

Selective logging and shifting cultivation practices significantly reduce ectomycorrhizal inoculum potential of humid forest soils of South Cameroon

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Abstract

Ectomycorrhizal (ECM) associations are key biological engineers of soil biodiversity in temperate, boreal and tropical humid forests. They play key roles in ecological functioning, fungal diversity, worldwide economy, food provisions and carbon sequestration. Yet, they are threatened by rampant man-made disturbances. Hitherto, little information and few data are available on effects of selective logging and shifting cultivation practices in tropical forests on ECM inoculum potential (ECMIP). ECMIP was investigated in rainforest patches of South Cameroon and assessed in intact soil cores, by baiting two ecologically dissimilar tree species, *Tetraberlinia bifoliolata* and *Afzelia bipindensis*. ECMIP's assessment was carried out by fractional ECM colonization rate and mushroom surveys. It was only in undisturbed ECM forest clumps that nearly most ECM fungal morphotypes and more than 150 putative ECM fruitbodies were recorded. There were strong fungal

specificity differences in ECM fungal compositions among ECM forest clumps. While native *Amanita* and *Russula* fungi were abundant and frequent in "Ekop" forest clumps, they were virtually absent in *Gilbertiodendron dewevrei* forest clumps. Both selective logging and shifting cultivation practices completely eliminated soil ECM inoculum and ECM fruitbodies. *Afzelia bipindensis* seedlings were colonized only in soils from the vicinity of ECM conspecific adult trees. *Tetraberlinia* seedlings were strongly colonized only in soils from ECM forest clumps. Seedlings of both tree species differed in fungal ECM colonization patterns owing to fungal specificity. Lack of ECMIP in soils from forestry practices and significant reduction of soil ECMIP in shifting cultivation practices adversely affect the conservation of soil ECMIP. Conservation of ECM forest clumps is recommended for ecologically sound forest management of tropical humid forests of the Congo Basin.

Mots clés : *Afzelia bipindensis*; Forest clumps; Fungal specificity

Résumé

Les associations ectomycorhiziennes (ECM) sont des ingénieurs biologiques clés de la biodiversité des forêts tempérées, boréales et humides. Elles jouent des rôles clés dans le fonctionnement écologique, la diversité fongique, l'économie mondiale, l'approvisionnement alimentaire et la séquestration du carbone. Cependant, elles sont menacées par des perturbations humaines rampantes. Jusqu'ici, peu d'informations et de données sont disponibles sur les effets des pratiques de coupe sélective du bois et d'agriculture itinérante sur brûlis sur le potentiel ectomycorhizien des sols (PECM) de forêts tropicales. Le PECM a été investigué le long de parcelles des forêts tropicales du Sud Cameroun et évalué à partir des carottes de sol intactes, en piégeant deux espèces d'arbres écologiquement dissimilaires, *Tetraberlinia bifoliolata* and *Afzelia bipindensis*. Le PECM a été évalué par la colonisation fractale ECM et des inventaires de carpophores fongiques. C'est seulement

dans des peuplements forestiers ECM (PFE) que presque tous les morphotypes et plus de 150 carpophores ECM putatifs ont été collectés. Une forte spécificité fongique a été observée dans les compositions fongiques ECM entre les PFE. Alors que les espèces d'*Amanita* et de *Russula* étaient abondantes et fréquentes dans les PFE à «Ekop», elles étaient virtuellement absentes dans les PFE à *Gilbertiodendron dewevrei*. Les deux pratiques de coupe sélective du bois et d'agriculture itinérante sur brûlis ont complètement éliminées le PECM et les carpophores ECM. Les semis d'*Afzelia bipindensis* n'ont été colonisés que dans les sols proches d'arbres adultes conspécifiques. Les semis de *Tetraberlinia* ont été fortement colonisés uniquement dans les sols des PFE ectomycorhiziens. Les semis des deux espèces ont différé dans les modes de colonisation ECM fongique en raison de la spécificité fongique.

L'absence de potentiel ectomycorhizien dans les sols provenant des pratiques coupe sélective de bois et sa forte réduction dans les sols provenant de l'agriculture itinérante sur brûlis ont négativement affecté la

conservation des PECM des sols. La conservation des peuplements forestiers ECM est recommandée pour la gestion écologiquement viable des forêts tropicales humide du Bassin du Congo.

Keywords : *Afzelia bipindensis*; *Peuplements forestiers équiennes* ; *Spécificité fongique*

1. Introduction

Sustainable functioning of tropical rain forest ecosystems depends on key ecological and biological processes that maintain soil fertility. These include carbon sequestration and organic matter decomposition, nutrient mineralization, carbon and water cycling and recycling, foraging and macrofungal grazing activities, and mycorrhizal activities. Mycorrhizae improve access to low available soil nutrients and water, and increase root resistance to soil pathogens for almost all terrestrial plants (Smith and Read, 1997; Bâ et al., 2012). Such key processes might be altered by deforestation resulting from logging and agricultural practices, if they lead to changes in species composition and disappearance. Decline in species richness of mycorrhizal fungi and a decrease in abundance of mycorrhizal propagules have been linked to changes in above-ground species diversity and altered ecosystem functioning (Perry et al., 1990; Janos, 1996). Yet, data on the impact of changes in land uses on mycorrhizal populations and dynamics remain scarce from tropical humid forests.

