SPATIAL STRUCTURE OF ECTOMYCORRHIZAL TREES IN WOODED SAVANNAS OF GUINEO-SUDANIAN ECOZONE IN WEST AFRICA

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The Guineo-Sudanian and Sudanian zones are home to predominantly ectomycorrhizal (EcM) plant communities dominated by members of the families Fabaceae (subfamily Ceasalpinioidae), Phyllanthaceae and Dipterocarpaceae. Numerous studies have shown that the aggregation of EcM trees is facilitated in part by the shared mycelial networks of EcM fungi. Mycelial networks involving mature trees would thus directly affect the survival of the seedlings of EcM trees and, thereby, the spatial structuring of the trees. In this study, we investigated the structure and spatial interactions of three vegetation types dominated by different EcM trees, namely, *Isoberlinia doka*, *I. tomentosa* and *Uapaca togoensis*. Three 50 m × 50 m plots were installed for each vegetation type. All EcM trees present in each plot were counted for estimation of density. Ripley's second order function K was used to estimate the spatial structure of EcMs trees. Spatial distribution of trees differed between species. Repulsion occurred at scales of 1 to 5 m between the different EcM trees species. By sharing nutrient through mycelial network, repulsion mechanisms observed during interaction between plants should have been cancelled but this was not observed in this study.

Keywords: Spatial distribution, facilitation, repulsion, Sudanian woodland

INTRODUCTION

West Africa is phytogeographically divided into three major domains, which are Guinean Regional Endemism Centre (GRE), Sudanian Regional Endemism Centre (CRE) and Guineo-Sudanian transitional zone (GSZ). Whilst the GRE covers large areas of southern and costal parts of West Africa, CRE is a narrow band stretching from Mali to Uganda between the 9° to 11° N, along an annual rainfall gradient from 700 to 1200 mm. CRE covers an area of 3.7 million km². GSZ is located between the GRE and the CRE, approximately between latitude 7° and 9° N. In contrast to GRE, both CRE and the GSZ harbour caesalpinioid-dominated woodlands and their subsequent degraded features. Woodlands of CRE and the GSZ have very simple floristic composition and is characterised by canopy trees from Fabaceae (subfamily Caesalpinioideae), Phyllanthaceae and Dipterocarpaceae (Bâ et al. 2010). The leguminous forests which once occupied considerable areas under the GSZ climate have shifted into woodlands or woody savannahs, and presently are represented by forests of other trees, including *Isoberlinia doka*, *I. tomentosa*, *Burkea africana* and *Uapaca* spp. (Bâ et al. 2011). Structurally speaking, they are mixed, woody and grassy forest types of dominant height varying between 12 and 18 m and whose canopy cover generally exceeds 50%.

The pronounced predominance of one or two species over large areas of woodland is an essential characteristic of the CRE and GSZ. The dominant species are usually *Isoberlinia* legumes, *Uapaca* spp. and more rarely the dipterocarp *Monotes kerstingii* (Bâ et al. 2011). One remarkable characteristic of these species is their common ectomycorrhizal (EcM) association with fungi (Yorou et al. 2014), an obligate symbiosis between both partners to promote plant growth and survival (Smith & Read 2008)

Factors such as water distribution, facilitation mechanism, fire and grazing, tree clustering, lack of exogenous disturbance, slow decomposition rate of leaf litter, soils and shade tolerance are the basis of this dominance and distribution of Caesalpinaceae and Phyllantaceae in CRE and GSZ woodland (Groen et al. 2008). One key factor responsible for the monodominance and distribution of Caesalpinaceae (mostly *Isoberlinia* spp.), Phyllantaceae (*Uapaca* spp.) and Dipterocarpaceae (*Monotes kerstingii*) in CRE and GSZ, is the belowground mycelial network of mycorrhizal fungi that putatively promote the establishment of monodominant trees (Mc Guire 2007, McGuire et al. 2008). EcM and dual mycorrhizal (i.e. ecto- and arbuscular mycorrhizal) associations with trees can increase nutrient supplies via a more efficient exploitation of larger volumes of soils (Agerer 2001) or through the direct decomposition of leaf litter. As many monodominant trees have such associations with telluric fungi, it has been hypothesised that these associations constitutes a competitive advantage for the host trees (McGuire et al. 2008), especially as EcM networks could enhance seedling survivorship near parent trees (McGuire 2007). Nevertheless, not all species that form monodominant stands are EcM. Also, many EcM-associated tree species that are not known to form monodominant stands are present in many mixed tropical forests. One example is *Aldina insignis* in Central Africa, which does not outcompete other species over large areas (Peh et al. 2011). Thus, EcM associations are not a prerequisite for a species be monodominant. However, whenever present, EcM symbiosis provides sufficient explanation for monodominance (Peh et al. 2011).

