Diversity of Endemic Ectomycorrhizae of Humid Forests of South Cameroon

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Abstract: The ecologically important below-ground ectomycorrhizal (ECM) biodiversity of tropical humid forests remain poorly known. Most ECM inventories have been based upon description and identification of fruitbodies with few work on ECM root tips of tropical tree species. Morpho-anatomical descriptions of root tips of 24 ECM Fabaceae/Detarioideae, *Uapaca* tree species, and *Gnetum* lianas were conducted in humid forest of South Cameroon. ECM forest clumps were the only resort sites for the more than 30 endemic ECM morphotypes, with apparently no host specificity. Distinguished by four colors – white, yellow, brown, and dark brown – and five textures – smooth, cottony, woolly, spiny and verrucose –, they differed from to the golden yellow coralloïdal *Gnetum* liana ECM with plectenchymatous mantle. Tree ECM were of monopodial-pinnate or -pyramidal types with external felt prosenchyma mantles shielded with abundant rhizomorphs, emanating hyphae and variously shaped cystida with clamp connections. These ECM fungal attributes may confer ECM associations with strong competitive abilities to strive at best on prevailing nutrient-poor acid soils and harsh conditions, thus better explaining tropical monodominance. Yet, much research is still needed to determine the role of below-ground ECM biodiversity on structure and functioning of tropical humid forests of the Congo basin.

Keywords: "Ekop", Cystidia, *Gnetum,* Emanating hyphae, rhizomorphs, Woronin bodies.

1. INTRODUCTION

The luxuriance of tropical humid forests appears to be maintained by biological components, which include processes such as transformation and decomposition of organic matter, biogeochemical cycles, water purification and nutrient cycling, greenhouse gas exchanges and carbon sequestration by consortia of soil micro- and macro-organisms, forming soil biodiversity (Suz *et al*., 2008). Particular soil chemical engineers provide mineral facilitation and control of environmental stresses, diseases and pests, for most terrestrial plants through perennial symbiotic relations, called "mycorrhizae" (Smith and Read, 2008). The kinds and amounts of such symbiotic associations however, are little accounted for in the management of humid forests in the Congo basin, the second largest tropical forest stretch in the world.

In the rain forests of tropical Africa, two types of mycorrhizal associations prevail, viz. arbuscular mycorrhiza (AM) and ectomycorrhiza (ECM) (Alexander, 1989; Onguene and Kuyper, 2001; Bâ *et al*, 2011). In the Congo basin, ECM associations occur as a forest continuum from the Cameroonian Atlantic Ocean coast to the "forêt Claire" in the Democratic Republic of Congo, through the Congo, southern parts of the Central African Republic and most of the Gabon (De Saint Aubin, 1963; Hart, 1990; Buyck, 1994; De Kesel *et al*., 2017; Onguene, 2021, in publication). These forest patches could be the hotspots for soil fungal biodiversity in the Congo basin. Nonetheless, few data and little information exist on their occurrence, regeneration requirements of ECM tree species and factors that effectively explain the present functioning of rain forests of the Congo Basin, under threats such as shifting cultivation, selective logging, climate change and mining.

Latest inventories on ectomycorrhizal fungi diversity using morpho-anatomical and molecular typing were based on observations, descriptions and identification of fruiting bodies (Waseem *et al*., 2017; Clasen *et al*., 2018; Vasco-Palacios *et al*., 2018). The drawback here is that of ECM fruitbodies' production is highly seasonal and patchy; some fungi may not fruit for years, and others are cryptic. In addition, the absence of fruitbodies does not imply that ectomycorrhizae are absent from the soil. Examination of root-tips therefore provides an alternative way to permanently determine ECM diversity of a particular plant community or ecological site. Thus, ECM morphotyping appears important because it provides ECM morphological and anatomical characteristics, producing useful

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information on functional roles of ECM fungi in the community with regards to nutrients and water absorption (Eberhardt *et al*., 2000; Anderson, 2006; Suz *et al*., 2008;). ECM morpho-anatomical characteristics have been previously grouped into four entities with respect to their value for classification (Agerer 1991). Most informative characters are the mantle structure, the organization of rhizomorphs and the attributes of emanating hyphae and cystidia. Sections of ECM are therefore very important in morphotyping. The ramification is influenced more by tree genus while the appearance and the color are caused by the fungus (Clasen *et al*., 2018). Ectomycorrhizae have been differentiated based on size and color of mycorrhizal system, external mantle surface texture, extra-radical mycelium, internal mantle, shape and size of rhizomorphs and emanating hyphae, presence or absence and shape of cystidia, cell shape of Hartig net, as well as the differing color reaction in Melzer's reagent (Agerer, 1991).

From observations of ectomycorrhizal fruitbodies, it was hypothesized that six major native ectomycorrhizae of *Aminata, Boletes, Cantharellus, Lactarius, Russula* and *Scleroderma* will be encountered in roots of ECM tree species. *Amanita* ECM have been shown to be monopodial-pinnate and tuberculate with undifferentiated rhizomorphs (Dell *et al*., 1990; Smith *et al*., 2009). For Boletales ectomycorrhizae, plectenchymatous and tuberculate mantles are known with very diverse rhizomorphs (Smith and Pfister, 2009). *Lactarius* ECM show smooth plectenchymatous mantles with laticifiers but lack cystidia (Mühlmann and Göbl, 2006; Eberhardt *et al*., 2000; Luppi and Gautero, 1967). *Russula* ECM depict a heterogeneous assemblage of mantles and rhizomorph types. They are typified by primitive and advanced types of surface mantles lacking very often rhizomorphs (Agerer *et al*. 1989). Ectomycorrhizae of *Scleroderma* possess ring-like, bundled hyphae with a Boletales-like mantle surface. However, descriptions of native ectomycorrhizae of tropical rain forests are lacking with very few work carried out on root tips of humid forests of South Cameroon (Moyersoen, 1996; Onguene, 2000; Onguene and Kuyper, 2001).