Mycorrhizal associations form the most widespread symbiotic relationships between roots of most vascular plants and both Basidiomycota and Ascomycota phyla of soil fungi (Smith and Read, 1997; Alexander and Selosse, 2009). Mutual fungal and plant partners benefit from each other from these mycorrhizal associations (Bâ et al., 2014; Jourand et al., 2014). The mutualistic fungi (Mycobiont) colonize the root system of a host plant, providing increased nutrient and water absorption capabilities and root bioprotection against soil pathogens while the plant (Phytobiont) provides the fungus with carbohydrates formed from photosynthesis and a secure habitat within the root cortex. Several other benefits have been reported viz. increased nitrogen uptake in Legumes, uptake of organic substrates by *Gnetum* lianas, alleviation of salt stresses, tree regeneration in Ultramafic soils and forest rehabilitation facilitation (Jourand et al., 2014; Onguene and Kuyper, 2003; Tambe, 2014).

Out of 7 types of mycorrhiza, the ectomycorrhizae predominate on forest trees and *Gnetum* lianas

(Alexander, 1989; Amaranthus, 1998; Onguene and Kuyper, 2001; McGuire et al., 2013; Tambe, 2014). In past literature, it was thought that ECM associations prevailed merely in temperate and boreal forests. Recent findings revealed that ECM 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; Sanon et al., 2014; Onguene et al., 2018). They occur as “islands” in “ocean” of arbuscular mycorrhizal (AM) forests forming either monodominant or oligo-dominant grooves where they significantly contribute to forest basal area. Such ECM forests have been denoted in East, South, South-East and South-West regions of Cameroon, in Gabon and the “Forêt Claire” of the Miombo in RD Congo (Newbery et al., 1988; Buyck et al., 1994, 1996; Hart, 1995; Onguene et Kuyper, 2001, 2012; Eyi et al., 2011; Bâ et al., 2012; De Kesel et al., 2017, Kaumbu et al., 2022). In such settings, ECM associations are threatened by rampant deforestation due to illegal mining, climate change, selective logging and shifting cultivation practices.

In Northern hemisphere, selective logging or partial forest removal is the practice of cutting down a few species of trees while leaving the rest of the forest more or less intact and unharmed. In tropical forestry practices, it consists of harvesting isolated and selected valuable timber tree species above a threshold stem diameter with official prescriptions designed to maintain the forest cover density. Consequently, the forest is damaged with skid trails and woodlot parks devoid of vegetation for dozens of years. Although selective logging has a far less impact on forest processes than deforestation, selectively logged sites experience higher rates of forest fires, tree fall, changes in microclimate, soil compaction and erosion among other ecological impacts on soil and plant biodiversity and ecosystem functioning (Baar et al., 1999; Barlow et al., 2016; Khabarov et al., 2016).

Shifting cultivation is a form of family agriculture, used especially in tropical Africa, in which a small

plot of forest land is cleared of vegetation by slash and burn at the onset of the dry season, followed by felling of large trees. During the raining season, the cleared plot is hand-hoed farmed and harnessed for two to three years, then abandoned to fallowing for several years to allow natural restoration of soil fertility. These anthropogenic activities lead to deforestation with induced serious negative consequences on terrestrial carbon sinks, balance of atmospheric greenhouse gases and soil biodiversity, particularly mycorrhizal fungal propagules.

Four major sources of ectomycorrhizal (ECM) fungal propagules prevail in forest soils viz. fruitbodies, spores, hyphae and sclerotia of ECM fragments, fragments of ECM mycelial strands (Bâ et al., 2012), constituting ECM inoculum. However, few data are available on impacts of selective logging and shifting cultivation practices on ECM inoculum potential (ECMIP) of rainforest soils. The objectives of this investigation were; (1) to assess changes in ECMIP during forest succession; (2) to determine the effects of selective logging and shifting cultivation practices on the ECMIP of humid forest soils of South Cameroon; and (3) to relate ECMIP to growth of two ecologically contrasted ECM timber tree species.

2. Material and methods

2.1. Study site

The study was undertaken in the western portions of the Atlantic Biafrean forest of South Cameroon (Letouzey, 1985). The research area covered nearly 2000 km². The climate is humid tropical with two distinct wet seasons and two dry seasons. Rainfall decreases in an easterly direction, with around 3000 mm in Kribi to nearly 1700 mm in Ebolowa. Soil texture ranges from sandy clay loam in the lowlands to very highly clayey in the hilly areas. Along the same gradient, pH and phosphorus availability decrease. Intensity of land use and consequently forest vegetation also change from the lowlands in the western parts to the hilly areas and plateaus in the eastern part of the area. In the lowlands only few fragments of undisturbed rain forests remained, and a large part of the forest was much degraded; in the hilly areas, late-secondary and undisturbed forests occurred more commonly. Within the research area, three sites were selected in

