of this lineage, particularly in undisturbed areas. Besides resupinate Thelephorales, many African EM fungi are still unidentified, and most of them are putative new species and require additional voucher material to confirm the descriptions. So far, three EM fungi have been formally identified as new species, *Russula* sect. *Archaeinae* sp. nov. (S53), *Russula* sp. nov. aff. *sesenagula* (S366) and *Lactarius* sect. *Plinthogali* sp. nov. (S13) (Bâ et al. 2000; Rivière et al. 2007).

The EM fruiting bodies were usually harvested aboveground, but there are also some hypogeous fruiting bodies in African tropical forests. For instance, two hypogeous sporocarps, *Austrogautieria* sp. and *Elasmomyces* sp., were found under one species of Phyllanthaceae (*Uapaca guineensis*), while three hypogeous species of *Sclerogaster* appeared to be common to several species of Caesalpinioideae, Dipterocarpaceae and Phyllanthaceae (Thoen and Bâ 1989; Sanon et al. 1997). A total of five species of hypogeous fungi were collected for the first time in tropical Africa (Thoen and Bâ 1989; Sanon et al. 1997), suggesting they were probably more abundant in tropical Africa than previously assumed (Thoen and Ducousso 1989).

In West Africa, some fungal species fruited after the first significant rainfall, others in the middle or at the end of the rainy season (Thoen and Bâ 1989). For example, *Scleroderma* spp. fruited during the rainy season, while *Colricia cinnamomea* fruited only at the end of the rainy season (Thoen and Bâ 1989, Sanon et al. 1997). Therefore, there was a fruiting phenology for some EM fungi in open forests characterised by a climate with very short rainy season and an erratic rainfall in time and space. However, sporocarp production is poorly understood and could depend on the accumulated rainfall, diversity of host trees, forest types and stand age (Fleming 1985; Lilleskov and Bruns 2003). In West Africa, the abundance of fungal species collected from different sites could be linked to forest types (rainforests versus open forests), number of host tree species and the climate characteristics (e.g. accumulation and distribution of rainfall, duration of rainy season) (Thoen and Bâ 1989; Thoen and Ducousso 1989; Sanon et al. 1997; Rivière et al. 2007). Fungal diversity in Guinean rainforests

Table 4 Diversity of ectomycorrhizal fungi based on sporocarps associated with EM native trees of West Africa (Burkina Faso, Guinea and Senegal) (from Bâ et al. 2011)

Basidiomycetous			
Orders	Families	Genera	Species
Amanitales	Amanitaceae	*Amanita*	30
Boletales	Boletaceae	*Austrogautiera*	1
		Boletellus	7
		Boletus	6
		Chalciporus	1
		Gyrodon	2
		Gyroporus	1
		Leccinum	5
		Mucilopilus	1
		Porphyrellus	2
		Pulveroboletus	2
		Scleroderma	11
		Sclerogaster	3
		Strobilomyces	6
		Tubosaeta	1
		Tylopilus	2
		Xerocomus	7
Cantharellales	Cantharellaceae	*Cantharellus*	3
Cortinariales	Inocybaceae	*Inocybe*	6
Hymenochaetales	Hymenochetaceae	*Coltricia*	1
Russulales	Russulaceae	*Russula*	33
		Lactarius	21
		Elasmomyces	1
Thelephorales	Thelephoraceae	*Thelephora/ Tomentella*	1
Tricholomatales	Tricholomataceae	*Tricholoma*	7
Total number of species			161

was higher than that reported in open and gallery forests (Table 3). These results should be interpreted cautiously as areas of surveyed plots and days spent in the field were different depending on sampling sites. For example, fungal species collected in open and gallery forests of Fouta Djallon was probably underestimated because the fungal surveys were conducted only during 10 days (Thoen and Ducousso 1989).

On the other hand, EM fungi displayed different putative host ranges (Table 5). For example, *Russula annulata* has a broad host range, while *Xerocomus hypoxanthus* has been observed only under *U. guineensis*. Several EM fungi harvested have a large distribution in tropical Africa (Table 6). For example, *Scleroderma dictyosporum* and *Scleroderma verrucosum* were recorded from all phytogeographical regions and forest types regardless of the level of rainfall. They have also been observed in Southeast Asian tropical forests (Watling 1993; Watling and Lee 1995; Yokota et al. 1996; Sims et al. 1999; Sanon et al. 2009). Some families of EM fungi in temperate regions are less represented in tropical Africa. This was the case of Tricholomatales represented by the genus *Tricholoma* and Cortinariales by the genus *Inocybe* and *Cortinarius* (Thoen and Bâ 1989; Onguene 2000; Rivière et al. 2007). These two groups of fungi are assumed to be adapted to cold climates (Buyck et al. 1996).

Diversity of ECMs

In some circumstances, mycelial strands and extensive masses of loose hyphae have been traced from the base of sporocarps to the most characteristic ECMs. For example, Thoen and Bâ (1989) established connections between yellow ECMs of *U. guineensis* and hypogeous sporocarps of *Austrogautiera* sp., pinnate, beige ECMs and *L. gymnocarpus*, pink ECMs and *Amanita* aff. *rubescens*, brown, bristly ECMs and *C. cinnamomea* and whitish ECMs with a sclerodermic smell of *S. verrucosum*. These observations were facilitated by the proximity and colour of sporocarps collected under *U. guineensis* in swamp forest. However, connections between sporocarps and the ECMs of *A. africana*, which were located deeper in the mineral soil, were more difficult to establish with certainty (Thoen and Bâ 1989; Sanon et al. 1997). Some chemical tests (Zak 1969) may also be used to link ECMs and sporocarps. For example, ECMs and sporocarps of *S. dictyosporum* are corn to amber yellow and specifically turn delphinium blue with sulphuric acid and dark blue with sulphoformol (Bâ and Thoen 1990). This empiric approach was often inconclusive to confirm EM fungal identity, and it was replaced by mycorrhizal syntheses or by the use of molecular tools (Bâ and Thoen 1990; Rivière et al. 2007; Sanon et al. 2009). Mycorrhizal syntheses allowed to confirm the symbiotic status of only some EM fungi, the majority of them not being cultivable (Bâ and Thoen 1990; Sanon et al. 1997).

It is well known that EM sporocarps do not provide a complete picture of EM fungal communities, and although sporocarps are necessarily linked to ECMs, a fungus forming ECMs may not always form sporocarps (Smith and Read 2008). Therefore, the inventory of ECMs is also an approach that provides access to the composition of belowground fungal communities (Horton and Bruns 2001). In tropical Africa, the first ECMs were described on *G. dewevrei* and *G. africanum* in rainforests of DR Congo (Fassi 1957, 1960). Subsequently, several ECMs were described on *Brachystegia laurentii*, *Afzelia bella*, *Anthonotha macrophylla*, *Paramacrolobium* spp. and *Julbernardia seretii* (Fassi and Fontana 1961, 1962). Jenik and Mensah (1967) have described for the first time two different ECMs on *Afzelia africana* based on the colour of

Table 5 Common ectomycorrhizal fungal species found fruiting beneath native trees from West Africa (Burkina Faso, Guinea and Senegal) (from Bâ et al. 2011)

Fungal species	Host plants	Countries
Amanita crassiconus Bas	*Aa*, *Uc*	FDG, SE
Amanita hemibapha (Berk. & Br.) Sacc.	*Aa*, *Ida*, *Ido*, *Us*	BF, SE
Cantharellus pseudofriesii Heinem.	*Aa*, *Ac*, *Ida*, *Ido*, *Mk*, *Ug*, *Us*	BF, FDG, SE
Coltricia cinnamomea (Pers.) Murr.	*Aa*, *Am*, *Ct*, *Ida*, *Ido*, *Ug*, *U* sp.	BF, FG, SE
Lactarius gymnocarpus Heim	*Aa*, *Ac*, *Ida*, *Ido*, *Mk*, *Ug*, *Uh*, *Us*	BF, FG, FDG, SE
Russula annulata Heim	*Ab*, *Af*, *Am*, *Ct*, *Gl*, *Pc*, *Uc*, *Ue*, *Ug*, *Uh*	BF, FG, FDG, SE
Russula discopus Heim	*Ug*, *Uh*	GF, FDG, SE
Scleroderma dictyosporum Pat.	*Aa*, *Abr*, *Ac*, *Ida*, *Ido*, *Mk*, *Ug*, *Us*	BF, FDG, SE
Scleroderma verrucosum Pers.	*Aa*, *Abr*, *Ac*, *Ida*, *Ido*, *Mk*, *Ug*, *Us*	BF, FDG, SE
Tubosaeta brunneosetosa (Sing.) Horak	*Aa*, *Ida*, *Ido*, *Gl*, *Pc*, *Uh*, *Ug*	BF, FG, FDG, SE
Xerocomus hypoxanthus Singer	*Ug*	FG, SE
Xerocomus subspinulosus Heinem.	*Aa*, *Ac*, *Ida*, *Ido*, *Ug*	BF, FDG, SE

BF Burkina Faso, *FG* Forest Guinea, *FDG* Fouta Djalon in Guinea, *SE* Senegal, *Aa Afzelia africana*, *Ab Afzelia bella*, *Abr Afzelia bracteata*, *Ac Anthonotha crassifolia*, *Af Anthonotha fragans*, *Am Anthonotha macrophylla*, *Ct Crysptosepalum tetraphyllum*, *Gl Gilbertiodendron limba*, *Ida Isoberlinia dalziellii*, *Ido Isoberlinia doka*, *Mk Monotes kerstingii*, *Pc Paramacrolobium coeruleum*, *Uc Uapaca chevalieri*, *Ue Uapaca esculenta*, *Uh Uapaca heudelottii*, *Ug Uapaca guineensis*, *Us Uapaca somon*, *U sp. Uapaca* sp. (compiled from Thoen and Bâ 1989; Thoen and Ducousso 1989; Sanon et al. 1997; Bâ et al. 2000; Rivière et al. 2007; Sanon et al. 2009)

the fungal mantle. Högberg and Nylund (1981) and Alexander and Högber (1986) described several ECMs on African Caesalpinioideae and Dipterocarpaceae. These ECMs were characterised by a relative thick fungal mantle that distinguished them from ECMs in temperate zones. These authors suggested that the relative thickness of fungal mantle increased the ability of fungi to store nutrients and protect roots against desiccation in the dry season. Observations made in Senegal (Thoen and Bâ 1989) and Guinea (Thoen and Ducousso 1989) also showed a wide variety of ECMs on African trees, while the average diameter and thickness of the fungal mantle were substantially identical in trees. In this respect, Thoen and Bâ (1989) observed on *A. africana* and *U. guineensis* that the percentage of area occupied by the fungal mantle over the surface of ECMs is comparable on average for both species. The depth of penetration of the Hartig net was similar in both trees. The epidermal cells form a basis palisade whose content was particularly rich in phenolic compounds in *U. guineensis* (Thoen and Bâ 1989). Most ECMs had mycelial strands with a possible role in the transfer of water and nutrients (Horton et al. 1999; He et al. 2004). The morphology and structure of ECMs on *A. africana* and *U. guineensis* were very close to those of ECM in temperate regions (Garbaye et al. 1986). In ecological studies, sorting of ECM based on morphological and structural characters often lead to false lumping and splitting of fungal taxa (Bâ et al. 1991; Wurzburger et al. 2001; Diédhiou et al. 2004b; Tedersoo et al. 2011). Although some taxa were difficult to recognise on the basis of morpho-anatomical characteristics of ECMs, it was not the case for all. Agerer's (1991) method can be very precise, but requires a lot of time and expertise. The first comprehensive descriptions of African ECMs using Agerer's (1991) method of classification were made on *T. bifoliolata* (Moyersoen 1996a, b, c). However, this method is much less convenient and efficient than molecular tools. To identify the fungal component of ECMs, internal transcribed spacer–restriction fragment length polymorphism (ITS-RFLP) patterns of ECMs were compared to those of sporocarps (Rivière et al. 2007). Whenever ITS-RFLP patterns of ECMs did not match sporocarps, fungi were identified using sequence analysis of either a portion of the mitochondrial large subunit or ITS (Gardes and Bruns 1996; Bruns et al. 1998; Diédhiou et al. 2004b; Rivière et al. 2007).