Ectomycorrhizal associations are widely distributed along the tropical humid forest corridor, from South-East Asia to the Neotropics, passing through the Congo basin (Baohanta *et al*., 2014; Haug *et al*., 2014; Jourand *et al*., 2014; Sanon *et al*., 2014; Yorou *et al*., 2014; Onguene, 2021, in publication). Elsewhere called as «Classical monodominance” where a single species or a group of genera dominates as ‡ 60% of canopy-level, 80–100% dominance in terms of total number of canopy trees is regularly attained in such ecosystems (Connell and Lowman, 1989; Onguene and Kuyper, 2001; Ebenye *et al*., 2017). Although the occurrence of such mono- or oligodominant forests may in some cases be explicable in terms of edaphic limitations or tree regeneration after large-scale disturbance (Grubb, 1977; Baohanta *et al*., 2014; Ramanakierana *et al*., 2014; Essene *et al*., 2017; Carriconce *et al*., 2019), the regeneration requirements of African ECM associations remain poorly understood. Do specific fungal attributes of indigenous ectomycorrhizae of tropical rain forests may explain the current structure and functioning of ECM forest clumps of the Congo Basin? At the onset of this study, it was assumed that there may exist in native forests of South Cameroon, specific forest hotspots of ECM diversity, probably dissimilar in fungal composition as in Australian, boreal and temperate forests, along with low host tree specificity. The primary goal of this study was to determine the richness of indigenous ectomycorrhizae through forest inventories describing ECM diversity of ECM forest clumps of South Cameroon.

2. MATERIALS AND METHODS

2.1. Study Sites

The study was carried out in western portions of the Atlantic Biafrean forest of South Cameroon, a humid tropical climate region with two distinct wet seasons (March-June and August-November) and two dry seasons. Rainfall decreases in an easterly direction (Waterloo *et al*., 2000). Soil texture ranges from sandy clay loam in the South-western lowlands to very highly clayey in the North-eastern hilly areas (Gemerden and Hazeu, 1999). Along the same gradient, pH and soil phosphorus availability decrease as well as land use intensity (Table **1**). In the lowlands, only few undisturbed, near native forest fragments remain with a large portion of the area being deforested; whilst in the hilly areas, undisturbed late-secondary forests occur more commonly. Four experimental sites were selected, which included Ebimimbang (low elevation; slightly acid sandy clay loam soils), Ebom (mid-elevation; clayey and acid clayey soils), Nyangong (high elevation and acid clayey soils); and Bityili (strongly acid very highly clayey soils) (Figure **1**). In each undisturbed forest, three 1-ha plots were laid out. Selected tree species were marked and the roots were sampled for three years. Plots were also laid out in the fallows and surveyed for the occurrence of ECM plant

Table 1: Localization, Elevation, Rainfall and Soil Physicochemical Characteristics of the Four Research Sites in Forest Clumps

Research Sites	Ebimimbang	Ebom	Nyangong	Bityili
Localization	3°02.67'N; 10°28.25'E	3°04.73'N; 10°41.24'E	2°58.11'N; 10°45.18'E	2°56.07'N; 10°49.55'E
Altitude (m.a.s.l)	0 – 350	350 – 500	500 – 800	>800
Rainfall (mm)	1556	1987	1677	1800
Soil texture	Sandy	Highly clayey	Highly clayey	Very highly clayey
pH	5 – 6	4 – 5	3 – 4	3 - 4
Carbon (%)	1.70	2.30	3.28	5.70
Nitrogen (%)	0.11	0.14	0.20	0.36
C/N ratio	15,5	16,4	16,4	15,9
Phosphorus (µm/ml soil)	0.01	0.005	0.002	0.000

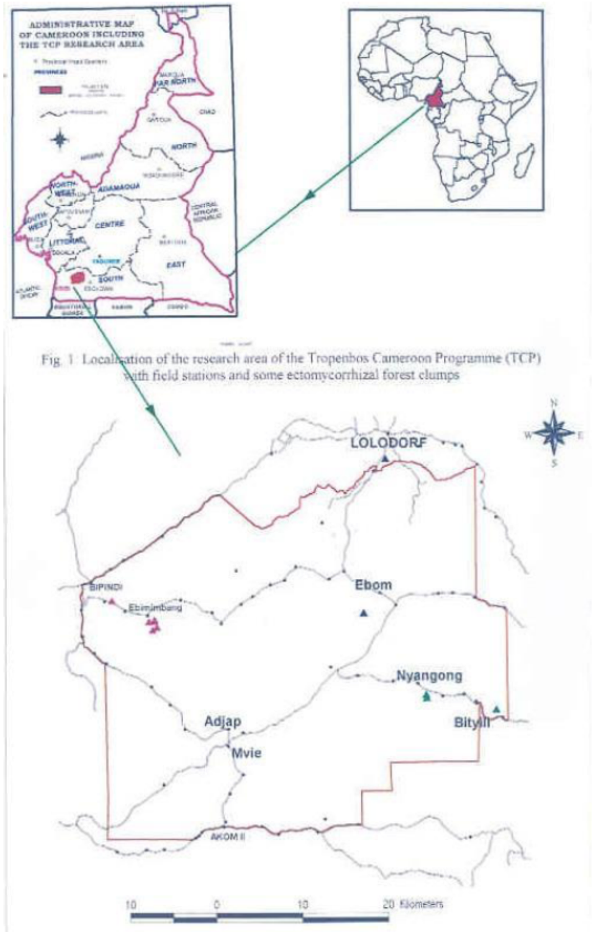


Figure 1: Localization of the research sites.

and *Gnetum* liana species and the roots were sampled. Data were pooled and analyzed.