Belowground mycorrhizal networks are composed of continuous fungal mycelia linking two or more plants of the same or different species (Gorzelak et al. 2015). These mycorrhizal networks provide pathways for reciprocal transfer of carbon (C) received from roots of host plant and nutrients taken up from the soil (Leake et al. 2004). They also transfer nutrients and C between plants interlinked by the same mycorrhizal network (Simard et al. 1997). Due to their direct impact on nutrition strategy and establishment of EcM forest trees, the EcM symbiosis is predicted to play an important role in density of trees, spatial distribution and forest regeneration. Thus, in the vegetation dominated by EcM plants, the repulsion mechanisms observed during interaction between certain plants (high competition for nutrients, allelopathy phenomenon, etc.) should be cancelled by interconnection and sharing of nutrients between different plants of the same and different species across the mycelial network.

In this paper, which is part of a larger study on the mutual influence of EcM fungi on their host forests in the face of microclimate variabilities, we analysed the existing spatial relationship between individuals of the same and different EcM trees using Ripley's K function. Assessing the current spatial structure of EcM trees would contribute to better understanding of the role of EcM networks in trees and forest regeneration in natural areas. This paper reports about the present representativeness and structure of EcM trees in the real environment.

MATERIALS AND METHODS

Study area

The present study was conducted in the Ouémé Supérieur Forest Reserve located between 9°11' and 9°47' N and 1°58' and 2°28' E (Figure 1). The study area has a rainy season from May till October which strongly contrasts with the long and severe dry season in October till April. The Ouémé Supérieur Forest Reserve is located in GSZ. The vegetation mosaic comprises woodland, wooded savannah, shrub savannah and gallery forests. The vegetation type in GSZ are dominated by members of Caesalpinioideae, Dipterocarpaceae, Phyllanthaceae and, Papilionoideae that are associated with high diversity of ectomycorrhizal fungi (Yorou et al. 2014, Bâ et al. 2011).

Sampling techniques and data collection

Three sites were investigated (Figure 1), and three permanent plots of 50 m × 50 m were installed at each site. Each plot was dominated by a different EcM forest tree: *I. doka* (P1), *I. tomentosa* (P2), *Uapaca togoensis* or *M. kerstingii* (P3). A complete survey of the trees was undertaken at each plot, and the identified EcM trees were recorded, numbered and mapped according to their geographic distance (X, Y) in meters from the north-western corner of the plot. Diameters > 10 cm at 1.3 m height (DBH) of EcM trees
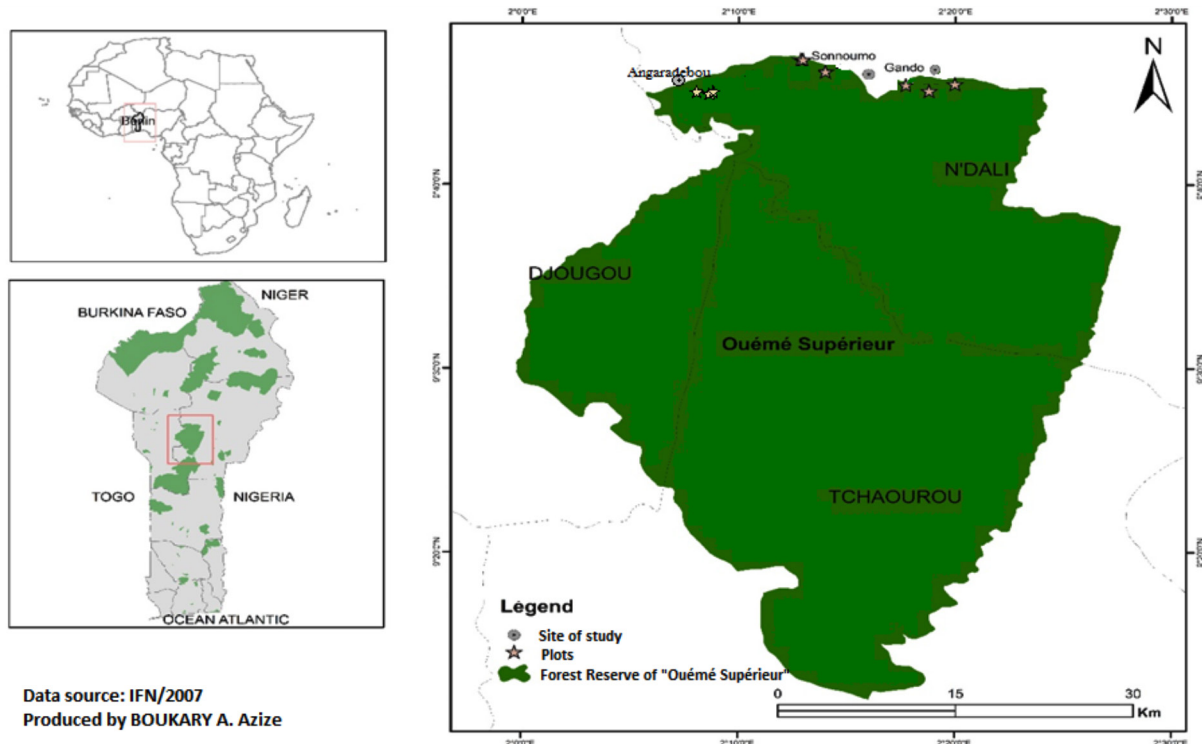
Figure 1   Ouémé Supérieur Forest Reserve (right) in Benin, with the study sites