Overall, Bâ et al. (2011) showed that 195 fungal taxa were identified in West Africa (e.g. Burkina Faso, Guinea and Senegal) using morphological descriptions and sequencing of the ML5/ML7 fragment (Table 3). Of the 119 fungal DNA sequences obtained, 78 were from sporocarps and 41 from ECMs. Only 12 DNA sequences obtained from ECMs displayed high similarity (100%) to that obtained from sporocarps (Diédhiou et al. 2004b; Rivière et al. 2007). Of the remaining 29 sequences obtained from ECMs, 21 were found to be closely related to thelephoroid taxa (Diédhiou et al. 2004b; Rivière et al. 2007). Thelephoroid fungi seem to invest more in vegetative growth than in sexual reproduction. In contrast, Amanitaceae, one of the most represented families in sampled sporocarps, was almost absent on the roots of the host plants (Table 3). It seems to invest more in sexual reproduction than in the reproduction by vegetative growth. The presence of small

Table 6 African distribution and habitat of some ectomycorrhizal fungi found fruiting under native trees from West Africa (Burkina Faso, Guinea and Senegal) (from Bâ et al. 2011)

Fungal species	Habitat and putative host tree	Country
Amanita annulatovaginata Beeli	Rainforest, nd	Cameroon
Amanita crassiconus Bas	Rainforest, open forest, nd	Nigeria
Amanita rubescens	Rainforest, nd	Cameroon
(Pers. : Fr.) S. F. Gray	Rainforest, *Uapaca bojeri*	Malagasy
Cantharellus congolensis Beeli	Rainforest, *Macrolobium* sp.	DRC, Cameroon
Cantharellus pseudofriesii Heinem.	Rainforest, *Macrolobium* sp.	DRC
Cantharellus rufopunctatus (Beeli) Heinem.	Rainforest, *Gilbertiodendron dewevrei*	DRC
Coltricia cinnamomea (Pers.) Murr.	Deciduous forest, nd	Burundi, Kenya, Sierra Leone, South Africa, Zambia
Gyrodon cupreus Heinem.	Open forest, nd	Ethiopia, Kenya, Malawi, Uganda
Gyroporus microsporus (Sing. & Grinl.) Heinem. & Rammeloo var. *congolensis* Heinem. & Rammeloo	Rainforest, *Macrolobium* sp. Open forest, *Brachystegia* sp.	Burundi, Zambia, DRC, Cameroon
Lactarius annulatoangustifolius Beeli	Rainforest, nd	Cameroon
Lactarius pulchrispermus Beeli	Rainforest, nd	Cameroon
Lactarius gymnocarpus Heim	Rainforest, open forest, nd	Cameroon, DRC, Tanzania, Ivory Coast
Lactarius zenkeri P. Henn.	Rainforest, nd	Cameroon
Porphyrellus niger Heinem. & Goos.	Rainforest, *Macrolobium* sp.	DRC
Russula annulata Heim	Rainforest, open forest, nd	Guinea, DRC, Tanzania
Russula discopus Heim	Rainforest, nd	Cameroon
Russula liberiensis Sing.	Rainforest, nd	Cameroon, Liberia
Russula pseudopurpurea Buyck	Rainforest, nd	Cameroon
Scleroderma dictyosporum Pat	Deciduous forest, open forest, nd	Ghana, DRC
Scleroderma verrucosum Pers	Deciduous forest, open forest, nd	Ghana, Sierra Leone, DRC, Cameroon, CAR, South Africa, Zimbabwe
Strobilomyces costatispora (Beeli) Gilb.	Rainforest, *Macrolobium* sp	DRC
Strobilomyces echinatus Beeli	Rainforest, nd	Cameroon
Strobilomyces luteolus Heinem.	Rainforest, nd	DRC
Tubosaete brunneosetosa (Singer) Horak	Rainforest, open forest, *Paramacrolobium* sp, *Brachystegia* spp., *Marquesia macroura*, *Uapaca guineensis, Gilbertiodendron dewevrei*	Cameroon, Liberia
Xerocomus spinulosus Heinem. & Goos.	Rainforest, nd	DRC
Xerocomus subspinulosus Heinem.	Rainforest, nd	DRC, Tanzania

nd host plant not determined, *DRC* Democratic Republic of Congo, *CAR* Central African Republic (compiled from Heim 1970; Heinemann 1954, 1959, 1966; Heinemann and Rammeloo 1983; Thoen 1971; Pegler 1977, 1983; Ryavarden and Johansen 1980; Thoen and Bâ 1989; Thoen and Ducousso 1989; Buyck et al. 1996; Bâ et al. 2000; Onguene 2000; Ramanankierana et al. 2007)

genets of Amanitaceae as indicative of colonisation via meiospore dispersal supports this hypothesis (Redecker et al. 2001).

By sequencing the rDNA ITS and nuclear large subunit (nLSU), Tedersoo et al. (2007) revealed 30 species of EM fungi on root tips of *Intsia bijuga* and *Vateriopsis seychellarum* from the Seychelles. Diédhiou et al. (2010) also analysed fungal ITS sequences from ECMs and thereby revealed 39 EM fungal taxa in a mixed forest stand of five tree species in Guinea. Recently, Tedersoo et al. (2011) identified, by sequencing of ITS and 28S rDNA from ECMs, 18 phylogenetic lineages including 94, 101, 46 and 111 putative species of EM fungi from Zambia, Gabon, Madagascar and Cameroon, respectively, with some shared species. Hence, the works of Tedersoo et al. (2011) confirmed the previous molecular studies of EM fungi from West Africa (Rivière et al. 2007; Diédhiou et al. 2010) and the Seychelles (Tedersoo et al. 2007), which reported the dominance of species of the /russula–lactarius, /tomentella–thelephora, /boletus and /pisolithus–scleroderma lineages. The remarkable dominance of the /russula–lactarius and /tomentella–thelephora lineages is reminiscent of temperate and other tropical forests (Horton and Bruns 1998; Sirikantaramas et al. 2003; Peay et al. 2010). Other EM fungal taxa such as /sebacina, /sordariales, /marcelleina-peziza gerardii and /elaphomyces lineages, which were absent or rarely encountered during previous surveys of ECMs from African tropical habitats (Rivière et al. 2007; Tedersoo et al. 2007; Diédhiou et al. 2010; Jairus et al. 2011) also displayed remarkable frequencies, whereas *Cenococcum geophilum*, one of the most widespread or dominant EM fungi in Holartic communities (e.g. Richard et al. 2005; Walker et al. 2005; Diédhiou et al. 2009) was absent. Finally, the three studies that investigated belowground EM fungi from six sites in different ecosystems (Guinea, Zambia, Gabon, Cameroon, Madagascar and the Seychelles) using molecular tools, support the hypothesis that some phylogenetic lineages of EM fungi were relatively low in African tropical forests (Tedersoo et al. 2007, 2011; Diédhiou et al. 2010). Furthermore, these studies confirm that ECMs and sporocarps studies are complementary to describe belowground EM community composition and structure. They also point out the importance of molecular analyses for the assessment of EM fungal communities (Gardes and Bruns 1996; Rivière et al. 2007).

Succession of EM fungi on *A. Africana* seedlings

Depending on the presence of host plants, and biotic (e.g. competition between soil fungi, spores predation) and abiotic (e.g. temperature, drought) factors, EM fungi are able to survive in soils in the form of spores, living hyphae in fragmented ECMs and mycelial strands and sclerotia, which are called propagules (Bâ et al. 1991; Jones et al. 2003). The life history strategies of fungal propagules depend partly on the accessibility of active roots of EM plants. The viability of vegetative propagules is about 2 years in the absence of host plants (Hagerman et al. 1999), while the spores have a longer shelf life (up to 5 years in a dry environment). Wind is the main factor of fungal spore dispersal from epigeous fungi, while small mammals are involved in the dissemination of spores from hypogeous fungi (Reddell et al. 1997; Ashkannejhad and Horton 2006). It is well known that spores with a mode of dispersal distance are very active during the colonisation of dune ecosystems by mycotrophic trees (Ashkannejhad and Horton 2006). Ingleby et al. (1998) showed that *Geastrum*, *Scleroderma* and *Suillus* form the major pioneer fungal communities of *Shorea parvifolia* due to their ability to produce abundant spores. Regarding their abundance and life history strategy span, spores are thought to be the most important source of viable propagules during primary succession in natural ecosystems (Jones et al. 2003).

During primary and secondary successions, a succession of different EM fungi occurs as trees age (Dighton and Mason 1985; Jones et al. 2003; Lilleskov and Bruns 2003). Based on the apparent succession of EM fungi on young birch used to reforest agricultural land, some EM fungi were referred to as early-seral fungi, which were thought to be replaced by other fungi named late-seral fungi (Deacon and Fleming 1992). Only early seral fungi appeared in young stand, whereas late-seral fungi were more abundant in older stands. Some fungi categorised as multi-seral fungi occurred in all stand ages. Two hypotheses have been proposed to explain this succession. The first hypothesis suggests that carbohydrate supply influenced by host plant age differentiates the behaviour of early and late-seral fungi (Dighton and Mason 1985; Jones et al. 2003). Late-seral fungi require higher amounts of carbohydrates than early seral fungi. The second hypothesis suggests that EM fungal succession depend on inoculum potential in terms of types and density of propagules in the soil. Early seral fungi particularly able to colonise from spore inocula will tend to colonise first, while late-seral fungi having high inoculum potential in the form of mycelia dominate later (Deacon et al. 1983; Fleming 1983, 1985). Some authors consider that this classification in two categories, early and late-seral, has a number of limitations, i.e. lack of precision in the terminology adopted and insufficient description of fungal species successional patterns (Twieg et al. 2007). In some studies (Bâ et al. 1991; Diédhiou et al. 2004a, b), a remarkable change in behaviour among early seral fungi has been noted in a relatively short time of EM colonisation.