2.2. Morphological and anatomical description of ectomycorrhizae

After identification and selection of ectomycorrhizal host trees in ectomycorrhizal forest clumps and isolated ones, four root samples were collected around each host tree. The color of the mantle was noted in the field before preservation in 50% alcohol or wrapped in aluminum foil with decomposed litter. All root samples were processed within 24 hours after collection. Whilst in the laboratory, root systems were cleared of soil debris by careful washing under a running tap water with the aid of a fine paint brush. Seven to 10 selected root tips for each representative morphotype were removed from the root sample and morphologically and anatomically described. The key morphological and anatomical features that were examined under a dissecting microscope at 40 x included: root tip branching, shape of branches, mantle color and surface texture, presence or not of rhizomorphs, emanating hyphae and, under a photonic microscope between 25 and 40x to confirm the mantle type and Hartig net, various layers of hyphal arrangement and to determine the presence of specialized cells, abundance and structure of rhizomorphs and cystidia, presence or not of Woronin bodies, using both cross - and longitudinal sections (Agerer 1995).

3. RESULTS

Ectomycorrhizal forest clumps were the only resort sites for the majority of indigenous ectomycorrhizae of humid forests of South Cameroon. Few ECM fungi were also collected around isolated ECM trees such as *Afzelia bipindensis* (Photo CMOAN106) and *Berlinia*

Table 2: List of Ectomycorrhizal Tree Species of the Detarioideae Sub-family by Types of Ectomycorrhizal Forest Habitats in South Cameroon

ECM forest clump types	Family/Sub-family [a]	Tree species	Common name [b]	Sites of occurrence
"Ekop" oligodominant ceasalp clumps	Fabaceae/ Detarioideae	*Aphanocalyx microphyllus* Harms *Bikinia le-testui* Pellegr. *Brachystegia cynometroides* L. *B. eurycoma* Harms *B. zenkeri* Harms *Didelotia africana* Baill. *Didelotia letouzeyi* Pellegr. *Didelotia brevipaniculata* J.Léonard Aubré and Pellegr. *Julbernardia pellegriniana* Pellegr. *J. seretii* (De Wild.) *Tetraberlinia bifoliolata* (Harms) Hauman	Ekop mayo ngang Ekop mayo Ekop evene Ekop naga Ekop spp Ekop rouge Ekop zing Ekop zing Ekop beli Ekop blanc Ekop ribi	All four sites
Uapaca monodominant clumps	Phyllanthaceae	*Uapaca acuminata* (Hutch.) Pax & K.Hoffm. *U. buchholizianum* Engl. *U. guineensis* Muell.Arg. *U. vanhouttei* De Wild.	Rikio Rikio Rikio Rikio	All four sites
Mixed *Uapaca* and ceasalp clumps	Phyllantaceae and Fabaceae/ Detarioideae	Various *Uapaca* and "Ekop" species	Rikio and "Ekop"	Nyangong, Bityili
Gilbertiodendron monodominant clumps	Fabaceae / Detarioideae	*Gilbertiodendron dewevrei* L. *G. brachystegioides* (Harms) J.Leonard	Limbali Limbali	Ebom, Dja, Ngoïla
Microberlinia monodominant clumps	Fabaceae / Detarioideae	*Microberlinia bisulcuta* [c] A. Chev.	Zingana	Korup National Park
Not observed in clumps	Fabaceae / Detarioideae	*Afzelia bipindensis* Harms *A. pachyloba* L.	Doussie rouge Doussie blanc	Only in Ebom
	Fabaceae / Detarioideae	*Anthonotha fragans* (Baker f.) Exell *A.macrophylla* P.Beauv. *Berlinia bracteosa* L. *B. confusa* Hoyle	Enak Enak Ebiara Ebiara	Ebom Nyangong

[a] All Fabaceae tree species listed in this table formerly belonged to the Caesalpiniaceae family according to Cronquist classification (1981) and are now ranged into Detarioideae sub-family following the new classification of the leguminosae (LPWG, 2017).

[b] Common names of "Ekop" were taken from Letouzey and Mouranche (1952).

[c] Data from Newbery *et al* (1988).

bracteosa (Photo CMOAN128). More than 30 endemic ECM tree species were described from 24 ECM tree species, with no apparent host specificity. Indigenous ectomycorrhizae of ECM Fabaceae and *Uapaca* tree species differed from the golden yellow ECM of *Gnetum* spp lianas. *Gnetum* ECM had a felt plectenchymatous mantle with few undifferentiated rhizomorphs of variable diameter (12.6-25.2 µm) and abundant hairy emanating hyphae with few clamp connections but devoid of cystidia (Photo CMOAN100). These ectomycorrhizae were observed more frequently in fallows of *Chromoleana odorata* (L.) R.M.King & H.Rob., and in secondary forests, on both sandy and clayey soils but *were* never found in ECM forest clumps. *Gnetum* ectomycorrhizae are widespread in the rain forest zone of South Cameroon.