were recorded with their circumference. Saplings (diameter < 10 cm at 4 m height) were only mapped without recording their circumference.

Data analysis

Structural parameters

Density of EcM trees in the stand (N), is the average number of trees per EcM species per plot, expressed as stems per hectare:

$$N = n/s$$

where n = overall number of EcM trees in the plot and s = area of the plot = 0.25 ha. G, basal area of the stand, is the sum of the cross-sectional areas at 1.3 m above ground of EcM tree on a plot and expressed in $m^2 ha^{-1}$:

$$G = \frac{\pi}{40000s}\left(\sum_{i=1}^{n} d_i^2\right)$$

where d_i = diameter (in cm) of the ith EcM tree of the plot.

Spatial analysis model

The analytical technique used in this work was Ripley's K(r) function (Ripley 1977). This technique makes it possible to analyse the spatial structure at different distance intervals and to detect mixed processes (for example, association at short distances and repulsion at long distances) (Fajardo et al. 2006). It is defined as the ratio of the mathematical expectation of the number of points (trees) located at a distance inferior to r from an arbitrary point, to the density of the species. To estimate this function, we used the usual estimator of expectation:

$$K(r) = \frac{Ax\sum_{j=i}^{N}\sum_{j=i}^{N} nij}{N^2}$$

where r = distance (m), A = area under consideration (m^2), N = total number of trees, and n_{ij} = 1 if the distance between tree i and tree j was less than r, otherwise n_{ij} = 0. In this approach, the trees were represented by points located at the projection on the ground of the centre of their trunk. The method has the advantage of expressing spatial distribution at different scales.

For interpretation purposes, as recommended by Collinet (1997), we used a linearised estimator of K(r) introduced by Besag (1977). The modified form of K(r) was:

$$L(r) = \sqrt{\frac{K(r)}{\pi}}$$

For any distribution, the value of L(r) gave an indication of the point seeding form at a scale of r. To test the significance of the L(r) function, 1000 Monte Carlo simulations (Metropolis et al. 1953) were performed (Figure 2). For the production of univariate graphs, we considered only the dimensions of representativeness (r) of each species in each plot by site. The point pattern dataset function of the spatstat package 45 in R version 3.4.0 (2017) was used to perform the analysis.

Calculation of intertypes

To study the interactions between species, the analysis focused on three EcM dominant species identified by site. The test of the null hypothesis of independence distribution between groups of dominant species by plot and site was done with Ripley's intertype estimator $K_{12}(r)$ whose modified function $L_{12}(r)$ was (Diggle 1983):

$$L_{12}(r) = \sqrt{\frac{K_{12}(r)}{\pi}} - r$$

R and K have the same meaning as explained above. The $L_{12}(r)$ function quantified the degree and type of spatial association between size classes and between species groups. The analysis of relationship between two types of points was analysed using the Diggle (1983) intertype method. This method is similar to the previously presented Ripley method. When the value of $L_{12}(r)$ was different from zero at a distance r, the hypothesis of independence of the groups of species (called marks) was rejected. Statistical significance of this difference was tested by Monte Carlo simulations. Each simulation consisted of randomly assigning new coordinates to trees while leaving unchanged those of other trees (Goreaud & Pelissier 2003). Attraction or repulsion between two trees occurred when $L_{12}(r)$ was above or below the confidence interval respectively. The point pattern dataset function of the spatstat package was used for this purpose (Baddeley et al. 2013).