Bâ et al. (1991) found a succession of EM fungi on lateral roots of *A. africana* seedlings grown in cores of soil taken beneath mature trees in a Bayottes forest of southern Senegal. Of the five EM fungi observed by the authors in the natural soil tested over a 6-month period, Thelephoroid fungal sp. XM002 and *S. verrucosum* were present on the roots soon after the germination of the seed and before the first leaf was formed, while two other *Scleroderma* species and one *Inocybe* sp. appeared later. These EM fungi are well known to be early seral fungi (Dighton and Mason 1985). At the end of the experiment, Thelephoroid fungal sp. and *S. dictyosporum* were the dominant EM fungi on roots. Nevertheless, the baiting method has the disadvantage of disrupting the connections between EM hyphae and living roots and consequently between root tips and their supply of photosynthetate (Jones et al. 2003). It tends to underestimate the pre-existing fungal flora under natural conditions particularly late-seral fungi, which require high amounts of carbohydrates from mature trees to colonise roots of seedlings. However, the baiting method is a good procedure that can be used to reveal which EM fungi, in particular early seral fungi, are suitable for artificial inoculation of seedlings in nurseries (Fleming 1985; Bâ et al. 1991).

The mechanisms by which some EM fungi are pioneers and others appear in later successional serals are not well understood (Bâ et al. 1991; Bâ et al. 1994a, b; Diédhiou et al. 2004a, b). Bâ et al. (1991) hypothesised that the initial colonisation of seedlings by Thelephoroid fungal sp. and *S. verrucosum* was linked to the viability of their vegetative propagules as well as their ability to colonise roots quickly (Table 7; Fig. 2). Indeed, vegetative propagules belonging to other fungi were present in the sampled soil cores but were not viable. These latter EM fungi probably employed other viable fungal propagules such as spores. For instance, *S. dictyosporum* was present in the soil in the form of viable spores that required more time for EM colonisation than viable vegetative propagules of Thelephoroid fungal sp. and *S. verrucosum*. Furthermore, the time required for EM colonisation was longer for the mycelium-based inoculum produced from *S. dictyosporum* alone or together at different porportions with Thelephoroid fungal sp. This EM fungus was dominant in time-course, irrespectively of its relative inoculum used. This suggests that the density of propagules did not determine the EM colonisation process (Diédhiou et al. 2004a). Diédhiou et al. (2004a) also found that Thelephoroid fungal sp. had a lower requirement for glucose than *S. dictyosporum*. This may be advantageous to Thelephoroid fungal sp. in colonising *Afzelia* roots more quickly than *S. dictysporum* knowing that the root carbohydrate status of seedlings increases with time. Similarly, Fleming (1985) found that early seral fungi required less glucose for growth in axenic culture than late-seral fungi. These results are in accordance with those reported by Bâ et al. (1994a), which showed that when translocation of reserves from cotyledons to the roots of *A. africana* seedlings was interrupted by partial or complete cotyledon excision, root soluble carbohydrate was drastically reduced, affecting the ability of *S. dictyosporum* to initiate ECMs and not that of Thelephoroid fungal sp.

Potential for the formation of common EM networks

Regeneration and recovery of tropical forests depend on the survival and establishment of seedlings, which in turn, depend on the rate at which they become mycorrhizal (Alexander et al. 1992; Newbery et al. 2000; Onguene and Kuyper 2002). In some circumstances, host tree species and soil properties may play an important role in structuring the EM fungal communities (Richard et al. 2005; Ishida et al. 2007; Tedersoo et al. 2008, 2010b; Morris et al. 2009; Smith et al. 2009). Nevertheless, EM fungal communities were little structured by host plants and soil properties in tropical forests of Continental Africa and Madagascar (Tedersoo et al. 2011). Furthermore, a low level of host preference of African EM fungi was revealed in a West African rainforest where the dominant EM fungal taxa colonised several host species and formed potential common ectomycorrhizal networks (CENs) (Diédhiou et al. 2010).

The existence of CENs implies that fungi have the potential to facilitate growth of regenerating seedling and to distribute resources among the involved tree species (van der Heijden and Horton 2009; Teste et al. 2010). In a monodominant tropical forest, in which the EM legume tree

Table 7 Density of fungal propagules and their ability to grow and colonise the roots of *Afzelia africana* seedlings

Propagules	Mean no. of propagules/g soil (n=20)	Percentage of propagules from which new hyphal growth arose in the presence of roots (n=25)	Time required for EM colonisation (weeks)
Thelephoroid fungal sp.			
Mycorrhizal root fragments	15.6 a	41	1–2
Fragments of mycelial strands	7.3 b	8	1–2
Sclerotia	1.8 c	0	>5
Scleroderma verrucosum			
Spores	nd	nd	4–5
Sclerotia	2.0 c	51	1–2
Scleroderma dictyosporum			
Spores	nd	nd	4–5
Mycorrhizal root fragments	7.9 b	0	>5
Fragments of mycelial strands	6.3 b	0	>5
Scleroderma sp.			
Mycorrhizal root fragments	6.4 b	0	>5
Fragments of mycelial strands	5.3 b	0	>5
Inocybe sp.			
Mycorrhizal root fragments	5.8 b	0	>5
Fragments of mycelial strands	4.9 b	0	>5

In each column, values followed by the same letter are not significantly different ($p \leq 5\%$) (compiled from Bâ et al. 1991, 2011)

nd not determined

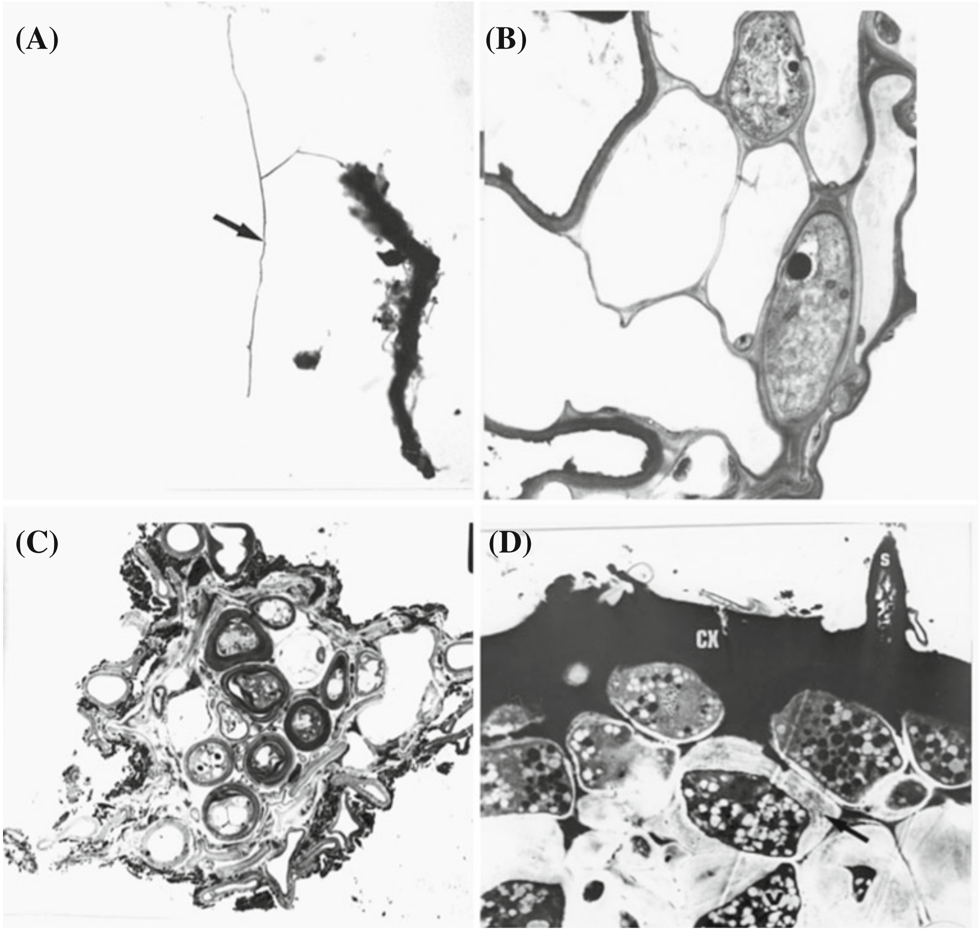

Fig. 2 Viable vegetative propagules of Thelephoroid fungal sp. XM002 from dried soil of the Bayottes forests, Senegal. **a** Hyphae (*arrowhead*) growing from a dark brown ECM, **b** higher magnification of inner mantle showing living hyphae, **c** higher magnification of a transverse section of a fragment of mycelial strand, **d** higher magnification of a partial view of transverse section of sclerotia (from Bâ et al. 1991)

D. corymbosa comprises more than 70% of the canopy, the CENs enhanced seedling survivorship near mature trees and therefore could contribute to the monodominance of this tree within the matrix of high diversity tropical rain forest (McGuire 2007). In the southern part of Korup National Park in Cameroon, Newbery et al. (2000) found that EM inoculum of three EM legume trees, *Microberlinia bisulcata*, *T. bifoliolata* and *Tetraberlinia moreliana*, forming patches was neither a prerequisite nor a guarantee of seedling establishment. Among tree species, only seedlings of *T. moreliana* were more colonised by EM fungi, probably because inoculum density of fungi specifically associated with conspecific mature trees was higher. In two sites of south Cameroon, Onguene and Kuyper (2002) showed that both survival and EM colonisation of seedlings in contact with their mature trees were significantly higher than those of isolated seedlings for four EM legume trees, *A. bipendensis*, *Brachystegia cynometroides*, *Paraberlinia bifoliolata* and *T. bifoliolata*. In these studies, the identity of EM fungi was not determined to clarify the extent to which the various hosts share EM partners. The complementary application of molecular typing and natural abundance of stable isotopes seems necessary to unravel the complexity of EM community structure and to determine whether some carbohydrates were transferred from mature trees to seedlings. In this respect, Diédhiou et al. (2010) analysed the diversity of ECMs on mature trees and understorey seedlings of five legume tree species, *A. fragrans*, *A. macrophylla*, *Cryptosepalum tetraphyllum*, *Paramacrolobium coeruleum* and *Uapaca esculenta*, forming patches in a 1,600 m^2 area of the Ziama rainforest in Guinea. Fungal taxa were identified by sequencing the rDNA ITS region. Among the 39 EM fungal taxa identified, 19 were multi-host found at least on two species of plants, nine were single-host and 11 singletons (Table 8). The multi-host EM taxa were much more abundant (89% and 92% when excluding singletons from the analysis of relative abundance) than the single-host EM taxa, suggesting that although this study has perhaps underestimated the number of multi-host EM taxa, there is a potential for the CEN formation. Moreover, Diédhiou et al. (2010) reported that seedlings tended to be more generalist and adults more specific, and therefore adults likely function as ‘nurse trees’ for conspecific and non-conspecific seedlings. Nevertheless, the hypothesis that C and N can be transferred from mature trees to seedlings through CENs was not confirmed in this study. Indeed, no significant difference for the delta ^{13}C and delta ^{15}N values were recorded between mature trees and