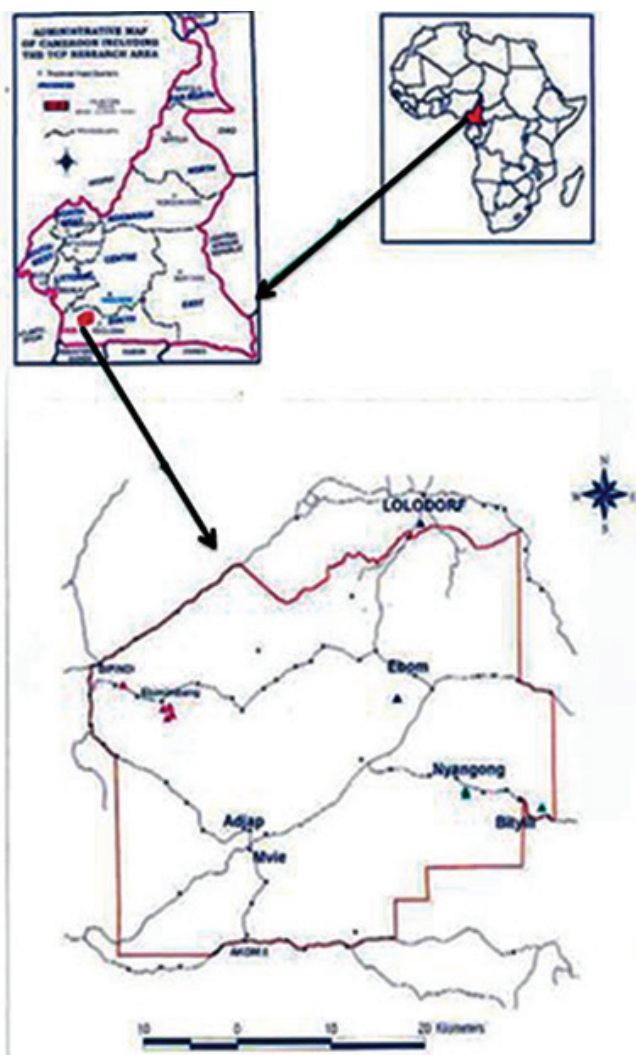


Figure 1: Map of localization of the research sites in portions of humid forests of South Cameroon

Ebimimbang (low elevation), Ebom (mid elevation), and Nyangong (high elevation).

Two types of mycorrhizal forests were sampled: ectomycorrhizal and Arbuscular Mycorrhizal (AM). ECM forest stands of the Detarioideae and Uapaceae tree species commonly occur in clumps where they tend to dominate the canopy (Onguene, 2000; Onguene and Kuyper, 2001; Onguene et al., 2018). Surrounding these clumps are old, predominantly AM forest stands. These stands sometimes constitute the rotational head of traditional shifting cultivation farms. Late-successional and undisturbed forest stands are given out as concessions or “vente de coupe” to logging companies. After exploitation, such stands are either

colonized by the exotic weed *Chromolaena odorata* (L.) R.M King and H.Rob. or the early-successional tree *Musanga cecropioides* R.Br. after which other early-successional trees re-establish, forming early-successional or secondary forest stands. In early-successional stands, most tree species are AM, but few isolated ECM trees could be found (Onguene and Kuyper, 2001). Age of undisturbed, late-successional and early-successional forest stands could not be accurately determined, due to lack of historical data on land and forest use. However, species composition, stem numbers, and basal area (the latter two parameters being inversely related during succession) can be used to infer their relative age. Data on forest vegetation in the area were provided by Van Gernerden et al (2003) and data on the mycorrhizal associations of the important tree species by Onguene and Kuyper (2001).

2.2. Soil sampling

In each site, nine 100 m² (10m x 10m) quadrats were selected in seven vegetation types (with different levels of disturbance), viz. (1) ECM forest clumps, (2) late-successional forest stands outside the crown projection of ECM clumps (LS), (3) early-successional forest stands, (4) agricultural fields of food crops with plantain (*Musa* spp (L.), cocoyam (*Xanthosoma sagittifolium* (L.) Schott)), groundnut (*Arachis hypogea* L.), and cassava (*Manihot esculenta* Crantz) as the major crops, (5) *Chromolaena odorata* fallow, (6) *Chromolaena* fallow with the liana *Gnetum* spp. Welw., and (7) sites of forestry practices such as skid trails and bare landings. The presence of *Gnetum*, an ECM plant was considered important as this liana might provide ECM inoculum to facilitate the establishment of ECM seedlings in formerly agricultural fields. The vegetation types will hereafter be referred to as disturbance stages. Canopy dominance in ECM clumps varied with site: in Ebimimbang dominants were “Ekop” species (a collective pilot name for a number of species of Amherstieae tribe), in Ebom *Gilbertiodendron dewevrei* (De Wild.), and in Nyangong Uapaca and “Ekop” species.

In each quadrat, soil cores were collected at three spots, each 50 m apart. Relatively undisturbed, intact, about 4.2-4.5 kg (wet weight basis) cylindrical soil monoliths were collected by driving a 15 cm diameter x 45 cm long PVC tube into the ground with a hammer dropped from a constant height (10-20 cm) onto a flat steel plate, placed on top of the PVC tubes.