RESULTS

Tree density, distribution and variation in basal area within the plots and between vegetation types

From the location of EcM trees within the plots, we observed high density of EcM trees in different plots at site 1 compared with sites 2 and 3 (Table 1). The highest number of trees was found in the plot dominated by *I. doka* at site 1, while the plots dominated by *I. doka* and *U. togoensis* at site 3 had the lowest EcM tree densities. Basal area of EcM trees varied greatly between the plots and the sites from 9.86 m² ha⁻¹ in plot 2 at site 1 to 4.77 m² ha⁻¹ in plot 3 at the site 3 (Table 1).
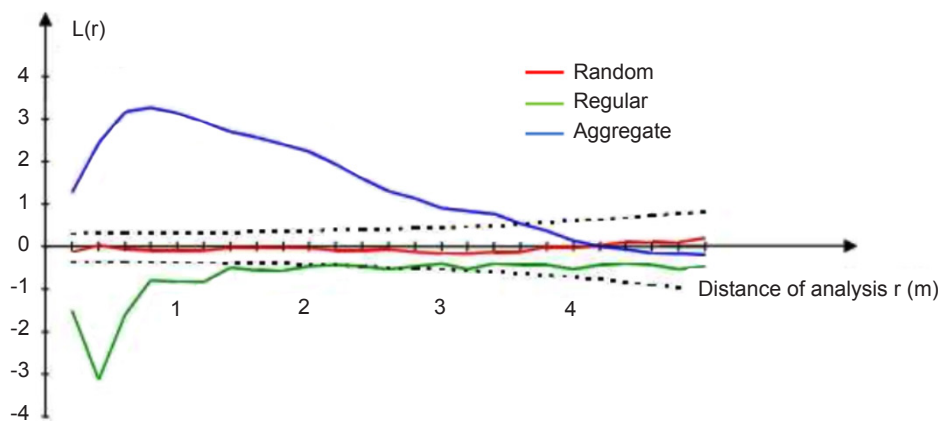

Figure 2   Example Ripley curves for regular, random and aggregated distribution

Table 1   Densitiy and basal area of EcM trees by site and by plot

Site	Species	Density (number 3600 m^{-2})			Basal area (m^2 ha^{-1})		
		Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
Site 1	*Isoberlinia doka*	51	8	25	8.46	9.86	6.37
	Isoberlinia tomentosa	1	33	4			
	Monotes kerstingii	15	16	44			
	Uapaca togoensis	41	-	22			
Site 2	*Isoberlinia doka*	91	-	17	8.40	6.39	5.40
	Isoberlinia tomentosa	-	57	-			
	Monotes kerstingii	3	2	-			
	Uapaca togoensis	2	1	85			
Site 3	*Isoberlinia doka*	46	13	-	8.23	7.20	4.77
	Isoberlinia tomentosa	-	17	-			
	Monotes kerstingii	1	-	6			
	Uapaca togoensis	4	-	74			

Spatial distribution of trees and their interdependencies

For site 1, analyses showed that the L(r) – r curves calculated for all species remained outside the confidence envelopes from 0 to 10 m radius, and thereafter remained close but within the confidence envelopes (Figure 3a). This indicated heterogeneity in the spatial distribution of trees within the study area. For site 2, the curve remained within the confidence interval, regardless of distance and confirmed the homogeneity of the trees distribution and their random character (Figure 3b). The curve for site 3 remained within the confidence interval and showed the homogeneity and random distribution of trees at this site (Figure 3c).

Intraspecific structures of each species within the plots and between the sites

Isoberlinia doka had regular distribution over a 1 m range (Figure 4a) in plot 1 of site 1. Beyond the 1 m radius, *I. doka* showed random distribution. *Uapaca togoensis* trees were distributed in aggregates from 2 to 12 m radius. *Monotes kerstingii* had regular distribution at 1.5 m range and random distribution ≥ 1.5 m radius. *Isoberlinia tomentosa* in plot 2 at site 1 showed regular distribution for r < 1 m and random distribution at greater distances while distribution of *M. kerstingii* was aggregative for r < 2.5 m and random at greater distances (Figure 4b). In plot 3 of site 1 (Figure 4c), *M. kerstingii* had regular distribution for r < 1 m and random distribution at greater distances. In the same habitat, *U. togoensis* showed aggregative

distribution for r < 6 m and random distribution at greater distances.

The distribution of *I. doka* in plot 1 at site 2, (Figure 5 a) showed regular distribution up to 0.5 m range and random distribution outside this range. The population of *I. tomentosa* in plot 2 at the same site had random distribution (Figure 5 b). In plot 3, distribution of *U. togoensis* was aggregative (Figure 5 c) while *I. doka* had aggregative distribution for r < 0.5 m and random distribution at greater distances.

At site 3, *I. doka* showed random distribution in plot 1 (Figure 6a). Regular distribution was observed for *I. doka* and *I. tomentosa* for r < 1 m and r < 2 m respectively and random distribution for greater distances in plot 2 (Figure 6b). *Uapaca togoensis* displayed aggregated distribution (Figure 6c) in plot 3. Table 2 summarises the distribution of all EcM trees at different sites and plots.