Table 8 Common fungal taxa identified from ECMs collected on mature trees and seedlings from the Ziama forest in Guinea forest

ECM taxa[a]	GenBank accession no.[a]	Best BLASTn full-length ITS match		Host species	Mature trees	Seedlings
		Specimen/accession no	Identity (%)			
Basidiomycota 1[b]	AM113461	Uncultured soil fungus/DQ420877	93	*Am*, *Ct*	+	+
Basidiomycota 2[b]	AM113462	Fungal endophyte/FJ450050	82	*Ue*	+	−
Basidiomycota 3[b]	AM113463	Uncultured Basidiomycota/AY969518	97	*Af*, *Am*, *Ct*, *Pc*, *Ue*	+	+
Boletaceae 1	AM113453	*Boletus bicolour*/GQ166877	80	*Af*, *Am*, *Pc*, *Ue*	+	+
Boletaceae 2	AM113454	*Bothia castanella*/DQ867114	84	*Af*, *Pc*	+	+
Boletaceae 3	AM113455	*Phylloporus rhodoxanthus*/DQ533980	79	*Af*	+	−
Clavulinaceae 1	AM113459	*Clavulina castaneipes*/EU669209	82	*Af*, *Ct*	−	+
Clavulinaceae 2	AM113460	*Clavulinaceae* sp./AJ534708	81	*Af*	−	+
Russulaceae 1	AM113427	*Russula compacta*/EU598172	83	*Am*, *Ct*, *Pc*, *Ue*	+	+
Russulaceae 2	AM113428	Uncultured Russulaceae/DQ777978	84	*Af*, *Pc*	+	−
Russulaceae 3	AM113429	Uncultured Russulaceae/DQ777978	82	*Ct*	+	−
Russulaceae 4	AM113430	*Lactarius pelliculatus*/AY606978	95	*Am*, *Pc*	−	+
Russulaceae 5	AM113431	*Lactarius pelliculatus*/AY606978	95	*Am*, *Ct*, *Pc*	+	+
Russulaceae 6	AM113432	*Lactarius pelliculatus*/AY606978	96	*Ue*	+	−
Russulaceae 7	AM113433	uncultured *Russula*/AY667426	89	*Pc*	+	−
Russulaceae 8	AM113434	*Lactarius pelliculatus*/AY606978	95	*Ct*	+	+
Russulaceae 9	AM113435	*Lactarius pelliculatus*/AY606978	95	*Ue*	+	−
Russulaceae 10	AM113436	*Lactarius pelliculatus*/AY606978	95	*Ue*	+	−
Russulaceae 11	AM113437	*Lactarius pelliculatus*/AY606978	95	*Pc*	+	+
Russulaceae 12	AM113438	*Lactarius pelliculatus*/AY606978	95	*Ue*	+	−
Russulaceae 13	AM113439	*Lactarius pelliculatus*/AY606978	95	*Pc*, *Ue*	+	+
Russulaceae 14	AM113440	*Lactarius pelliculatus*/AY606978	95	*Ue*	−	+
Russulaceae 15	AM113441	Uncultured fungus/FM999659	85	*Af*, *Am*, *Ct*, *Pc*, *Ue*	−	+
Russulaceae 16	AM113442	*Lactarius pelliculatus*/AY606978	96	*Af*, *Am*, *Ct*, *Pc*, *Ue*	+	+
Sclerodermataceae 1	AM113464	*Scleroderma* sp./AB099900	93	*Am*, *Ct*, *Ue*	−	+
Sclerodermataceae 2	AM113465	*Scleroderma* sp./AB099900	94	*Af*, *Am*, *Ct*, *Pc*, *Ue*	+	+
Thelephoraceae 1	AM113443	Uncultured *Tomentella*/EF218826	91	*Af*	+	−
Thelephoraceae 2	AM113444	Uncultured Thelephoraceae/DQ273420	89	*Am*, *Pc*	−	+
Thelephoraceae 3	AM113445	Uncultured ectomycorrhizal fungus/FM993211	92	*Ct*, *Pc*	+	+
Thelephoraceae 4	AM113446	Uncultured *Tomentella*/GQ240908	92	*Ct*	−	+
Thelephoraceae 5	AM113447	Uncultured Thelephoraceae/GQ240903	90	*Ct*	+	−
Thelephoraceae 6	AM113448	Uncultured fungus/GQ205372	88	*Af*, *Am*, *Ct*, *Pc*, *Ue*	+	+
Thelephoraceae 7	AM113449	Uncultured ectomycorrhizal fungus/FM993262	88	*Af*	−	+
Thelephoraceae 8	AM113450	Uncultured fungus/GQ205372	88	*Af*, *Am*	+	−
Thelephoraceae 9	AM113451	Uncultured fungus/FJ820581	89	*Pc*	−	+
Thelephoraceae 10	AM113452	Uncultured fungus/GQ205371	88	*Af*, *Am*, *Ct*, *Pc*, *Ue*	+	+
Tricholomataceae 1	AM113456	Uncultured fungus/FJ820560	97	*Ue*	+	−
Tricholomataceae 2	AM113457	*Tricholoma atroviolaceum*/AY750166	91	*Pc*	−	+
Tricholomataceae 3	AM113458	Uncultured mycorrhizal fungus/AB454382	94	*Am*	+	−

The closest BLAST match represents the most accurate taxonomic match between the ITS sequences of Diédhiou et al. (2010) and those in the NCBI database

+ presence, − absence, *Af Anthonotha fragrans*, *Am Anthonotha macrophylla*, *Ct Cryptosephalum tetraphyllum*, *Pc Paramacrolobium coeruleum*, *Ue Uapaca esculenta*

[a] Diédhiou et al. (2010)

[b] The fungi corresponding to these sequences were considered ectomycorrhizal since Blast analysis revealed a lot of sequences amplified from ectomycorrhizas in GenBank (but an unclear taxonomic position)

their seedlings suggesting that seedlings did not receive detectable C and N via their EM fungi. The existence of CENs and their impact on growth and fitness of seedlings remain to be assessed in the tropical forests of Africa.

Growth response of seedlings to EM inoculation

In temperate regions, EM fungi improve significantly the growth and mineral nutrition of trees (Smith and Read 2008). They also allow the trees to better withstand some root diseases and exploit the water resources. In tropical Africa, using highly efficient EM fungi, controlled ectomycorrhization experiments have pointed out the importance of root symbionts in establishment and growth of exotic tree species such exotic pines and Australian acacias (Bâ et al. 2010). In contrast, there are very little equivalent data on the role of EM fungi for native tree species growth despite their economic importance as timber of high commercial value and fodder in reforestation programs in tropical Africa (Bâ 1990; Moyersoen et al. 1998a; Bâ et al. 1999, 2002; Diédhiou et al. 2005; Ramanankierana et al., 2007).

Garbaye (1991) reviewed the advantages and disadvantages of the use of natural inoculant or pure strain inoculants. Less expensive natural inoculants have the disadvantage of introducing undesirable pathogens. Therefore, despite its higher costs, use of pure cultures of selected EM fungi remains the better practice to optimise the efficiency of fungal inoculum to improve tree growth (Bâ et al. 2010). This was repeatedly illustrated in seedling nurseries in a range of situations (Table 9). However, the performance of fungi involved in EM symbiosis and biology of seeds of native trees are well known in tropical Africa (Bâ and Thoen 1990; Thoen and Ducousso 1989; Sanon et al. 1997, 2009; Diédhiou et al. 2004a, b, 2005; Bechem and Alexander 2009, 2011).

Bâ (1990) compared four EM fungi in sterilised or unsterilised soil with non-limiting P availability and found that Thelephoroid fungal sp. XM002 is more efficient on biomass production and mineral nutrition of *A. africana* than the other EM fungi (Table 9). These results were confirmed by an experiment that compared *A. africana* from two different provenances (Senegal and Burkina Faso) inoculated with four EM fungi under low soil P availability conditions (Bâ et al. 1999). Growth of *A. africana* from

Table 9 Compiled results of controlled ectomycorrhizal fungus inoculation trials of some African trees in seedling nurseries (from Bâ et al. 2011)

Reference	Host plant	Type of soil	Parameter	Fungal inoculant	Effect of inoculation compared to the uninoculated treatment
Bâ (1990)	*Afzelia africana* (provenance of Senegal)	Sterilised sandy soil at 44 ppm available P	Total biomass after 6 months	Thelephoroïd fungal sp. XM002	×1.54
				Scleroderma dictyosporum	×1.35
				Scleroderma verrucosum	×1.03
				Scleroderma sp.	×1.01
Bâ et al. (1999)	*A. africana* (provenance of Burkina Faso)	Unsterilised sandy soil at 2.7 ppm available P	Total biomass after 4 months	Thelephoroïd fungal sp. XM002	×1.48
				Scleroderma dictyosporum	×1.27
				Scleroderma sp1	×1.46
				Scleroderma sp2	×1.25
	A. africana (provenance of Senegal)	Unsterilised sandy soil at 2.7 ppm available P	Total biomass after 4 months	Thelephoroïd fungal sp. XM002	x 1.28
				Scleroderma dictyosporum	×0.99
				Scleroderma sp1	×1.10
				Scleroderma sp2	×1.09
Bâ et al. (2002)	*A. quanzensis* (provenance of Kenya)	Unsterilised sandy soil at 2.7 ppm available P	Total biomass after 4 months	Thelephoroïd fungal sp. XM002	×1.28
				Scleroderma sp1	×0.99
Ramanankierana et al. (2007)	*Uapaca bojeri* (provenance of Madagascar)	Unsterilised sandy soil	Shoot biomass after 5 months	*Scleroderma* sp. Sc1	×0.77
		Sterilised sandy soil	Shoot biomass after 5 months	*Scleroderma* sp. Sc1	×0.70
Bâ et al. (2011)	*Isoberlinia dalziellii* (provenance of Burkina Faso)	Unsterilised sandy soil at 2.7 ppm available P	Total biomass after 4 months	Thelephoroïd fungal sp. XM002	×1.08
				Scleroderma dictyosporum	×1.26

nd not determined

both provenances was more improved by Thelephoroid fungal sp. XM002 than the other EM fungi. However, the provenance of *A. africana* from Burkina Faso responded better to inoculation than the provenance from Senegal irrespective of the EM fungi.