2.3. Experimental bioassays

Two native timber species, both belonging to the Detarioideae, were used for the bioassays. *Tetraberlinia bifoliolata* Harms Troupin is an ECM tree (with very occasional AM structures: Moyersoen and Fitter, 1999) that is a valuable potential novel timber tree. *Afzelia bipindensis* Harms is a dual mycorrhizal tree (Newbery et al., 1988; Onguene and Kuyper, 2001) that provides a highly priced timber. Hereafter, the trees will be designated by their generic names only. *Tetraberlinia* occurred usually in ECM forest clumps together with other “Ekop” species, while *Afzelia* tree species usually grew isolated between AM trees and had not been observed in ECM clumps. Both tree species had large pods (10-20 x 5-8 cm) with a small number of large and heavy seeds; average seed size of *Tetraberlinia* was 20-30 x 15-25 x 5-7 mm and that of *Afzelia* 30-40 x 20-30 x 10-20 mm; average seed mass of *Tetraberlinia* was 1.5 g (0.8-2.7 g) and of *Afzelia* 11.5 g (6.2-17.4 g). Seedlings of both species possessed coarsely branched seedlings with few root hairs. Seeds were germinated for a week in steam-sterilized sand without pregermination treatment. One (1)-week old seedling of each tree was placed in a small hole in the centre of the soil core. Cores were placed on benches and grown under natural light conditions in a shade house in Kribi (02°57'N; 09°59'E) in a randomized complete block design, and watered every three days to maintain soils at field capacity. Soil cores did not receive nutrient amendments. Seedlings of *Tetraberlinia* and *Afzelia* were grown for five months. At harvest, shoots and roots were separated. Shoots were dried at 70°C for 72 hours and shoot dry weight subsequently determined. Root systems were cleared of soil debris by gently washing under a water flow, immersed in tap water, and observed under a dissecting microscope at 40x magnification. Fractional ECM colonization was assessed by the gridline intersect method (Brundrett et al., 1996; Agerer, 2001). Afterwards, portions of the root sample of *Afzelia* were stained with acid fuchsin and fractional colonization by AM fungi was assessed by the gridline intersects method (Hayman, 1970; Kormanik and McGraw, 1980).

2.4. Experimental design and statistical analysis

For *Tetraberlinia*, the experiment was a full factorial with two factors, site (3 levels) and disturbance stage (7 levels). Because of a limited number of seeds of

Afzelia, a full factorial experiment was not possible. A smaller factorial experiment was executed with soils from three sites and three disturbance stages (ECM forest clumps, late-successional forest stands, early-successional forest stands). For the Ebom site, where *Afzelia* was fairly common and widespread, soils from forestry practices, agricultural fields, and fallow were included but differentiated by fallow with and without *Gnetum*. We also investigated ECM inoculum potential of soils directly under *Afzelia* mother trees as positive controls. ECM fungal fruitbodies were scrutinized both in the fields and in the shade house along the disturbance stages.

The SPSS package (SPSS v.2020 Inc, 2014) was used for statistical analysis. Data were tested first for normality and homogeneity of variances using the Levene test in the one-way analysis of variance (ANOVA). Data on fractional ECM root colonization by *Tetraberlinia* contained many zeroes and did not meet the requirements of normal distribution and homogeneous variances. Therefore, the non-parametric Kruskal-Wallis test was applied. When the analysis was restricted to the three forested disturbance stages (ECM forest clumps, late-successional forest stands, early-successional forest stands) data of fractional ECM root colonization, after arc sin square root transformation, did meet

the requirements for ANOVA. For *Afzelia*, fractional ECM colonization in soils from the three forested disturbance stages was very variable, resulting in variances that did not meet the requirement of homogeneity. Again, the non-parametric Kruskal-Wallis test was applied. For the Ebom soils, data did meet the assumptions for ANOVA after arc sin square root transformation. Data on AM colonization were also arc sin square root transformed. Shoot dry weights of both species was square root transformed and analyzed by ANOVA. Average means were separated by Duncan's multiple range tests. Spearman's rank correlation coefficients between fractional ECM colonization, fractional AM colonization, and shoot dry weights were calculated for seedlings of both tree species.

3. Results

3.1. Effects of disturbance stages on ectomycorrhizal inoculum potential

Non-parametric analysis of variance indicated that fractional ectomycorrhizal colonization of *Tetraberlinia* seedling roots was significantly influenced by disturbance stages ($p < 0.001$), but not by site ($p > 0.1$). Seedlings grown in soils from sites of forestry practices, agricultural fields and fallow without *Gnetum* remained devoid of ECM

Table 1: Localization, elevation, rainfall and soil physico-chemical characteristics of research sites in portions of the Atlantic rain forest of South Cameroon

Research sites	Ebimimbang	Ebom	Nyangong
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
Altitude (m.a.s.l)	0 – 350	350 – 500	500 – 800
Rainfall (mm)	1556	1987	1677
Soil texture	Sandy	Highly clay	Highly clay
pH	5 – 6	4 – 5	3 – 4
Carbon (%)	1.70	2.30	3.28
Nitrogen (%)	0.11	0.14	0.20
C/N ratio	15,5	16,4	16,4
Phosphorus (µm/ml soil)	0.01	0.005	0.002

Table 2 : Two-way analysis of variance of site and disturbance stage on shoot dry weight of five-month old seedlings of *Tetraberlinia* and *Afzelia*

Source of variation	Df	F	p	Df	F	p
	<i>Tetraberlinia</i>			<i>Afzelia</i>		
Site	2	4.36	0.019*	2	13.2	0.000**
Disturbance stage	6	4.39	0.001**	2	0.7	0.529ns
Site x Disturbance stage	12	2.44	0.017*	4	3.3	0.036*

Table 3 : Fractional ectomycorrhizal (ECM) colonization (measured as percent root length) of five-month-old seedlings of *Tetraberlinia* and *Afzelia* in fonction of three forest vegetation stages at three experimental sites