Indigenous endemic tree ectomycorrhizal morphotypes were demarcated by their surface mantle textures and types, colors, abundance and structures of rhizomorphs, shapes and structures of emanating elements, cystidia and presence of Woronin bodies in one case. Three types of cystidia were noted awl-shaped, bottle-shaped and fusiform cystidia to different extent, though (Table **2**). Native ectomycorrhizae of ECM tree species covered the entire root system with various colors viz. white, yellow, brown and dark brown. White and yellow colors dominated. Textures varied from smooth, woolly, cottony, spiny, cotton-hairy to verrucose. They were of monopodial pinnate or pyramidal types and formed felt prosenchymal external mantle on top of an irregular or a regular synenchyma and a simple Hartig Net layer. Their thickness varied from 100 µm or less for smooth texture to 255-650 µm coarse texture. External mantles were generally shielded by undifferentiated or differentiated rhizomorphs, numerous emanating hyphae with variously shaped cystidia with clamp connections in some cases (Table **2**; Photographs). Cottony and woolly textures ECM generally had a thicker mantle than ECM morphotypes of *U. guineensis* and *G. dewevrei*. Most indigenous Cameroonian ECM were found on surface layers, sometimes even on decomposing leaves' surface like in *G. dewevrei* clumps (Photo CMOAN107) or directly on mineral red soil as for *T. bifoliolata* ECM (Photo CMOAN101) or *A. bipindensis* (Photo CMOAN106).

4. DISCUSSION

4.1. Endemic Indigenous Ectomycorrhizae in the Tropics

More than 30 endemic indigenous ectomycorrhizae were morphotyped from 24 ectomycorrhizal tree species, forming ECM forest clumps, on a vast array of ecosystems. None of indigenous ECM was observed neither in pine nor in eucalyptus plantations in Cameroon. It is the first report of such a high number of below-ground ECM biodiversity from rain forests of the Congo Basin. However, this sheer ECM number is lower than the above-ground biodiversity obtained from the same ECM forest clumps (Onguene, 2000) owing to few work on this mycological aspect and lack of African mycologists. Using molecular techniques, a high diversity of endemic ECM taxa associated with *Tristaniopsis* species were recorded from both Ultramafic and volcano-sedimentary soils in New Caledonia, with no significant differences In ECM genera between both soil types (Waseem *et al*., 2017). Similarly, high endemic ECM diversity was also observed in roots of *Acacia spirorbis* on calcareous, ferralitic and volcano-sedimentary soils (Houles *et al*., 2018). In the Neotropics coastal forests of Guadeloupe, ECM fungal community associated with *Coccoloba uvifera* was equally endemic. Endemic ECM fungi were confirmed associated with three species of *Dycimbe* and *Aldinia insignis* on widely varying chemical and textural soils in the Pakaraïma Mountains in Western Guyana (Henkel *et al*., 2002). All Dipterocarp species of the lowland tropical rain forests of South-East Asia were shown to be colonized by endemic ECM fungi (Essene *et al*., 2017). Endemicity of indigenous ECM may be a general trait in the tropics. Their life history attributes large abundance and diversity in a wide variety of habitats with nutrient-poor soils, thereby suggesting that endemic ECM fungi enhance their competitive abilities to optimize host tree nutrition and may contribute to the maintenance of tropical monodominant forests (Essene *et al*., 2017; Henkel *et al*., 2002; Corrales *et al*., 2018).

4.2. Diverse Habitats for Tropical Ectomycorrhizae

Historically, ectomycorrhizal associations were considered rare or absent from tropical rain forest ecosystems (Corrales *et al*., 2018; Verbeken and Bucyk, 2002). Tropical ectomycorrhizal habitats may be widespread as earlier thought (Carriconde *et al*., 2019). In humid forests of South Cameroon, ECM associations prevailed in five diversely ECM forest clumps on widely varied forest ecosystems, including both acid sandy and clayey soils, and widely varied ecosystems (Onguene and Kuyper, 2012). In the Pakaraïma Mountains of Western Guyana and Venezuela, they prevailed on sandstone highlands with the leguminous canopy tree *Dicymbe corymbosa* (Henkel, 2003; Smith *et al*., 2013) as well as on ultramafic rain forest in New Caledonia where they predominantly associated with *Cortinarius* fungi (Carriconde *et al*., 2019). In Asia, they are found in the tropical moist deciduous forests of India forming ECM associations between endemic *Russula* species and the endemic dipterocarp tree *Shorea robusta* (Kumar and Astri, 2019). In Indonesia, their habitats include *Shorea* plantations (Sukarno and Nara, 2019). In Brazil, indigenous ECM associations are found predominantly in pine and eucalyptus plantations, occasionally in species of *Rosaceae*, *Fabaceae* and in “Campinarama” vegetation type (flooded shrublands) in the Amazon region and, *Bauhinia forficata* and *Campomanesia xanthocarpa* in the Cerrado vegetation (Moreira and Siqueira, 2002; Carvalho and Amazonas, 2002). Endemic ECM associations are also common in the genera *Dycimbe* and *Aldina* in white sand forests in South Columbia Amazonia, in Amazonian lowland white-sand forests in Brazil and French Guyana (Vasco-Palacios *et al*. 2018; Roy *et al*., 2016). It is evident that ECM forests prevail in the Tropics with endemic ECM fungi for each habitat. Yet, ECM habitats remain poorly known in tropical humid forests and deserve more research attention to clarify the role of these symbioses in carbon and nutrient cycling as well in the ecological monodominance by some tree species of particular botanical families.

In temperate and boreal forests, ectomycorrhizal associations are formed predominantly on short root tips (fine roots) of host plants, unevenly distributed throughout the soil profile. Indigenous ectomycorrhizae of ECM tree species of forest clumps of South Cameroon covered the entire root system, similarly to those of *Gnetum* lianas (Figure **2**; Bechem and Alexander, 2011). It is plausible that individual trees, either of the same or different species could be linked spatially and temporally by hyphal ECM fungi that allow carbon and nutrients to pass among them and promote forest establishment after disturbance (Amaranthus *et al*., 1994; Onguene and Kuyper, 2002; Pena and Polle, 2014). In temperate and boreal forests, ECM fungal diversity was shown to play a key role in nitrogen cycling (Zhu *et al*., 2018). It may be assumed that ECM associations of humid forests of South Cameroon achieve strong gregarious behavior in low N and P acid clayey soils, thereby providing the competitive capacities to their host tree species with no host specificity owing to abundant rhizomorphs and emanating hyphae.