In some circumstances, P content in seeds could be a critical key factor for the initial mycorrhizal colonisation and plant growth (Allsopp and Stock 1992; Zangaro et al. 2000). As an example, 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 arbuscular mycorrhizal habit than large-seeded plants for growth in P-deficient soils. Seeds of caesalpionioid legumes and Phyllanthaceae species also exhibit a considerable range in seed mass (Thoen and Bâ 1989; Green and Newbery 2001; Diédhiou et al. 2005; McGuire 2007). In this respect, Diédhiou et al. (2005) showed that seed mass of different African legume and Phyllanthaceae tree species was negatively related to their EM dependency, so that plants with larger seeds (e.g. *A. macrophylla*) exhibited lower relative mycorrhizal dependency (RMD) values than those with smaller seeds (e.g. *U. somon*) (Fig. 3). Furthermore, *U. bojeri*, which produces small seeds, was highly dependent on AMs and ECMs, and controlled ectomycorrhization of this tree species strongly influenced soil microbial catabolic diversity (Ramanankierana et al. 2007). In contrast, *A. quanzensis*, which produces large seeds, showed little mycorrhiza dependency (Bâ et al. 2002). Besides seed mass, the length of time that cotyledons remain attached is an important factor influencing response of tree species to EM colonisation. Diédhiou et al. (2005) showed that this parameter varied approximately from 5 to 6 weeks for tree species having the highest RMD values (e.g. *U. somon*) and from 9 to 14 weeks for plants with low RMD values (e.g. *A. macrophylla*). This study hypothesises that in the large-seeded species such as *A. macrophylla* and *A. africana*, the benefits of the EM symbioisis may be delayed 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 EM development (Diédhiou et al. 2005). This hypothesis should be tested by determining how much P in Caesalps and Phyllanthaceae seedlings derived from seed reserves and whether the seedlings with the emptying of the cotyledonary reserves become dependent on the capacity of their EM roots to mobilise P from nutrient-deficient soil.

Although the major contribution of EM symbiosis is to improve P uptake by trees in P-deficient soil (Smith and Read 2008), the low soil P level was not a limiting factor

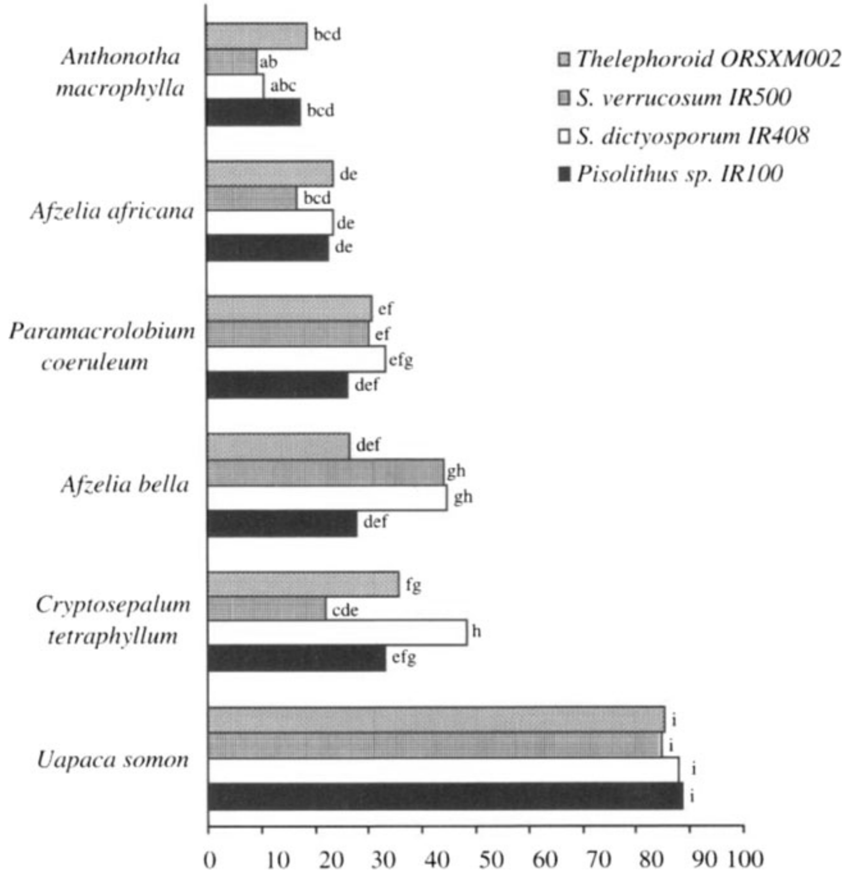

Fig. 3 Relative mycorrhizal dependency (RMD) of five Caesalpinioideae (*Afzelia africana*, *Afzelia bella*, *Anthonotha macrophylla*, *Cryptosepalum tetraphyllum* and *Paramacrolobium coeruleum*) and one Phyllanthaceae (*Uapaca somon*) inoculated with *Scleroderma dictyosporum* IR408, *Scleroderma verrucosum* IR500, *Pisolithus albus* IR100 and Thelephoroid fungal sp. XM002 ($p \leq 5\%$) (from Diédhiou et al. 2005)

for growth and P nutrition of the *U. somon* and Caesalps seedlings in most cases during the 4 month's experiment (Diédhiou et al. 2005). These results support previous data that suggested that soil P deficiency may not limit the growth of some tropical African EM tree species (Bâ 1990; Bâ et al. 1999, 2002; Newbery et al. 2002). Interestingly, the P uptake by *T. moreliana* seedlings was correlated with EM colonisation at both low and high P availability in a greenhouse experiment (Moyersoen et al. 1998a). *T. moreliana* produces litter with high P content. EM associations might be advantageous both in low soil P availability and in soil with high P input from *T. moreliana* litter. However, some studies (Bâ et al. 1999, 2002; Diédhiou et al. 2005) indicated that K uptake seemed to be more related to biomass production of caesalps and *U. somon* than P. It is well known that K plays an important role in water stress tolerance by regulating stomata and vacuolar osmotic potential (Lindhauer 1985; Bandou et al. 2006). Such a physiological effect of EM symbiosis could be of great advantage to the development of African trees during the dry season and deserves further investigation under conditions of soil water stress, which are more relevant to the ecological conditions of low rainfall in Africa.

A research program is underway in Senegal to select EM fungi to improve the growth of *A. africana* in forest nurseries (Bâ et al. 1999, 2002, 2010; Diédhiou et al., 2004a, b, 2005). Forest soils from native stands of *A. africana* are often used in nursery substrates for seedling production by the forest Services in Senegal. This raised the question of how the selected Thelephoroid fungal sp. XM002 competed and improved *Afzelia* growth with the indigenous mycorrhizal populations in three different nursery soils (Diédhiou et al. 2004b). Using morphotyping and molecular analyses, Diédhiou et al. (2004b) detected the early colonisation, persistence and effectiveness of the introduced Thelephoroid fungal sp. XM002. This fungus was not found in any of the three analysed soils and did not induce a consistent change in fungal species composition following inoculum application. This result is not in agreement with some studies indicating that fungi introduced in nurseries can either decrease the native fungal species richness or completely replace some indigenous EM fungi (Villeneuve et al. 1991). Therefore, Thelephoroid fungal sp. XM002 appeared to be an early coloniser, a good competitor and an efficient fungus in promoting seedling growth.

Conclusions and research priorities

From the works reported in this review, it is conclusive that ECMs are an integral part of African tree's physiology. Nevertheless, the EM status of tropical African tree species was examined only in 25% of tree species belonging to known EM genera. Further works are necessary to determine the EM status of African tree that are not examined until now. This may lead to reconsider a widespread view that the EM African trees are scarce both in species number and as phylogenetic groups. Not only the EM status of many trees remains underinvestigated in tropical forests but also the EM fungal diversity which could be as great as temperate forests. An unsuspected richness and diversity of EM fungi and ECMs were found in the vicinity of some EM tree species forming groves in rainforest and open forests. Many unidentified EM fungi remain to be described. As in temperate forests, sporocarps surveys were insufficient to estimate true ECMs diversity. Again, as in temperate forests, the /russula–lactarius and /tomentella–thelephora lineages dominated EM fungal flora. In addition African EM fungi displayed a low level of host preference. Besides the low level of host preference of African EM fungi, the dominance of multi-host fungal taxa suggests a potential for the formation of CENs, which could play an important role not only as a source of inoculum for regenerating seedlings, but also in the transfer of nutrients from mature trees to understorey seedlings. However, the existence of CENs and their impact on growth and fitness of different tree species during their life cycle remain to be rigorously assessed in African tropical forests. To date, no published literature exists on the inoculation trials of African trees in plantations. Further efforts should be done in this direction due to the importance of African trees in the reforestation programmes in agroforestry systems. For establishment of plantations, it is necessary to select fungal isolates for their ablity to improve plant growth, survive competition from other soil microbes and withstand to the local soil constraints. In this respect, Thelephoroid fungal sp. XM002, which is an efficient and competitive EM fungus in nurseries, appears to be a good candidate for the inoculation trials on African EM trees in plantations.

References

Agerer R (1991) Characterization of ectomycorrhizae. In: Norris JR, Read DJ, Varma AK (eds) Methods in microbiology techniques for the study of mycorrhiza. Academic, London, pp 25–73

Alexander IJ (1989) Systematics and ecology of ectomycorrhizal legumes. Monogr Syst Bot Missouri Bot Gard 29:607–624

Alexander IJ (2006) Ectomycorrhizas-out of Africa. New Phytol 172:589–591

Alexander IJ, Högber P (1986) Ectomycorrhizas of tropical angiosperm trees. New Phytol 102:541–549

Alexander IJ, Ahmad N, Lee SS (1992) The role of mycorrhizas in the regeneration of some Malaysian forest trees. Philos Trans R Soc London B 335:379–388

Allen EB, Allen MF (1981) The leguminosae. A source of book of characteristics, uses and nodulation. Macmillan, London

Allsopp N, Stock WD (1992) Mycorrhizas, seed size and seedling establishment in low nutrient environment. In: Read DJ, Fitter DH, Alexander IJ (eds) Mycorrhizas in ecosystems. CAB International, Wallingford, pp 59–64

Ashkannejhad S, Horton TR (2006) Ectomycorrhizal ecology under primary succession on coastal sand dunes: interactions involving *Pinus contorta*, suilloid fungi and deer. New Phytol 169:345–354

Bâ AM (1986) Premiers résultats sur l'infection ectomycorhizienne chez deux essences forestières du Sud du Sénégal: *Afzelia africana* Sm. et *Uapaca guineensis* Mull.Arg. In: les arbres fixateurs d'azote et l'amélioration biologique de la fertilité du sol (Eds. CRDI/NFTA/IFS/ORSTOM), Dakar, 17–25 mars, pp. 243–255.