Forest vegetation types	Ebimimbang		Ebom		Nyangong	
	<i>Tetraberlinia</i>	<i>Afzelia</i>	<i>Tetraberlinia</i>	<i>Afzelia</i>	<i>Tetraberlinia</i>	<i>Afzelia</i>
ECM forest clumps	48 ^{bc}	26	32 ^{cd}	0	81 ^a	13
Late-successional forests	28 ^d	22	12 ^e	5	52 ^b	34
Early-successional forests	4 ^f	1	0 ^f	11	20 ^{de}	0

Table 4 : Two-way analysis of variance of site and disturbance stage on arbuscular mycorrhizal fractional colonization of five-month old seedlings of *Tetraberlinia* and *Afzelia*

Source of variation	Df	F	p	Df	F	p
	<i>Tetraberlinia</i>				<i>Afzelia</i>	
Site	2	52.7	0.000**	2	15.6	0.553ns
Disturbance stage	6	88.9	0.000**	2	0.003	0.045*
Site x Disturbance stage	12	0.836	0.017*	12	1.31	0.403ns

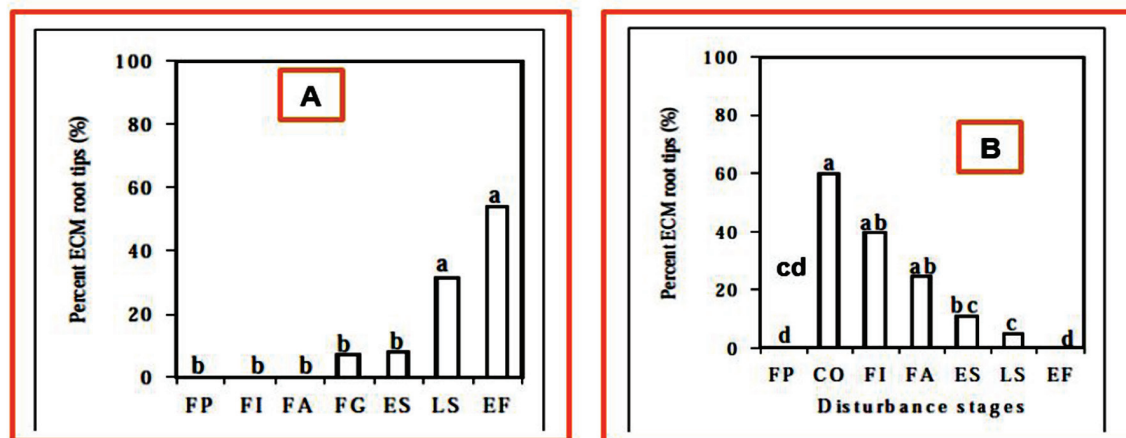


Figure 2: Ectomycorrhizal fractional colonization of *Tetraberlinia* (A) and *Afzelia* (B) seedlings grown in soils from different disturbance stages (average from three sites). Significant differences between disturbance stages (Mann-Whitney U-test; $p < 0.05$) are indicated by different letters. Abbreviations are as follows: EF = ectomycorrhizal forest clumps; LS = late-successional forest stands outside the crown projection of ectomycorrhizal clumps; ES = early-successional forest stands; FI = agricultural fields of food crops with plantain (*Musa* spp), cocoyam (*Xanthosomas esculenta*), groundnut (*Peanut hypogea*), and cassava (*Manihot esculenta*) as the major crops; FA = *Chromolaena odorata* fallows; FG = *C. odorata* fallows with the liana *Gnetum*; FP = sites of forestry practices such as skid trails and Bare landings

colonization. No ECM fungal fruitbodies were recorded in disturbed sites. In soils from fallow with *Gnetum* from all three sites, roots of *Tetraberlinia* seedlings were lightly colonized to some extent. ECM colonization was highest in soils from ECM forest clumps (figure 2A). A two-way analysis of variance for fractional ECM colonization of only the three forest stands indicated that both site and disturbance stages were statistically significant, whereas the interaction was not (table 2). ECM

inoculum increased during succession with ECM forest clumps showing a significantly higher ECM colonization than late-successional stands, and fractional ECM colonization being lowest in early-successional stands (figure 2A). Fractional ECM colonization was highest in soils from Nyangong and lowest in soils from Ebom (table 3).

Non-parametric analysis of variance indicated that ectomycorrhizal colonization of *Afzelia* seedling roots in soils from the three forest stands was