In Northern hemisphere, ectomycorrhizal shapes in which the host plant roots and the fungi grow simultaneously are found in favorable environmental conditions. ECM associations are abundant in soils rich in organic matter (Brundrett *et al*., 1996). It was not the case in this study. ECM root tips were observed on a vast array of harsh and nutrient-poor forest ecosystems including, mineral soils, decomposing leaves, litter, and swamps, on both sandy and clayey soils. Yet, these red sandy or clayey soils were acid and nutrient-poor, thereby confirming earlier hypotheses that ECM associations are often more abundant and diverse in sites with nutrient-poor soils, where they can optimize plant nutrition and may contribute to the maintenance of tropical monodominant forests (Pey *et al*., 2011a,b; Corrales *et al*., 2018). Local subsistence dwellers of the Congo Basin claimed that ECM forest clumps, even close to houses are nutrient-poor. Consequently, they never slash them for food crop farming but systematically used them to harvest wild *Cantharellus* and other edible mushrooms at the onset of the heavy rainy season (Onguene *et al*., 2015; Dijk *et al*., 2003; Eyi *et al*., 2011; De Kessel *et al*., 2017).

4.3. Distinctive Ectomycorrhizal Morphological Characters

Most investigations on ectomycorrhizal biodiversity were concentrated on the above-ground diversity and molecular identification. For the first time, more than 30 indigenous ECM morphotypes were described from the roots of 24 ECM host tree species belonging to the Fabaceae and Phyllanthaceae. They were recruited mostly in ECM forest clumps, and occasionally around isolated ECM tree species. Indigenous Cameroonian ECM showed distinctive ECM structures. They varied in color with rough textures; a generally well-developed external felt prosenchymatous mantle and a thin Hartig Net shielded by undifferentiated or differentiated rhizomorphs, septate emanating hyphae with clamp connections and bottle-shaped cystidia. Our data depict dissimilarities with results from Australian, temperate and boreal forests with smooth ectomycorrhizae of dark colors like *Coenoccum geophilum*, apparently absent from tropical rain forests (Brundrett *et al*., 1996; Smith and Read, 1997). In boreal and temperate forests, several ECM genera showed tuberculate mantle types for *Amanita* and Boletales, and heterogeneous mantle assemblages for *Russula* species devoid of rhizomorphs (Luppi and Gautero, 1967; Agerer *et al*. 1989; Brundrett *et al*., 1996; Smith and Read, 1997). Whereas indigenous ECM from this study seldom shows smooth plectenchymatous mantles as in temperate and boreal forests, they mostly harbored rough textures with abundant undifferentiated or differentiated rhizomorphs and emanating hyphae, sometimes sheltered by mostly bottle-shaped cystidia. No tuberculate ECM was noted in roots of local ECM tree species.

Table 3: Preliminary Accounts of Indigenous Ectomycorrhizae of Ectomycorrhizal Forest Clumps of South Cameroon

N°ECM	Color	Texture	Shape	Type	Mantle	Thickness (µm)	Rhizomorphs	Emanating hyphae	Cystidia	Host tree/liana
CMOAN101	Golden Yellow	Twisted with felt strings	Corralloïdal	Threadlike	F.p	12.6-25.2	Undiff.	+		*Gnetum africanum*
CMOAN102	Yellow	Cottony	Straight	Monopin	F.p	255-408	-	+	+b	*Paraberlinia bifoliolata*
CMOAN103	Milky white	cottony	Tortuous	Monopin	F.p	110-119	Undiff.	+	+b	“Ekop”
CMOAN104	White	Woolly	Tortuous	Monopin	F.p		Diffirentiated	+	+b	“Ekop”
CMOAN105	Yellow	Smooth	Straight	Monopin	F.p		Undiff	+	+b	“Ekop”
CMOAN 106	White	Woolly	Straight	Monopin	F.p		Undifff	+	+a	*Afzelia bipindensis*
CMOAN 107	Chestnut brown	Woolly	Smooth	Monopyr	F.p	100.2	-	+	-	*Uapaca guineensis*
CMOAN 108	Brown/cchestnut/chestnut brown	cottony	Straight/curved	Monopin	F.p	510-765	Undiff	-	+a	*Tetraberlina bifoliolata*
CMOAN 109	Brown	Woolly	Sinuous/ curved	Monopin	F.p	403-502.3	Diff; broown	+	+b	*Tetraberlina bifoliolata*
CMOAN 110	Orange	Woolly	Straight	Monopin	F.p	>650	Diff	+	+b	*Didelotia africana*
CMOAN 111	Brown	Woolly	Straight/ curved	Monopyr	F.p	540-615	Undiff	+	-	*Didelotia africana*
CMOAN 112	Brown yellow	Woolly	Straight	Monopin	F.p	556-712	Diff	+	+b	Ekop
CMOAN 113	Whitish	Cotton-like	straight	Monopin	F.p	390-650	Diff	*	+a	*Gilbertiodendron dewevrei* a
CMOAN 114	Dark	hairy	Straight	Monopin	f.p	350-475	Diff rhizo	+	+b	*Uapaca* spp
CMOAN 115	Brown white	Woolly	Straight	Monopin	F.p	150	Absent	+	-	Ekop
CMOAN 116	Brown/Dark	Verrucose	Straight	Monopin	F.p	100	Diff	+	+b	*Uapaca guineensis*
CMOAN 117	Brown red	Smooth	Straight	Monopin	F.p	45-75	Absent	-	-	*U. acuminata***
CMOAN 118	White	Hirsute	Straight	Monopin	F.p	25-30	Absent	+	+b	*U. acuminata***
CMOAN 119	Brown	Smooth to woolly	Straight	Monopin	F.p	162-200	Absent	+	+b	Ekop
CMOAN 120	Brown	Woolly	Straight	Monopin	F.p	280-315	Undiff	+	+b	Ekop
CMOAN 121	brown	woolly	Straight	Monopin	F.p	300-400	diff	+	+b	Ekop
CMOAN 122	White	cottony	Straight	Monopin	F.p	420-470	Diff	+	+b	Ekop
CMOAN 123	brown	cottony	Straight	Monopin	F.p	580-625	Diff	+	+b	Ekop
CMOAN 124	Dark brown	Cottony	Straight	Monopin	F.p	481-510	Undiff	+	+b	*Uapaca* spp
CMOAN 125	Dark	Woolly/ cottony	Tortuous	Monopin	F.p	306-459	Undiff	+	+b	Ekop
CMOAN 126	Brown white	cottony	Straight/ slightly curved	Monopyr	F.p	405-510	Diff	-	-	*Julbernadia seretti*
CMOAN 127	Yellow	Mat	Straight	Monopin	F.p	175-325	Short rhizo	-	+f	*Berlinia grandiflora*