Bâ AM (1990) Contribution à l'étude de la symbiose ectomycorhizienne chez deux essences forestières d'Afrique intertropicale: *Afzelia africana* et *Uapaca guineensis*. Université Montpellier II, France, Thèse de Doctorat, p 193

Bâ AM, Thoen D (1990) First syntheses of ectomycorrhizas between *Afzelia africana* Sm. (Caesalpinioideae) and native fungi from West Africa. New Phytol 103:441–448

Bâ AM, Sougoufara B, Thoen D (1987) The triple symbiosis of *Casuarina equisetifolia* in Senegal. In: Sylvia DM, Hung LL, Graham JH (eds) Mycorrhizae in the next decade. University of Florida, Gainesville, p 121

Bâ AM, Garbaye J, Dexheimer J (1991) Influence of fungal propagules during the early stade of the time sequence of ectomycorrhizal colonization on *Afzelia africana* Sm. Seedlings. Can J Bot 66:2442–2447

Bâ AM, Garbaye J, Dexheimer J (1994a) The influence of culture conditions on mycorrhiza formation between the ectomycorrhizal fungus *Pisolithus* sp. and *Afzelia africana* seedlings. Mycorrhiza 4:121–129

Bâ AM, Garbaye J, Martin F, Dexheimer J (1994b) Root soluble carbohydrate of *Afzelia africana* Sm. seedlings and modifications of mycorrhizal establishment in response to the cotyledon excision. Mycorrhiza 4:269–275

Bâ AM, Balaji B, Piché Y (1994c) Effect of time of inoculation on *in vitro* ectomycorrhizal colonization and nodule initiation in *Acacia holosericea* seedlings. Mycorrhiza 4:109–119

Bâ AM, Sanon KB, Duponnois R, Dexheimer J (1999) Growth responses of *Afzelia africana* Sm. seedlings to ectomycorrhizal inoculation in nutrient-deficient soil. Mycorrhiza 9:91–95

Bâ AM, Buyck B, Deschères P, Eyssartier G, Ifolno FG, Ducousso M, Wey J, Giraud E, Fontana A, Diallo MAK, Dreyfus B (2000) Diversity and use of ectomycorrhizal fungi in Guinea tropical rain forest. In: Garbaye J, Lugtenberg B, Sörensen J (eds) Selection strategies for plant-beneficial microorganisms. INRA, Nancy, p. 1

Bâ AM, Sanon KB, Duponnois R (2002) Influence of ectomycorrhizal inoculation on *Afzelia quanzensis* Welw. seedlings in a nutrient-deficient soil. For Ecol Manag 161:215–219

Bâ AM, Diédhiou AG, Prin Y, Galiana A, Duponnois R (2010) Management of ectomycorrhizal symbionts associated to useful exotic tree species to improve reforestation performances in tropical Africa. Ann For Sci 67:301–310

Bâ AM, Duponnois R, Diabaté M, Dreyfus B (2011) Les champignons ectomycorhiziens des arbres forestiers en Afrique de l'Ouest. Institute of Research for Development, Montpellier, p. 252

Bandou E, Lebailly F, Muller F, Dulormne M, Toribio A, Chabrol J, Courtecuisse R, Plenchette C, Prin Y, Duponnois R, Thiao M, Sylla S, Dreyfus B, Bâ AM (2006) The ectomycorrhizal fungus *Scleroderma bermudense* alleviates salt stress in seagrape (*Coccoloba uvifera* L.) seedlings. Mycorrhiza 16:559–565

Béreau M, Gazel M, Garbaye J (1997) Les symbioses mycorhiziennes des arbres de la forêt tropicale humide de Guyane française. Can J Bot 75:711–716

Bakarr MI, Janos PJ (1996) Mycorrhizal associations of tropical legume trees in Sierra Leone, West Africa. For Ecol Manag 89:89–92

Bechem EET, Alexander I (2009) Inoculum production and inoculation of *Gnetum africanum* rooted cuttings using a range mycorrhizal fungi. Int J Biol Chem Sci 3:23–32

Bechem EET, Alexander I (2011) Mycorrhiza status of *Gnetum* spp. in Cameroon: evaluating diversity with a view to ameliorating domestication efforts. Mycorrhiza. doi:10.1007/s00572-011-0384-0

Beeli M (1935) Genres *Aminata* et *Volvaria.* Flore Iconographique des Champignons du Congo. Fascicule 1–17:5–45

Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77

Bruneau A, Forest F, Herenden PS, Klitgaard BB, Lewis GP (2001) Phylogenetic relationships in the Caesalpinioideae (Leguminosae) inferred from chloroplast *trnL* intron sequences. Syst Bot 26:487–514

Bruns TD, Szaro TM, Gardes M, Cullings KW, Pan JJ, Taylor DL, Horton TR, Kretzer A, Garbelotto M, Li Y (1998) A sequence database for the identification of ectomycorrhizal basidiomycetes by phylogenetic analysis. Mol Ecol 7:257–272

Buyck B (1993) Russula I (Russulaceae). Flore illustrée des Champignons d'Afrique Centrale 15:335–408

Buyck B, Thoen D, Walting R (1996) Ectomycorrhizal fungi of the Guinea–Congo region. Proc Royal Soc Edinburgh 104:313–333

Chalermpongse A (1987) Mycorrhizal survey of dry deciduous and semi-evergreen dipterocarp forest ecosystems in Thailand. In: Kostermans ACJH (ed) Proceedings of the Third Round Table Conference on Dipterocarps. East Kalimantan, Mulawarman University, pp 81–103

Corby HDL (1974) Systematic implications of nodulation among Rhodesian Legumes. Kirkia 9:301–329

Corner EJH, Heinemann P (1967) Clavaires et *Thelephora*. Flore Iconographique des Champignons du Congo, 309–322, pl. 50–51

de Alwis DP, Abeynayake K (1980) A survey of mycorrhizae in some forest trees of Sri Lanka. In: Mikola P (ed) Tropical mycorrhiza research. Clarendon, Oxford, pp 146–153

de Faria SM, Lewis GP, Sprent JI, Sutherland JM (1989) Occurrence of nodulation in the leguminosae. New Phytol 111:607–619

de Faria SM, Diédhiou AG, de Lima HC, Ribeiro RD, Galiana A, Casthilo AF, Henriques JC (2010) Evaluating the nodulation status of leguminous species from the Amazonian forest of Brazil. J Exp Bot 61:3119–3127

Deacon JW, Fleming LV (1992) Interactions of ectomycorrhizal fungi. In: Allen MF (ed) Mycorrhizal functioning: an integrative plant–fungal process. Chapman & Hall, New York, pp 249–300

Deacon JW, Donaldson SJ, Last FT (1983) Sequences and interactions of mycorrhizal fungi on birch. Plant Soil 71:257–262

Diédhiou AG, Verpillot F, Guèye O, Dreyfus B, Duponnois R, Bâ AM (2004a) Do concentrations of glucose and fungal inoculum influence the competitiveness of two early-stage ectomycorrhizal fungi in *Afzelia africana* seedlings? For Ecol Manag 203:187–194

Diédhiou AG, Bâ AM, Sylla S, Dreyfus B, Neyra M, Ndoye I (2004b) The early-stage ectomycorrhizal Thelephoroid fungal sp. is competitive and effective on *Afzelia africana* Sm. in nursery conditions in Senegal. Mycorrhiza 14:313–322

Diédhiou AG, Guèye O, Diabaté M, Prin Y, Duponnois R, Dreyfus B, Bâ AM (2005) Contrasting responses to ectomycorrhizal inoculation in seedlings of six tropical African tree species. Mycorrhiza 16:11–17

Diédhiou AG, Dupouey J-L, Buée M, Dambrine E, Laüt L, Garbaye J (2009) Response of ectomycorrhizal communities to past Roman occupation in an oak forest. Soil Biol Bioch 41:2206–2213

Diédhiou AG, Selosse M-A, Galiana A, Diabaté M, Dreyfus B, Bâ AM, de Faria SM, Béna G (2010) Multi-host ectomycorrhizal fungi are predominant in a Guinean tropical rainforest and shared between canopy trees and seedlings. Env Microb 2:2219–2232

Dighton J, Mason PA (1985) Mycorrhizal dynamics during forest tree development. In: Moore D, Casselton LA, Wood DA, Frankland JC (eds) Developmental biology of higher fungi. Cambridge University Press, London, pp 117–139

Dissing H, Lange M (1963) Gasteromycetales I. Flore Iconographique des Champignons du Congo, pp 215–232

Dissing H, Lange M (1964) Gasteromycetales II. Flore Iconographique des Champignons du Congo, pp 233–252

Ducousso M, Béna G, Bourgeois C, Buyck B, Eyssartier G, Vincelette M, Rabevohitra R, Randrihasipara L, Dreyfus B, Prin Y (2004) The last common ancestor of Sarcolaenaceae and Asian dipterocarp trees was ectomycorrhizal before the India–Madagascar separation, about 88 million years. Mol Ecol 13:231–236

Ducousso M, Ramanankierana H, Duponnois R, Rabévohitra R, Randrihasipara L, Vincelette M, Dreyfus B, Prin Y (2008) Mycorrhizal status of native trees and shrubs from eastern Madagascar littoral forests with special emphasis on one new ectomycorrhizal endemic family, the *Asteropeiaceae*. New Phytol 178:233–238

Fassi B (1957) Ectomycorhize chez le *Gnetum africanum* Welw. due à *Scleroderma* sp. Bull Soc Mycol France 73:280–285

Fassi B (1960) The distribution of ectotrophic mycorrhizae in the litter and upper soil layer of *Gilbertiodendron dewevrei* (Caesalpiniaceae) forest in the Congo. In: Mykorrhizae, Internationales Mykorrhizas symposium (Ed. DEU), pp 297–302

Fassi B, Fontana A (1961) Le micorrize ectotrofiche di *Julbernadia seretii*, Caesalpiniaceae del Congo. Allionia 7:131–157

Fassi B, Fontana A (1962) Micorrize ectotrofiche di *Brachystegia laurentii* e di alcune altre di Caesalpiniaceae minori del Congo. Allionia 8:121–131

Fleming LV (1983) Succession of mycorrhizal fungi on birch: infection of seedlings planted around mature trees. Plant Soil 71:263–267

Fleming LV (1985) Experimental study of sequences of ectomycorrhizal fungi on birch (*Betula* sp.) seedling root systems. Soil Biol Biochem 17:591–600