Interspecific structures of dominant EcM tree species

Distribution parameters between EcM tree species taken two by two per plot at each site were studied using intertype estimator. At all study sites, EcM trees species maintained distancing relationship (i.e. repulsive interaction between individuals of two different species). At site 1, repulsion in plot 1 between *M. kerstingii* and *U. togoensis* was about 1 m and that between *I. doka* and *M. kestingii* was about 2 m. Repulsion between *I. doka* and *U. togoensis* was 1 m at site 1 but it was 0.5 m at site 2 in plot 3. Repulsion between *I. tomentosa* and *M. kerstingii* at site 1 in plot 2 was 1.5 m while that between *U. togoensis*
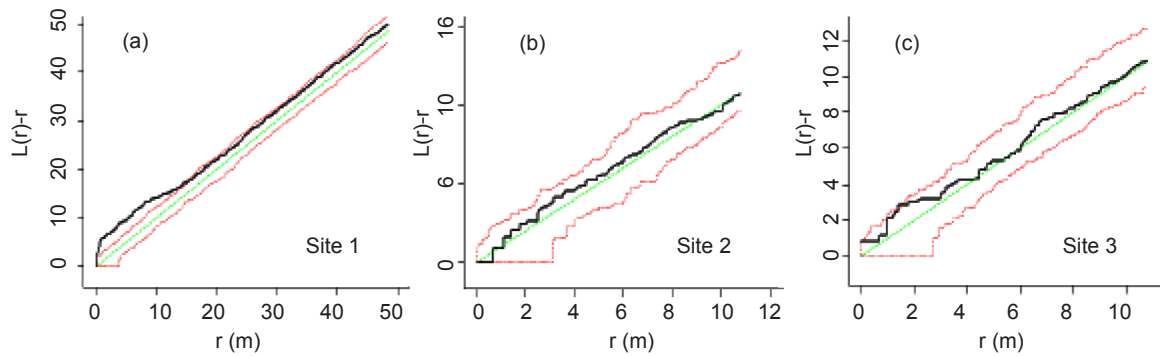
Figure 3   L(r) curves (black line) for spatial distribution of trees of sites 1, 2 and 3 and their corresponding confidence envelopes (dotted line)
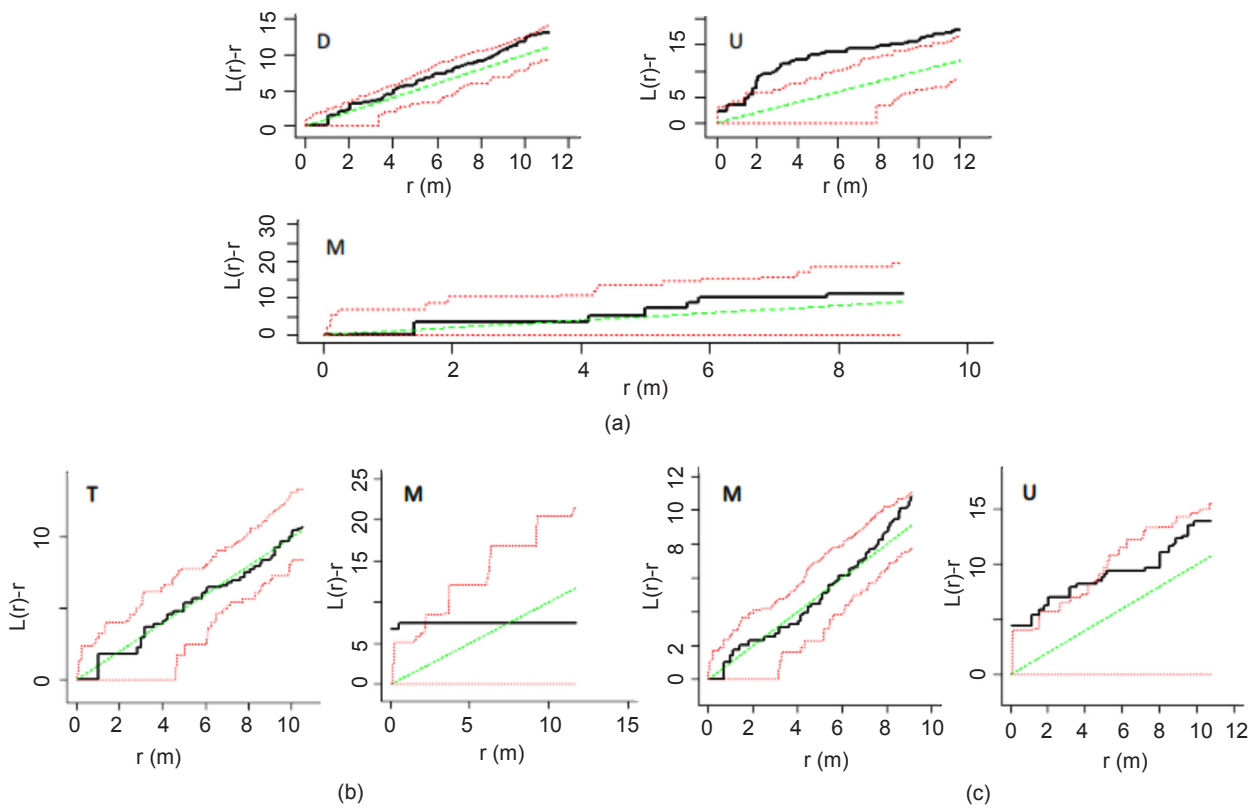