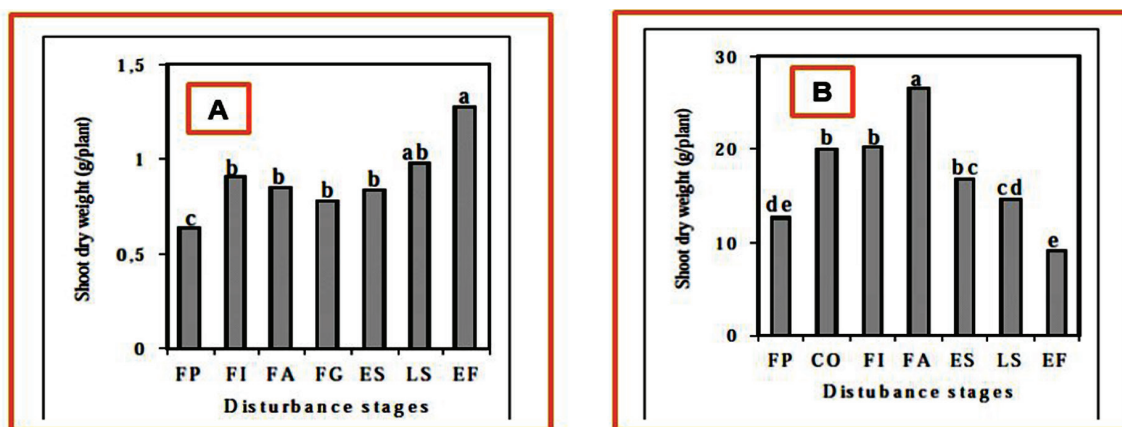


Figure 3: Shoot dry weights of *Tetraberlinia* (A) and *Afzelia* (B) seedlings grown in soils from different disturbance stages (Average from three sites). Significant differences between disturbance stages (Duncan's Multiple Range Tests; $p < 0.05$) are indicated by different letters. Abbreviations are similar to figure 2.

significantly influenced neither by site nor by disturbance stage ($p > 0.1$). No or very little ECM colonization by native ECM fungi was observed in soils from a Gilbertiodendron forest clump of Ebom and in soils from early-successional forests from Ebimimbang and Nyangong (table 3). For the Ebom soils only, soil cores taken under a mature *Afzelia* tree resulted in the highest fractional ECM root colonization. Fractional ECM colonization was high in sites of agricultural practices (fields, fallow) and declined in soils from late-successional forest stages. In soils from forestry practices (Skid trails and bare landings) and ECM forest clumps, no fractional ECM colonization was observed (figure 2B). In the three forested disturbance stages, there was no correlation between ECM fractional colonization of *Tetraberlinia* and *Afzelia* seedling roots ($r = 0.50$, $n = 9$; $p > 0.1$).

3.2. Effect of disturbance regimes on abundance and diversity of ectomycorrhizal fungi and fruitbodies

No ectomycorrhizal fruitbodies was observed in any disturbance stage in the three sites for three years of mushroom excursions (figure 2A). It was only in undisturbed ECM forest clumps that nearly 90 intact ECM fungal morphotypes (Photos 1 to 6) and more than 150 putative ECM fruitbodies (Photos 7 to 18) were identified. However, the consortia of native ECM fruitbodies differed among the four ECM forest clumps, in particular, *Amanita* fruiting bodies were nearly absent from *G. dewevrei* forest clumps conversely to other ECM forest clumps. Indigenous *Amanita* and *Russula* fruiting bodies were particularly abundant in "Ekop" forest clumps.

3.3. Arbuscular mycorrhizal inoculum in ectomycorrhizal forest clumps

In soil cores from ectomycorrhizal forest clumps, fractional arbuscular mycorrhizal colonization was almost always lower than 5%. Neither site and disturbance stage, nor the interaction were significant for the three forest stands (table 4). No colonization by AM fungi was observed in soil cores from neither forestry practices nor ECM forest clumps. Fractional colonization by ECM and AM fungi in *Afzelia* seedling roots was neither correlated for the range of disturbance stages of Ebom soils, nor for the three forest stands ($p > 0.1$ in both cases).

3.4. Effect of ectomycorrhizal inoculum on shoot dry mass

Shoot dry mass of *Tetraberlinia* seedlings was significantly affected by disturbance stage, site, and the interaction between both factors (table 5). Seedlings growing in soils from ECM forest clumps and late-successional forests outside clumps had largest dry mass, in soils from forestry practices the smallest mass was recorded (figure 3). Analysis of variance of shoot dry mass restricted to the three forest types yielded similar results. There was a significant low positive correlation between fractional ECM colonization and seedling dry weight ($r = 0.324$; $n = 63$; $p < 0.01$). However, for the three forested disturbance types, fractional ECM colonization was not correlated with seedling weight ($r = 0.175$, $n = 27$, $p > 0.1$). Shoot dry mass of *Afzelia* seedlings, grown in soils from the three forest types was significantly affected by site and by the site x disturbance stage

interactions, but not by disturbance stage (table 4). However, for the data set from Ebom, shoot dry mass was significantly affected by disturbance stage ($p < 0.001$). Seedlings grown in soils from fallow had the highest biomass, and seedlings grown in soils from forestry practices and from ECM forest clumps had the smallest biomass (figure 3). For the Ebom soils, fractional ECM colonization was significantly and positively correlated with seedling dry mass ($r = 0.596$, $n = 21$, $p < 0.01$). However, for the three forested disturbance stages, fractional ECM colonization was not correlated with seedling dry mass ($r = 0.163$, $n = 27$, $p > 0.1$).

Fractional arbuscular mycorrhizal colonization of *Vigna unguiculata* roots was not significantly correlated with seedling dry weight both for the Ebom soils and for the three forested disturbance types ($p > 0.1$). Most soil cores did not produce abundant AM fungal colonization. AM colonization was detected in 56% (54 out of 96) soil cores from ECM forest clumps. Sparse AM colonization varied with sites; it was very low to low in clumps in Ebimimbang and Ebom, and completely absent in Nyangong. No AM colonization was observed in soil cores taken 5 m and 10 m away from the stem base of *Azelia*, *Brachystegia*, and *Paraberlinia*, but AM colonization was observed in soils from *Tetraberlinia* and varied from 2.5 to 22.5%.

4. Discussion

4.1. Ectomycorrhizal forest clumps are the only refuge stands of ectomycorrhizal inoculum potential including ECM fruitbodies.