Garbaye J (1991) Utilisation des mycorhizes en sylviculture. In: Lavoisier (ed) Les mycorhizes des arbres et plantes cultivées Technique et documentation. Lavoisier, Paris, pp 197–250

Garbaye J, Menez J, Wilhelm ME (1986) Les mycorhizes des jeunes chênes dans les pépinières et les régénérations naturelles du Nord-Est de la France. Acta Oecol 7:87–96

Gardes M, Bruns TD (1996) ITS-RFLP matching for identification of fungi. In: Clapp JP (ed) Methods in molecular biology. Species diagnostics protocols: PCR and other nucleic acid methods, vol 50. Humana Press, Totowa, pp. 177–186

Green JJ, Newbery DM (2001) Light and seed size affect establishment of grove-forming ectomycorrhizal rain forest tree species. New Phytol 151:271–289

Hagerman SM, Jones MD, Bradfield GE, Sakakibara S (1999) Ectomycorrhizal colonization of *Picea engelmannii* x *Picea glauca* seedlings planted across cut blocks of different sizes. Can J For Res 29:1856–1870

Haug I, Weiß M, Homeier J, Oberwinkler F, Kottke I (2004) Russulaceae and Thelephoraceae form ectomycorrhizas with members of the Nyctaginaceae (Caryophyllales) in the tropical mountain rain forest of southern Ecuador. New Phytol 165:923–936

He XH, Critchley C, Ng H, Bledsoe C (2004) Reciprocal N (NH_4^+)-N^{15} or (NO_3^-)-N^{15} transfer between non $N_{(2)}$-fixing *Eucalyptus maculata* and N_{-2}-fixing *Casuarina cunninghamiana* linked by the ectomycorrhizal fungus *Pisolithus* sp. New Phytol 163:629–640

Heim R (1955) Les Lactaires d'Afrique Intertropicale (Congo Belge et Afrique Noire Francaise). Bull Jard Bot Etat Bruxelles 25:1–91

Heim R (1970) Particularités remarquables des Russules tropicales pelliculariae lilliputiennes: Les complexes *annulata* et *radicans*. Bull Soc Mycol France 86:59–77

Heinemann P (1954) Boletineae. Flore iconographique des champignons du Congo. Fasc., 3, pp. 50–80, pl. 9–12

Heinemann P (1959) Cantharellineae. Flore iconographique des champignons du Congo. Fasc. 8, pp. 153–165, pl. 26–28

Heinemann P (1966) Hygrophoraceae, *Laccaria* et Boletineae II (compléments). Flore iconographique des champignons du Congo. Fasc. 15, pp. 279–308. pl. 47–49

Heinemann P, Rammeloo J (1983) Gyrodontaceae p.p. (Bolitineae). Flore illustrée des champignons de l'Afrique Centrale Fasc. 10, 183–198, pl. 32–35

Henkel TW, Terborght J, Vilgalys R (2002) Ectomycorrhizal fungi and their leguminous hosts in the Pakaraima Mountains of Guyana. Mycol Res 106:515–531

Hennings P (1895) Fungi austro-africani. Hedwigia 34:325–327

Herendeen PS, Bruneau A, Lewis GP (2003) Phylogenetic relationships in Caesalpinioid legumes:a premliminary analysis based on moprhological and molecular data. In: Klitgaard BB, Bruneau A (eds) Advances in legume systematic. Part 10: higher level systematics. Royal Boatnic Gardens, Kew, pp 37–62

Högberg P (1982) Mycorrhizal associations in some woodland and forest trees and shrubs in Tanzania. New Phytol 92:407–415

Högberg P, Nylund JE (1981) Ectomycorrhizae in coastal miombo woodland of Tanzania. Plant Soil 63:283–289

Högberg P, Piearce GD (1986) Mycorrhizas in Zambain trees in relation to host taxonomy, vegetation type and successional patterns. J Ecol 74:775–785

Horton TR, Bruns TD (1998) Multiple-host fungi are the most frequent and abundant ectomycorrhizal types in a mixed stand of Douglas fir (*Pseudotsuga menziesii*) and bishop pine (*Pinus muricata*). New Phytol 139:331–339

Horton TR, Bruns TD (2001) The molecular revolution in ectomycorrhizal ecology: peeking into the black box. Mol Ecol 10:1855–1871

Horton TR, Bruns TD, Parker VT (1999) Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. Can J Bot 77:93–102

Ingleby K, Munro RC, Noor M, Mason PA, Clearwater MJ (1998) Ectomycorrhizal populations and growth of *Shorea parvifolia* (Dipterocarpaceae) seedlings regenerating under three different forest canopies following logging. For Ecol Manag 111:171–179

Ishida TA, Nara K, Hogetsu T (2007) Host effects on ectomycorrhizal fungal communities: insight from eight host species in mixed conifer-broadleaf forests. New Phytol 174:430–440

Jairus T, Mpumba R, Chinoya S, Tedersoo L (2011) Invasion potential and host shifts of Australian and African ectomycorrhizal fungi in mixed eucalypt plantations. New Phytol 192:179–187. doi:10.1111/j.1469-8137.2011.03775.x

Jenik J, Mensah KOA (1967) Root system of tropical trees. I. Ectotrophic mycorrhizae of Afzelia africana Sm. Preslia 39:59–65

Jones MD, Durall DM, Cairney JWG (2003) Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. New Phytol 157:399–422

Le Tacon F, Garbaye J, Bâ AM, Beddiar AF, Diagne O, Diem HG (1989) Importance des symbioses racinaires pour les arbres forestiers en zone tropicale sèche et en zone tropicale humide. In: Trees for development in Sub-Saharian Africa, ICRAF HQ, Nairobi, Kenya, pp 302–318

Lilleskov EA, Bruns TD (2003) Root colonization dynamics of two ectomycorrhizal fungi of contrasting life history strategies are mediated by addition of organic nutrient patches. New Phytol 159:141–151

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM (2002) Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83:104–115

Lindhauer MG (1985) Influence of K nutrition and drought on water relation and growth of sunflower (*Helianthus annuus* L.), *Zeitung Pflanzenernähr*. Bodenk 148:654–669

Martin F, Delaruelle C, Ivory M (1998) Genetic variability in intergenic spacers of ribosomal DNA in *Pisolithus* isolates associated with pine, eucalyptus and *Afzelia* in lowland Kenyan forests. New Phytol 139:341–352

McGuire KL (2007) Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88:567–574

Molina R, Massicotte H, Trappe JM (1992) Specificity phenomena in mycorrhizal symbioses: community-ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning: an integrative plant-fungal process. Chapman and Hall, New York, pp 357–423

Morris MH, Perez-Perez MA, Smith ME, Bledsoe CS (2009) Influence of host species on ectomycorrhizal communities associated with two co-occurring oaks (*Quercus* spp) in a tropical cloud forest. FEMS Microbiol Ecol 69:274–287

Moyersoen B (1996a) Tetraberliniaerhiza bicolor on *Tetraberlinia bifoliolata* (Harms) Hauman. Descr Ectomyc 1:137–141

Moyersoen B (1996b) Tetraberliniaerhiza cerviformis on *Tetraberlinia bifoliolata* (Harms) Hauman. Descr Ectomyc 1:143–147

Moyersoen B (1996c) Tetraberliniaerhiza heterocystidiae on *Tetraberlinia bifoliolata* (Harms) Hauman. Descr Ectomyc 1:149–153

Moyersoen B (2006) *Pakaraimaea dipterocarpacea* is ectomycorrhizal, indicating an ancient Gondwanaland origin for the ectomycorrhizal habit in Dipterocarpaceae. New Phytol 172:753–762

Moyersoen B, Fitter AH (1999) Presence of arbuscular mycorrhizas in typically ectomycorrhizal host species from Cameroon and New Zealand. Mycorrhiza 8:247–253

Moyersoen B, Alexander IJ, Fitter AH (1998a) P nutrition of ectomycorrhizal and arbuscular mycorrhizal tree seedlings from Korup National Park rainforest, Cameroon. J Trop Ecol 14:47–61

Moyersoen B, Fitter AH, Alexander IJ (1998b) Spatial distribution of ectomycorrhizas and arbuscular mycorrhizas in Korup National Park rainforest, Cameroon. New Phytol 139:311–320

Moyersoen B, Becker P, Alexander IJ (2001) Are ectomycorrhizas more abundant than arbuscular mycorrhizas in tropical heath forests? New Phytol 150:591–599

Munyanziza E, Kuyper TW (1995) Ectomycorrhizal synthesis on seedlings of *Afzelia quanzensis* Welw. using various types of inoculum. Mycorrhiza 5:283–287

Nataranjan K, Senthilarasu G, Kumaresan V, Rivière T (2005) Diversity in ectomycorrhizal fungi of a dipterocarp forest in Western Ghats. Curr Sci 88:1893–1895

Newbery DM, Alexander IJ, Thomas DW, Gartlan JS (1988) Ectomycorrhizal rain-forest legumes and soil phosphorus in Korup National Park, Cameroon. New Phytol 109:433–455

Newbery DM, Alexander IJ, Rother JA (2000) Does proximity to conspecific adults influence the establishment of ectomycorrhizal tree species inanAfrican rain forest? New Phytol 147:401–409

Newbery DM, Chuyong GB, Green JJ, Songwe NC, Tchuenteu F, Zimmermann L (2002) Does low phosphorus supply limit seedling establishment and tree growth in groves of ectomycorrhizal trees in a central African rainforest? New Phytol 156:297–311

Onguene NA (2000) Diversity and dynamics of Mycorrhizal associations in tropical rain forests with different disturbance regimes in South Cameroon. Tropenbos Cameroon Series 3. P 167

Onguene NA, Kuyper TW (2001) Mycorrhizal associations in the rain forest of South Cameroon. For Ecol Manag 140:277–287

Onguene NA, Kuyper TW (2002) Importance of the ectomycorrhizal network for seedling survival and ectomycorrhiza formation in rain forests of south Cameroon. Mycorrhiza 12:13–17

Pegler DN (1977) A preliminary Agaric Flora of East Africa. Kew Bulletin Additiona Series VI: 1–615, fig. 1–129. HMSO, London

Pegler DN (1983) Agaric Flora of the Lesser Antilles. Kew Bulletin Additiona Series IX, 1–668, pl. 1–27, figs. 1–129. HMSO, London

Peay KG, Kennedy PG, Davies SJ, Tan S, Bruns TD (2010) Potential link between plant and fungal distribuions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. New Phytol 185:529–542

Peyronel B, Fassi B (1957) Micorrize ectotrofiche in una caesalpiniacea del Congo Belga. Atti Accademia delle Scienze di Torino 91:569–576

Peyronel B, Fassi B (1960) Nuovi casi de simbiosi ectomicorrizica in Leguminose della famiglia delle Caesalpiniacea. Atti Accademia delle Scienze di Torino 94:36–38