Figure 4   Spatial distribution of *Isoberlinia doka* (D), *I. tomentosa* (T), *Monotes kerstingii* (M) and *Uapaca togoensis* (U) in plots (a) 1, (b) 2 and (c) 3 at site 1 with Ripley's function; L(r) curves (black line) and confidence envelopes (dotted line) are based on the distance r

and *M. kestingii* at site 1, plot 3 was 1 m. Repulsion was more pronounced between *I. doka* and *I. tomentosa* at site 3, plot 2, i.e. about 4.5 m. Table 3 summarises the interspecific structures of dominant EcM trees.

DISCUSSION

The results of our study confirmed the co-existence of the four EcM species, i.e. *M. kerstingii*, *U. togoensis* with *I. doka* and *I. tomentosa*. *Monotes kerstingii*, the only Dipterocarpaceae in West Africa, occurs in association with mixed stands of *Isoberlinia* spp. (Bâ et al. 2010). *Uapaca togoensis* has also been frequently identified in woodlands and savannahs dominated by *Isoberlinia* spp. *Isoberlinia* spp. woodland is one of the two major plant communities (the other being *Vitellaria paradoxa* woodland) in West Africa (Downing 2010). *Isoberlinia* stands are young,

Table 2 Distribution of EcM trees at different sites and plots of this study

Species	Site 1			Site 2			Site 3		
	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
D	Regular at 1 m	-	-	Regular at 0.5 m	-	Aggregate at 0.5 m	Random	Regular at 1 m	-
M	Regular at 1.5 m	Aggregate at 2.5 m	Regular at 0.75 m	-	-	-	-	-	-
U	Aggregate	-	Aggregate at 5 m	-	-	Aggregate at 3 m et > 10 m	-	-	Aggregate
T	-	Regular at 1 m	-	-	Random	-	-	Regular at 2 m	-

D = *Isoberlinia doka,* M =*Monotes kerstingii,* U = *Uapaca togoensis* and T = *Isoberlinia tomentosa*

Table 3 Mode of distribution of EcM species taken two by two per plot at each study site by radius reach

Species	Site 1			Site 2			Site 3		
	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3	Plot 1	Plot 2	Plot 3
D:M	Repulsive at 1.8 m	-	-	-	-	Repulsive at 0.5 m	-	-	-
D:U	Repulsive at 1.5 m	-	-	-	-	-	-	-	-
D:T	-	-	-	-	-	-	-	Repulsive at 1.8 m	Repulsive at 4.5 m
M:U	Repulsive at 1.5 m	-	Repulsive at 1.8 m	-	-	-	-	-	-
M:T	-	Repulsive at 1.8 m	-	-	-	-	-	-	-

D = *Isoberlinia doka,* M =*Monotes kerstingii,* U = *Uapaca togoensis* and T = *Isoberlinia tomentosa*

with individuals aged 30 to 40 years, indicating a very dynamic system. This is highlighted in this study by the low basal area of the trees, varying from 4.77 to 9.86 m²ha⁻¹. The predominance of *U. togoensis* and *M. kerstingii* in *Isoberlinia*-dominated stands could be explained by two essential factors, namely, the canopy effect on the reduction of fire frequency (Hennenberg et al. 2005) and the mycelial network effect (Mcguire 2007). *Isoberlinia* species are good early coloniser as it can reproduce from root suckers (in secondary succession) and it grows quickly (Fonton et al. 2012). Once the *Isoberlinia* spp. get large enough, their canopy are able to reduce the presence of grass in the undergrowth, which in turn reduces the fuel available for burning while providing a cooler, wetter environment that can withstand fire (Nangendo et al. 2005). This environment will encourage the growth of other woodland understorey species such as *U. togoensis, M. kerstingii, Gardenia* spp., *Pteleopsis*