In humid forests of South Cameroon, the unique refuge stands of native ectomycorrhizal inoculum potentials are the five different types of ECM forest clumps, 1) “Ekop” oligo-dominants, 2) mixed “Ekop” and *Uapaca* oligo-dominants, 3) *Uapaca* monodominants, 4) *G. dewevrei* monodominants; and 5) *Microberlinia bisulcata* monodominants. The last ECM forest clumps occurred in Korup National Park, South-West Cameroon (Newbery et al., 1988). They are mutually associated with 25 tree species belonging to either Detarioidaeae or Uapacaceae (Newbery et al., 1988; Onguene et al., 2014, 2018). At least, 90 different ECM fungal morphotypes were recorded in ECM forest clumps with very low soil P availability. This high ECM fungal diversity might increase P uptake efficiencies

by ECM host tree species under harsh soil conditions. For the European beech (*Fagus sylvatica* L.), similar observations of ECM tree species striving in low fertile soil conditions were recently made (Köhler et al., 2018). At the continental and Sub-Saharan regional scales, tropical ECM ecosystems are highly diverse and vary widely in ECM plant and fungal abundance, diversity, composition and phylogenetic affinities (Newbery et al., 1988; Buyck et al., 1997; Rivière et al., 2007; Abdala et al., 2010; Tedersoo et al., 2014). Both ECM trees and fungi also exhibit strong turnover along altitudinal and soil fertility gradients, suggesting niche differentiation among taxa. ECM fungi are often more abundant and diverse in sites with nutrient-poor soils, suggesting that ECM associations can optimize plant nutrition and may contribute to the maintenance of tropical monodominant forests (Corrales et al., 2018). In this research area, four distinct ECM forest clumps were recorded showing strong development under very poor nutrient soils. In humid forest of South Cameroon, small to medium-sized forest clumps of *G. dewevrei* are the most common. Henceforth the regeneration niche is more likely to explain the widespread occurrence of “Islands” of ECM forest clumps within an “Ocean” of AM rainforests in humid forests of South Cameroon of the Congo Basin (Buyck et al., 1997; Newbery et al., 1997; Onguene, 2000).

4.2. Selective logging and shifting cultivation practices are no guarantee for ectomycorrhizal inoculum potentials.

Anthrogenic disturbances like selective logging and shifting cultivation practices are no guarantee for ECM inoculum potentials in tropical forestry and agriculture. Seedlings of both *Tetraberlinia* and *Azelia* were not colonized in soil cores from skid trails, woodlot parks, food farms and *Chromolaena* fallows, with the exception of *Gnetum* fallow's soils, for only *Tetraberlinia* seedlings. It is clear from these data that ECM fungal propagules of mature trees are crucial for ECM colonization of ECM host saplings and consequently the survival of ECM host tree seedlings (Onguene and Kuyper, 2002) as similarly observed in rainforests of Upper Guinea (Thoen and Decouso, 1989; Rivière et al., 2007). Deforestation and conversion of forest land to agricultural uses have resulted in the loss of vast areas of lowland rain forest in Southeast Asia (Ingleby et al., 2000)

and subsequent ECM biodiversity losses. It is most likely that lowland humid forests of South Cameroon run similar loss risks of ECM biodiversity following the coming decentralization and regionalization in Cameroon. Hence, future replanting programmes will be a priority in the agendas of local administrations in order to preserve the unique ECM biodiversity inoculum potentials and native ECM fruitbodies of rainforests of South Cameroon. Alexander et al, (1992), and Onguene and Kuyper, (2002) have shown that early colonization of naturally regenerating Detarioideae and Dipterocarp seedlings depends on mycelial connections made by the ECM fungi associated with adjacent mature trees. It has also been shown that ECM mycelial networks are particularly sensitive to disturbance (Read and Birch, 1988) and that forest clearance leads to rapid depletion of these sources of ECM inoculum in the soil (Brundrett, 1991). For three years of observations, neither ECM inoculum nor ECM fruitbodies were detected in soils of skid trails, woodlot parks, Chromolaena fallows and food farms. In fallow lands invaded by *Chromolaena odorata* weeds, only fruitbodies of *Scleroderma sinnamariensis* Mont. were often observed during the dry seasons. They were never observed in ECM forest clumps nor close to conspecific *Afzelia* adult trees in Ebom. However, other species of *Scleroderma* fungal strains were observed in ECM forest clumps, thereby suggesting tree fungal specificity in humid forests of South Cameroon.

4.3. Tropical ectomycorrhizal associations also depict fungal specificity depending on types of ectomycorrhizal forest clumps.