Pirozynski KA, Malloch DW (1975) The origin of land plants: a matter of mycotrophism. Biosystems 6:153–164

Ramanankierana N, Ducousso M, Rakotoarimanga N, Prin Y, Thioulouse J, Randrianjohany E, Ramaroson L, Kisa M, Galiana A, Duponnois R (2007) Arbuscular mycorrhizas and ectomycorrhizas of *Uapaca bojeri* L. (Euphorbiaceae): sporophore diversity, patterns of root colonization and effects on seedling growth and soil microbial catabolic diversity. Mycorrhiza 17:195–208

Rambelli A (1973) The rhizosphere of Mycorrhizae. In: Marks GC, Kozlowski TT (eds) Ectomycorrhizae: their ecology and physiology. Academic, New York, pp 299–349

Read DJ, Perez-Moreno J (2004) Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? New Phytol 157:475–492

Reddell P, Foster RC, Bowen GD (1986) The effects of sodium chloride on growth and nitrogen fixation in *Casuarina obese* Miq. New Phytol 102:397–408

Reddell P, Spain AV, Hopkins M (1997) Dispersal of spores of mycorrhizal fungi in scats of native mammals in tropical forests of northeastern Australia. Biotropica 29:184–192

Redecker D, Szaro TM, Bowman RJ, Bruns TD (2001) Small genets of *Lactarius xanthogalactus*, *Russula cremoricolor* and *Amanita francheti* in late-stage ectomycorrhizal successions. Mol Ecol 10:1025–1034

Redhead JF (1968a) Mycorrhizal associations in some Nigerian forest trees. Trans Brit Mycol Soc 51:377–387

Redhead JF (1968b) *Inocybe* sp. associated with ectotrophic mycorrhiza on *Afzelia bella* in Nigeria. Commonwealth For Rev 47:63–65

Redhead JF (1974) Aspects of the biology of mycorrhizal associations occurring on tree species in Nigeria. PhD thesis. University of Ibadan, Nigeria

Redhead JF (1979) Soil mycorrhiza in relation to soil fertility and productivity. In: Mongi HM, Huxley PA (ed.), Soils Research in Agroforestry. Tech., David Spurgeon, ICRAF, pp. 175–204

Richard F, Millot S, Gardes M, Selosse M-A (2005) Diversity and specificity of ectomycorrhizal fungi retrieved from an old-growth

Mediterranean forest dominated by *Quercus ilex*. New Phytol 166:1011–1023

Rivière T, Diédhiou AG, Diabate M, Senthilarasu G, Natarajan K, Verbeken A, Buyck B, Dreyfus B, Bena G, Bâ AM (2007) Genetic diversity of ectomycorrhizal basidiomycetes from African and Indian tropical forests. Mycorrhiza 17:415–428

Ryavarden L, Johansen J (1980) A preliminary polypore flora of East Africa. Fungiflora, Oslo

Sanon KB, Bâ AM, Dexheimer J (1997) Mycorrhizal status of some fungi fruiting beneath indigenous trees in Burkina Faso. For Ecol Manag 98:61–69

Sanon KB, Bâ AM, Delaruelle C, Duponnois R, Martin F (2009) Morphological and molecular analyses in *Scleroderma* species associated with some Caesalpiniaceae, Dipterocarpaceae and Phyllanthaceae trees in southern Burkina Faso. Mycorrhiza 19:571–584

Sims KP, Sen R, Watling R, Jeffries P (1999) Species and population structures of *Pisolithus and Scleroderma* identified by combined phenotypic and genomic marker analysis. Mycol Res 103:449–458

Sirikantaramas S, Sugioka N, Lee SS, Mohamed LA, Lee HS, Szmidt AE, Yamazaki T (2003) Molecular identification of ectomycorrhizal fungi associated with Dipterocarpaceae. Tropics 13:69–77

Smith S, Read J (2008) Mycorrhizal Symbiosis (Ed. Hardcover), p 800

Smith ME, Douhan GW, Fremier AK, Rizzo DM (2009) Are true multihost fungi the exception or the rule? Dominant ectomycorrhizal fungi on Pinus sabiniana differ from those on co-occurring *Quercus* species. New Phytol 182:295–299

Schüßler A, Schwarzott D, Walker C (2001) A new fungal phylum, the *Glomeromycota*: phylogeny and evolution. Myco Res 105:1413–1421

Tedersoo L, Nara K (2010) General latitudinal gradient of biodiversity is reversed in ectomycorrhizal fungi. New Phytol 185:351–354

Tedersoo L, Suvi T, Beaver K, Kõljalg U (2007) Ectomycorrhizal fungi of the Seychelles: diversity patterns and hosts shifts from the native *Vateriopsis seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpinioideae) to the introduced *Eucalyptus robusta* (Myrtaceae), but not *Pinus caribea* (Pinaceae). New Phytol 175:321–333

Tedersoo L, Jairus T, Horton BM, Abarenkov K, Suvi T, Saar I, Kõljalg U (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxonspecific primers. New Phytol 180:479–490

Tedersoo L, May TW, Smith ME (2010a) Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20:217–263

Tedersoo L, Sadam A, Zambrano M, Valencia R, Bahram M (2010b) Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. ISME J 4:465–471

Tedersoo L, Bahram M, Jairus T, Bechem E, Chinoya S, Mpumba R, Ml L, Randrianjohany E, Razafimandimbison S, Sadam A, Naadel T, Kõljalg U (2011) Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests of Continental Africa and Madagascar. Mol Ecol 20:3071–3080

Teste FP, Simard SW, Durall DM, Guy RD, Berch SM (2010) Net carbon transfer between *Pseudotsuga menziesii* var. *glauca* seedlings in the field is influenced by soil disturbance. J Ecol 98:429–439

Thiès E (1995) Principaux Ligneux Forestiers de la Guinée (Eds. Deutsche Gesellschaft fr Technische Zusammenarbeit), n. 253.

Thoen D (1971) Etude mycosociologique de quelques forêts des districts picardo-brabançons, mosan et ardennais de Belgique. Bull Rech Agro Gembloux 5:309–326

Thoen D (1993) Looking for ectomycorrhizal trees and ectomycorrhizal fungi in tropical Africa. In: Aspects of tropical mycology (Ed. Cambridge University Press), Cambridge University Press, pp 193–205

Thoen D, Bâ AM (1987) Observations on the fungi and the ectomycorrhizae of *Afzelia africana* and *Uapaca guineensis* in southern Senegal. In: Sylvia DM, Hung LL, Graham JH (eds) Mycorrhizae in the next decade, NACOM 7, IFAS, University of Florida, Gainesville, FL, 3–8 May 1987, p 132

Thoen D, Bâ AM (1989) Ectomycorrhizas and putative ectomycorrhizal fungi of *Afzelia africana* Sm. and *Uapaca guineensis* Müll. Arg. in southern Senegal. New Phytol 113:549–559

Thoen D, Ducousso M (1989) Champignons et ectomycorhizes du Fouta Djalon. Bois For Trop 221:45–63

Torti SD, Coley PD (1999) Tropical monodominance: a preliminary test of the ectomycorrhizal hypothesis. Biotropica 31:220–228

Torti SD, Coley PD, Kursar TA (2001) Causes and consequences of monodominance in tropical lowland forests. Am Nat 157:141–153

Trappe JM (1962) Fungus associates of ectotrophic mycorrhiza. Bot Rev 28:538–606

Twieg BD, Durall DM, Simard SW (2007) Ectomycorrhizal fungal succession in mixed temperate forests. New Phytol 176:437–447

van der Heijden MGA, Horton TR (2009) Socialism in soil ? The importance of mycorrhizal fungal network for facilitation in natural ecosystems. J Ecol 97:1139–1150

Villeneuve N, Le Tacon F, Bouchard D (1991) Survival of introduced *Laccaria bicolor* in competition with native ectomycorrhizal fungi and effects on the growth of outplanted Douglas-fir seedlings. Plant Soil 135:95–107

Walker JF, Miller JRO, Horton JL (2005) Hyperdiversity of ectomycorrhizal fungus assemblages on oak seedlings in mixed forests in the southern Appalachian Mountains. Mol Ecol 14:829–838

Wang B, Qiu Y-L (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363

Warcup JH (1980) The mycorrhizal relationships of australian orchids. New Phytol 87:371–381

Watling R (1993) Comparison of the macromycete biotas in selected tropical areas of Africa and Australia. In: Isaac S, Frankland JC, Watling R, Whalley AJS (eds) Aspects of tropical mycology. Cambridge University, Cambridge, pp 171–191

Watling R, Lee SS (1995) Ectomycorrhizal fungi associated with Members of the Dipterocarpaceae in peninsular Malaysia I. J Trop For Sci 7:657–669

Wurzburger N, Bidartondo MI, Bledsoe CS (2001) Characterization of *Pinus* ectomycorrhizas from mixed conifer and pygmy forests using morphotyping and molecular methods. Can J Bot 79:1211–1216

Yokota A, Neda H, Erdy S (1996) Ectomycorrhizal fungi in an Indonesian *Dipterocarpus* forest in Laut Island, South Kalimantan province. Abstracts of the 48th Annual Meeting of the Kanto Branch of the Japanese Forestry Society, vol. 48, p 35

Yorou SN, Agerer R (2007) *Tomentella furcata*, a new species from Benin (West Africa) with basidia forming internal hyphae. Mycol Prog 6:239–247

Yorou SN, Agerer R (2008) *Tomentella africana*, a new species from Benin (West Africa) identified by morphological and molecular data. Mycologia 100:68–80

Yorou SN, Köljalg U, Sinsin B, Agerer R (2007) Studies in African thelephoroid fungi 1. *Tomentella capitata* and *Tomentella brunneocystidia*, two news species from Benin (West Africa) with capitate cystidia. Mycol Prog 6:7–18

Yorou NS, Diabaté M, Agerer R (2011a) Phylogenetic placement and anatomical characterisation of two new West African Tomentella (Basidiomycota, Fungi) species. Mycol Prog. doi:10.1007/s11557-011-0739-0

Yorou NS, Gardt S, Diabaté M, Guissou M-L, Agerer R (2011b) Three new Tomentella species from West Africa identified by anatomical and molecular data. Mycol Prog. doi:10.1007/s11557-011-0760-3

Yorou NS, Guelly AK, Agerer R (2011c) Anatomical and ITS rDNA-based phylogenetic identification of two new West African resupinate thelephoroid species. Mycoscience. doi:10.1007/s10267-011-0117-4

Zak B (1969) Characterisation and classification of ectomycorrhizae of Douglas fir. I. *Pseudotsuga menziesii* + *Poria terrestry* (blue and orange staning strains). Can J Bot 47:1833–1840

Zangaro W, Bononi VLR, Truffen SB (2000) Mycorrhizal dependency, inoculum potentiel and habitat preference of native woody species in South Brazil. J Trop Ecol 16:603–622