suberosa and *Piliostigma thonningii* (Akpado 2000). The predominance of EcM species, notably *U. togoensis* and *M. kerstingii,* in *Isoberlinia*-dominated stands could also be explained by the positive effect of the mycelial network on the survival and growth of EcM seedlings. It has been reported that almost 100% of the surviving seedlings of EcM trees planted on EcM mycelium-rich substrates, were all colonised by EcM fungi (Mcguire 2007, Diédhiou et al. 2010). Thus, it has been suggested that the connection of seedlings to the existing mycorrhizal network is an important advantage. As EcM symbiosis in general is not species-specific, the EcM mycorrhizal network will connect and facilitate the establishment of any EcM tree species. This may explain the presence of *U. togoensis* and *M. kerstingii* in *Isoberlinia*-dominated stands.

This study generally showed random distribution of EcM trees with aggregates varying in radius from 1 to 10 m. The aggregate
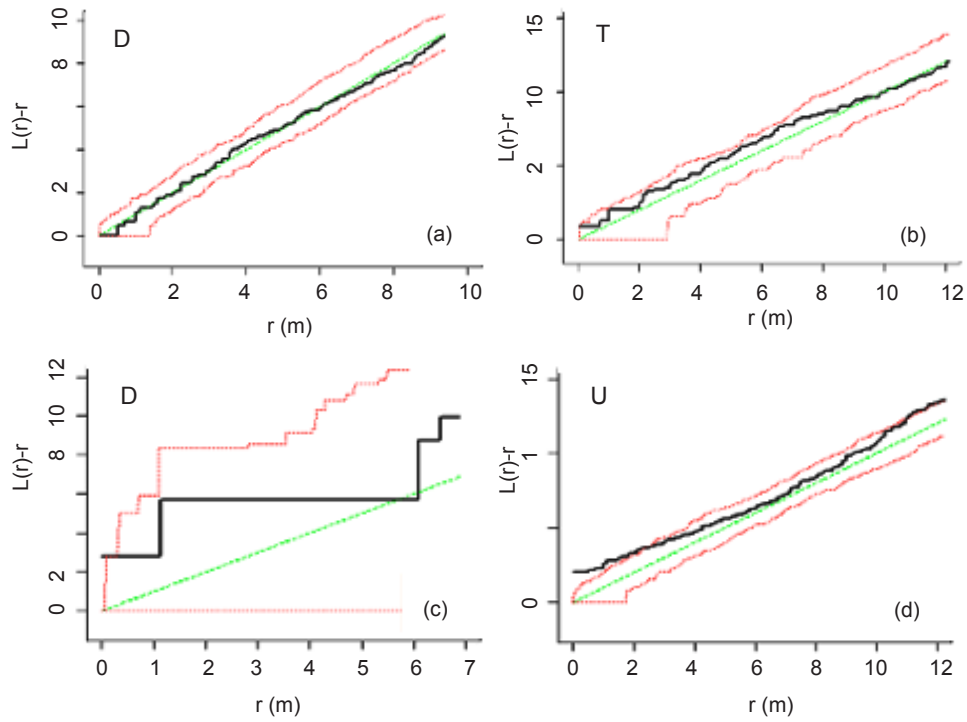
Figure 5   Spatial distribution of EcM trees at site 2; (a) *Isoberlinia doka* (D) in plot 1, (b) *I. tomentosa* (T) in plot 2 and (c) *I. doka* (D) and (d) *Uapaca togoensis* (U) in plot 3; L(r) curves (black line) and confidence envelopes (dotted line) are based on the distance r
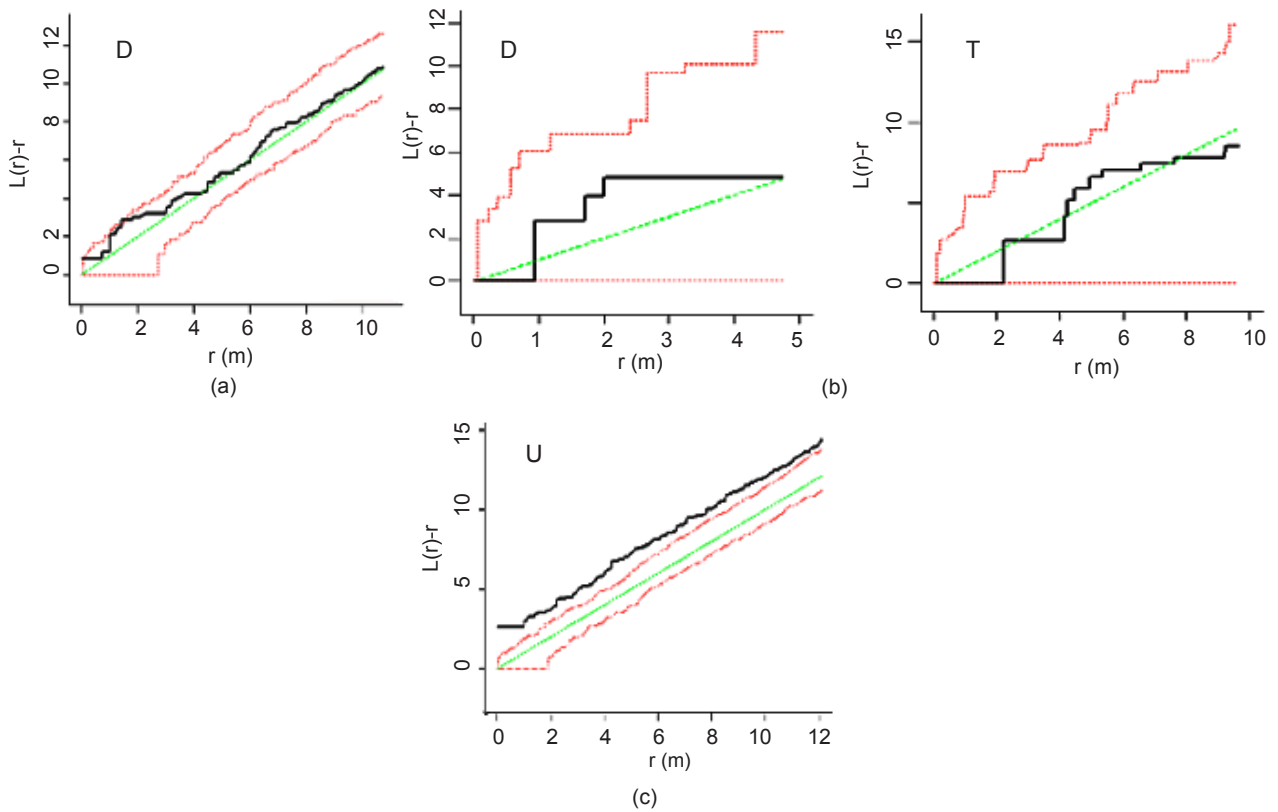