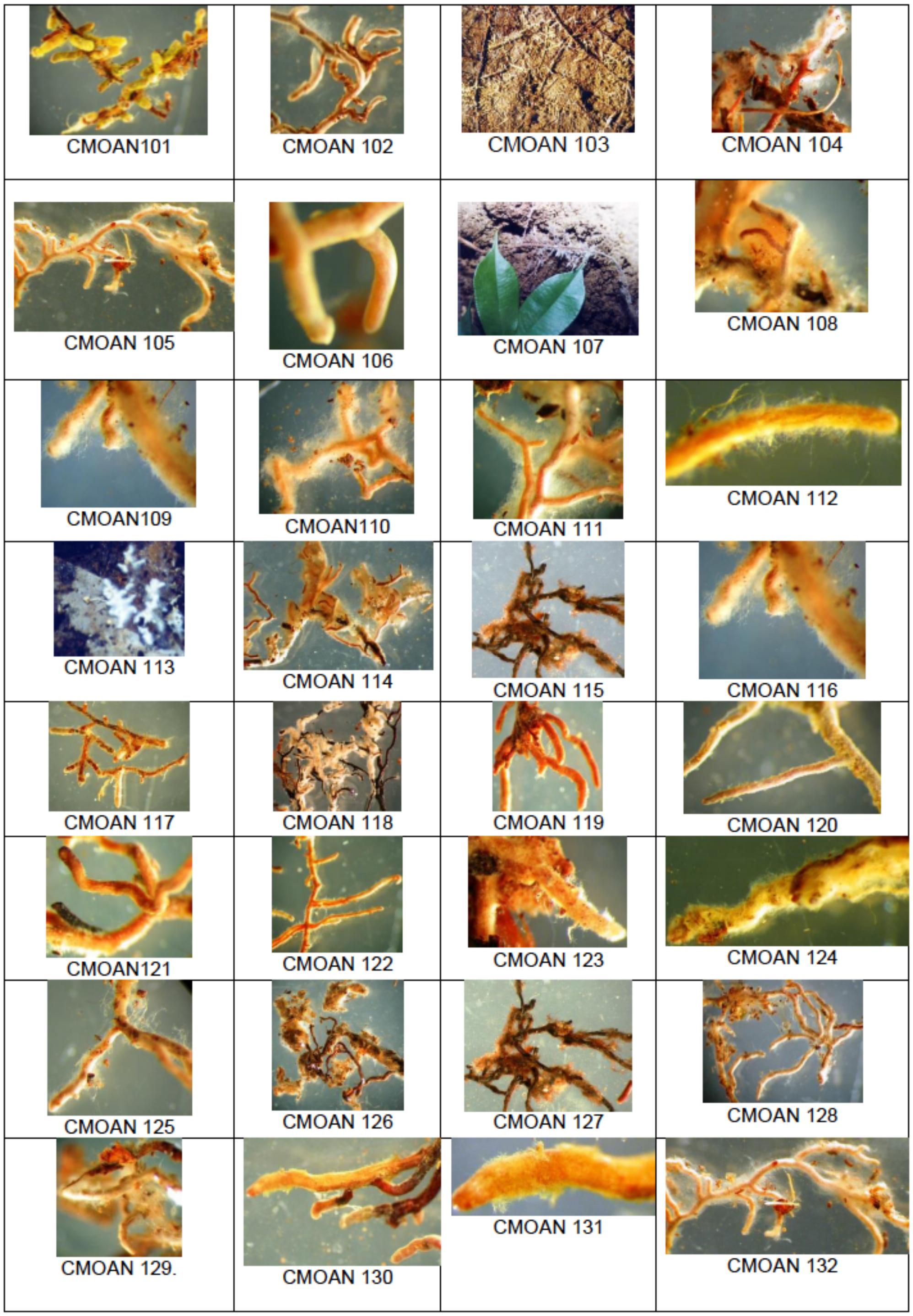
CMOAN 128			Straight	Monopin	F.p			+	+b	Ekop
CMOAN 129	Brown	Monopyr	Smooth	Monopin	R.s	25-30	-	+	+a	*Uapaca acuminate*
CMOAN 130	White	Monopyr	Felty	Monopin	F.p	207-275		-	+f	*Monopetalanthus letestui* Pellegr
CMOAN 131	white			Monopin	F.p	378		+	-	*G. dewevrei*
CMOAN 132	Brown	Woolly	Felty	Monopyr	F.p	306-561	+	-	+f	*Monopetalanthus letestui*
CMOAN133	Brown	Woolly	Straight	Monopin	F.p	110-119.2	+	-	+b	*Paraberlinia bifoliolata*
CMOAN134	White	Woolly	Straight	Monopyr	F.p	255	+	-	+b	*Didelotia brevipaniculuta*
CMOAN134	White	Cottony	twisted	Monopyr	F.p	162-200.4	+	+	+b	*Didelotia brevipaniculuta*
CMOAN 135	White	Woolly	Felty	Monopyr	F.p	108-183.9	*	+	+f	*Monopetalanthus letestui*
CMOAN 136	White	Velvety	Straight	Monopyr	F.p	>533	Diff	+	+b	*Didelotia letouzeyi*
CMOAN 137	Milky white	Smooth	Straight/ curved	Monopin	F.p	255-408	Undiff	+	+f	*Tetraberlina bifoliolata*