During ectomycorrhizal ontogeny, mutualistic associations do not randomly occur: both symbionts choose one or more associated microorganisms among a complex population of rhizospheric microorganisms. In general, the ECM symbiosis does not seem strictly specific. ECM fungi α diversity is a major factor contributing to root functioning under global change. In temperate forests, it has been hypothesized that plant specificity among ECM fungi would be common in a closed *Pinus* canopy forest conversely to early-successional forest (Culling et al., 2011). In this study, some strict affinities were observed under natural conditions viz. *Gnetum* spp and *S. sinnamariense*, *A. bipindensis* and native ECM fungi from the rhizosphere of conspecific *Afzelia* adult

trees. However, *Amanita* fungal species were nearly absent in *G. dewevrei* forest clumps conversely to “Ekop” and *Uapaca* forest clumps rich in indigenous *Amanita* and *Russula* fungal species in Cameroonian humid forests. In these forest ecosystems, the large number of ECM tree species occur uniquely in ECM forest clumps while a minority grow isolated among AM forests like *Afzelia bipindensis*, *Anthothoa* spp, *Berlinia bracteosa* (Onguene and Kuyper, 2001). This suggests the low fractional arbuscular mycorrhizal reported in this work in *Afzelia* seedling roots. These results are also in agreement with those of Djotan et al. 2020 who reported AMF in roots of *Afzelia africana*, *Entada africana*, and *Pterocarpus erinaceus* in Benin, using morphological and molecular analyses. Consortia of indigenous ECM fruitbodies of *G. dewevrei* differed from those of “Ekop” and *Uapaca* forest clumps, depicting really fungal specificity in tropical rainforests of South Cameroon. *G. dewevrei* forest clumps strikingly lacked *Amanita* fungal species. In temperate and boreal forests, high affinities have also been noticed between many *Betulaceae* and some *Suillus* and *Leccinum* genera, or some *Lactarorussulaceae*, or *Hygrophoraceae* (Guillot, 1997). In humid forests of South Cameroon, fungal specificity appears dependent on clumpiness of host ECM tree species. This information is crucial for ECM tree regeneration programmes. However, more research is still needed to elucidate the diversity patterns of native ECM fungi and trees in humid forests of the Congo Basin, a hotspot biodiversity, and to clarify the roles of ECM symbioses on ECM tree regeneration, nutrient and carbon cycling, and climate change.

4.4. In tropical acid soils of rainforests, ectomycorrhizal inoculum exerts a negative feedback on arbuscular mycorrhizal inoculum.

A basic tenet in ecology is that negative feedbacks on abundance play a crucial role in the coexistence of species within guilds (Bever, 2000). Basal area of ECM *Ceasalp* tree species varied from 80% to 100% in ECM forest clumps (Newbery et al. 1997; Onguene and Kuyper, 2001). In shade house experiments with intact soil cores from ECM forest clumps close to four different ECM tree species, AM root colonization of *V. unguiculata*, a highly AM mycorrhizal plant, was always very low to null. Hence, positive phylogenetic plant-soil feedbacks for ECM tree species in low fertile soils are coupled with negative feedbacks for AM tree

and plant species, thereby, explaining clumpiness of ECM tree species in humid forests. Family dominance has also been noted for Dipterocarpaceae in South-East Asia (Whitmore, 1984; Richards, 1996). Differences in plant-soil feedbacks may stem from variation among AM and ECM fungi in host specificity dispersal ability, enzymatic capacities and interactions between soil pathogens and nutrients (Bruns and Shefferson, 2004; Morris et al., 2007; Hoeksema et al., 2010). Thus, while AM and ECM symbioses are both expected to be more beneficial to host trees and plants in low fertile soils that prevail in the Tropics, these benefits should be greater for ECM-hosting tree and liana species because ECM fungi have greater capacity to access nutrients bound in plant litter of nutrient-depleted soils (Read and Perez-Moreno, 2000), since they evolved from saprotrophic ancestor. ECM associations show more positive feedbacks than AM ones in particular forest ecosystems. Therefore, positive feedbacks shape monodominance while negative feedbacks determine diversity in tropical rainforests.

4.5. Ectomycorrhizal inoculum differently influences seedling growth depending on phylogenetics.

Numerous examples depict that ECM inoculation improves growth of ECM seedlings in nurseries and in the fields (Smith and Read, 2008). Different fungal associations do not provide the same benefit to the host. A pronounced variability in response depending on the nature of the fungal-plant association has been observed (Chalot et al., 1988; Guehl et al. 1990). Yet, correlations between ECM colonization and seedling growth of this study were contrasted. For the clumping ECM *Tetraberlinia* seedlings, there was no correlation conversely to ECM *Afzelia* non-clumping. Considerable data on ECM fungi and their effects on plant growth and nutrient uptake have been purported under various ecological conditions (Castellano and Molina, 1989; Roldan et al. 1996; Garbaye and Churin 1997). Thus, for successful tree regeneration, it is essential for controlled mycorrhization in nurseries that tree seedlings be inoculated with with ECM fungi that are ecologically adapted to the tree species and the replanting sites. In this study, it seems clear that reforestation with *Tetraberlinia* seedlings will require fine soil and root samples from ECM clumps forests while for *Afzelia* seedlings, inoculum will be collected in the vicinity

of conspecific *Afzelia* adult trees. It is recommended that adult *Afzelia* trees which occur within secondary forests and fallow lands close to villages be protected as sources of ECM inoculum.

Conclusion

The results of this study show that in humid forests of South Cameroon, ectomycorrhizal inoculum potentials including native ECM fruitbodies are found only in ECM forest clumps. Selective logging and shifting cultivation practices are no guarantee for ECM inoculum potentials since both significantly eliminate or reduce ECMIP. Tropical ECM associations equally depict fungal specificity depending on types of ECM forest clumps with *Amanita* fruiting bodies almost absent from *G. dewevrei* clumps. In tropical acid soils of rainforests, ECM inoculum exerts a negative feedback on AM inoculum. If most ECM tree species behave similarly to *Tetraberlinia*, conservation of forest patches and clumps where these tree species occur is urgently needed, including their regeneration requirements.

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