Notes. F.p: felt prosenchyma mantle; R.s: regular synenchyma; Monopin: monopodial-pinnate; Monopyr: monopodial-pyramidal;** Presence of Woronin bodies; +: present; -: absent; +b: bottle-shaped cystidia; +f: fusiform cystidia; *a: awl-shaped cystidia.

The Hartig Net, one of the three components required to form ectomycorrhizal roots, is a network of inward growing fungal hyphae that extend into the root, penetrating between the epidermia and cortex of ectomycorrhizal plants. It is a specialized bi-nutritional nutrient exchange organ between ECM fungi and host plants found in ectomycorrhizal associations. The Hartig Net supplies chemical elements required for plant growth, such as potassium and provide compounds such as nitrate, used in combination with ectomycorrhizal symbiosis to host tree species which has shown to protect the fungi against heavy metal toxicity (Guerroro-Galan *et al*., 2018 Yao *et al*., 2019; Zhang *et al*., 2019). The Hartig Net is limited to the proximal zone of the root cap as a result of a mechanical ECM fungal penetration at early plant growth stages double with a higher concentration of cell wall pectin cellulose than fully mature trees (Nylund *et al*., 1982; Smith *et al* 2008). The Hartig Net of native ECM of local tree species of this study was restricted to a few epidermal layers conversely to those of *Gnetum* liana which was deeper. Our results corroborate with earlier findings that the Hartig network is limited in Angiosperms while that of Gymnosperms progress and surround both epidermal and cortical cells (Fassi, 1957; Massicotte *et al*., 1989; Theon and Ducousso, 1989: Brundrett *et al*., 1996; Ingleby, 1999; Bechem and Alexander, 2011).

Utilization of only morphological and anatomical criteria can be used in some cases to identify the mycorrhizal fungal species, at least at the genus level (Zak, 1975). In this study, morphological features allowed to identify fungal species similar to *Scleroderma sinnamariense* (Mont.) as the ECM root samples were directly traced under these fruitbodies. Formed only by *Gnetum* species, they are distinctive by their golden yellow color, felt or string-like texture and coralloïdal shape (Onguene, 2000; Tambe and Alexander, 2003). The yellow golden *Gnetum* ECM was never observed in ECM forest clumps, suggesting ECM ecological specificity. However, other *Scleroderma* species were found in ECM *G. dewevrei* clumps (Ebenye *et al*., 2017). On *Figus sylvaticus* L., ECM of *S. areolatum* were silvery white with abundant rhizomorphs; all mantle layers were plectenchymatous with type E rhizomorphs, prominent emanating hyphae and thick cell wall. The distal ends of emanating hyphae of rhizomorphs were inflated and often merged with other emanating hyphae. All parts of the ectomycorrhiza were clampless. White *Scleroderma* fungal strains were also observed on roots of some *Gnetum* spp lianas in secondary forests and fallows of *Chromoleana odorata* in South Cameroon (Onguene, 2000; Bechem and Alexander, 2012). However, only few studies have been carried out on African ectomycorrhizae (Diedhiou *et al*., 2004).

In temperate forests, shape of ectomycorrhizae often varied with plant-fungus interactions or is influenced by the fungal type involved in the association (Agerer, 1990). *Gnetum* ECM were of


CMOAN101 CMOAN 102 CMOAN 103 CMOAN 104
CMOAN 105 CMOAN 106 CMOAN 107 CMOAN 108
CMOAN109 CMOAN110 CMOAN 111 CMOAN 112
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CMOAN121 CMOAN 122 CMOAN 123 CMOAN 124
CMOAN 125 CMOAN 126 CMOAN 127 CMOAN 128
CMOAN 129. CMOAN 130 CMOAN 131 CMOAN 132

Photographies A: Putative native ectomycorrhizae from ectomycorrhizal forest clumps of rainforests of South Cameroon.

coralloïdal type whilst ECM of tree species were either monopodial-pinnate or monopodial-pyramidal. Similar observations were made on *Afzelia africana* Baill. ectomycorrhizae in forests of South-West of Burkina Faso (Sanon, 1999). Apparently, *Gnetum* ECM belonged to Ascomycetes while those of trees were mainly from Basidiomycetes. This distinction is inferred from specialized elements like Woronin bodies, clamp connections, septa and presence of cystidia (Agerer, 1999; Brundrett *et al*., 1996). With the exception of one ECM morphotype associated with *U. acuminata* with Woronin bodies, suggesting an Ascomycete ECM fungus, all other native tree ECM of this study carried distinctive characters of ECM Basidiomycetes as those of boreal and temperate forests.

Ectomycorrhizal thickness varies with texture. In this study, cottony and woolly textures ectomycorrhizae

Russula camerunensis *R. annulatobadia* *Lactarius rubroviolascens* *Xerecomus spinolosus*

Amanita gigavolvata *Amanita bicolor* *Amanita afrorubensis* *Amanita zingui*

Cantharellus sp1 *Inocybe zingii* *Cortinarius ionopygmaeus* *Scleroderma sinnamariense* *Ramaria* sp1

Photographies B: Some native ectomycorrhizal *Amanita* and *Russula* fungal strains from ectomycorrhizal forest clumps of South Cameroon.

generally had a thick mantle than ECM morphotypes of *Uapaca guineensis* and *Gilbertiodendron dewevrei*. Ectomycorrhizal thickness varied from 100 µm or less thick in smooth texture ECM to 255-650 µm in coarse texture. Narrow mantle with a single tissue layer densely arranged and organized as a net synenchyma with elongated hyphae were observed in Pine ECM associations (Landeweert et. al, 2005). Indigenous ectomycorrhizae of selected tree species of this study were monopodial-pinnate or pyramidal types with thick mantles, undifferentiated or differentiated rhizomorphs, septate emanating hyphae with clamp connections and variously shaped cystidia. Abundance of cystidia could suggest *Russula* ectomycorrhizae as observed by the dominance of above-ground ECM fungal fruitbodies (Onguene, 2000). ECM roots of Sal (*Shorea robusta*) associated with *Russula* species were light brown to greyish brown, and have plectenchymatous gelatinised outer mantle layers having abundant cystidia elements in India (Kumar and Atri, 2019).

Cystidia, sterile and variously shaped hyphal ends, are possibly appropriate for preventing animal attack and moreover can cover mantles and rhizomorphs (Agerer, 2006; Roman *et al*., 2005; Beenken, 2001). Cystidia occur not only on the cap skin, gills, and stipe of sporocarps but also on the ectomycorrhizae (Agerer 2006). Although they are not very common, the 15 types compiled by Agerer (1991) are distinctive for some fungal groups. Cystidia seem to be specialized in short distance nutritional processes, increasing the mantle's field of influence. In most cases, ECM morphotypes in this study carried bottle-shaped cystidia. Bottle-shaped cystidia were also described in temperate ECM for different *Russula* species (Agerer, 1994; Ceruti and Busseti, 1962).

4.4. Ectomycorrhizal Fungal Rhizomorphs and Emanating Hyphae: Ectomycorrhizal Specialized Organs that Better Explain Monodominance of ECm Associations under Nutrient-poor Soils and Harsh Forest Ecosystems

Ectomycorrhizae are characterized by particular components for nutrient scavenging, water absorption and protection against soil pests, cystidia, rhizomorphs and emanating hyphae. Rhizomorphs are multi-hyphal linear aggregates (Agerer 1999), divided into seven types by their structure (Agerer 1999; Agerer and Iosifidou 2004). ECM rhizomorphs are thick-walled hyphae of uniform diameter running in parallel with a simple apex or with ramified tortuous hyphae with protusions and protuberance at the tip and frequently or less septa. They are highly differentiated or undifferentiated hydrophobic enduring transport hyphae whilst emanating are fine hydrophilic hyphae that explore and exploit soil matrix or may aggregate to form rhizomorphs.

Despite few studies of tropical ectomycorrhizae (Moyersoen, 2014), few data show that ectomycorrhizal rhizomorphs and emanating hyphae are commonplace in the tropics. In the Pakaramaïmaea forest of Southern Venezuela, Sebacinales ectomycorrhizal fungi associated with *Parakamaea dipterocarpacea* spp.*nitida* harbored emanating hyphae and rhizomorphs throughout (Moyersoen, 2014). Ectomycorrhizas of three species of Nyctaginaceae in tropical mountain rain forest of South Ecaduor did not show any rhizomorphs (Haug *et al*., 2014). In this study, most indigenous ectomycorrhizae harbored abundant undifferentiated or differentiated rhizomorphs and emanating hyphae (Onguene *et al*., 2014). Both particular extrametrical mycelia may justify ECM competitive abilities on prevailing poor nutrient soils or in temporarily inundated swamps in tropical forest ecosystems.

It is recognized that ectomycorrhizal rhizomorphs and their mycelium are capable of long-distance uptake and transport of water and nutrients (Duddridge *et al*.; 1980; Finlay *et al*.; 1988; Kammaerbauer *et al*., 1989). Their function is directly related to nutrient uptake and transport with capacity of exploring large distances from the mantle. They enable ectomycorrhizae to develop on hard conditions. ECM symbiosis may contribute to limit heavy metal accessibility and uptake by host plants (Colpaert *et al*., 2011). In ultramafic soils of New Caledonia, some isolates of *Pisolithus tinctorus* could tolerate high levels of Nickel (Aggaran *et al*., 1998). In experimental soils containing 60 mg of Ni, ectomycorrhizal *Eucalyptus globulus* seedlings could strive conversely to controls after 12 weeks of growth (Jourand *et al*., 2014). In this study, soils were often very low in available P and N. Native ECM strive at best in three-months temporary inundated soils on riversides and harbored abundant rhizomorphs and emanating hyphae. Thus, ectomycorrhizal fungal rhizomorphs and emanating hyphae could be ECM specialized organs adapted to such forest ecosystems and better explain tropical monodominance of ECM associations under nutrient-poor soils and harsh forest ecosystems.

CONCLUSION

In fine, tropical ectomycorrhizal forest clumps constituted hotspots of the below-ground ectomycorrhizal diversity, similar in fungal composition to Australian, temperate and boreal forests, along with low host tree specificity. However, their endemicity is coupled with three fungal attributes, rhizomorphs, emanating hyphae and cystidia that confer them with strong competitive abilities to strive at best on prevailing nutrient-poor acid soils and harsh conditions. However, more research is still needed on tropical ECM diversity to study their roles in the structure and functioning of humid forests of the Congo basin.

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