Figure 6   Spatial distribution of EcM trees at site 3; (a) *Isoberlinia doka* (D) in plot 1, (b) *I. doka* (D) and *I. tomentosa* (T) in plot 2 and (c) *Uapaca togoensis* (U) in plot 3

distribution of trees in CRE and GSZ ecozones is limited to small patches (Fonton et al. 2012). *Isoberlinia doka*, *M. kerstingii* and especially *U. togoensis* had aggregate distribution, as shown by Fonton et al. (2012). Similarly, the authors observed the stands of *M. kerstingii* in small aggregates in ecologically similar area in northern Benin. The aggregate distribution of *U. togoensis* induced greater diversity of EcM fungi (De Kesel et al. 2002) than under more disseminated species.

The distribution of trees in relation to each other showed a distancing relationship, which was much more pronounced between *I. doka* and *I. tomentosa*. Numerous studies supported the distancing relationship of native CRE and GSZ forest trees. For example, the distribution of *Parkia biglobosa* and *Vitellaria paradoxa*, *Vitex doniana*, *Anogeissus leiocarpa* and *Tectona grandis* are characterised by a repulsion process of about 1 to 10 m, meaning that the probability of finding the other tree species is lower within 1–10 m from the first tree species (Dotchamou et al. 2016). The repulsion process has been attributed to dissemination strategy of the trees (Fonton et al. 2012), and also the allelopathy phenomenon (Dale 1999) and morphology of the trees (Dotchamou et al. 2016). Nevertheless, EcM symbiosis could strongly affect the distribution of forest trees in their natural environment. The extent of fungal mycelium in the soil is large and the mutualisms between fungal species and host plants are usually diffuse, enabling the formation of mycorrhizal network (Gorzelak et al.2015). Mycorrhizal networks can influence the physiology (Wu et al. 2001), growth (Teste et al. 2010) and defense chemistry (Song et al. 2010) of plants. Ectomycorrhizal saplings that are connected via mycorrhizal network can rapidly modify their behaviour in response to fungal colonisation and interplant biochemical communication (Gorzelak et al. 2015). Mycorrhizal networks can influence sapling establishment and enhance seedlings survival (Nara 2006, Teste et al. 2008). If EcM networks enhance seedling survival, it could be predicted that a positive dependent distance of seedling survival will be observed in these systems. This prediction was based on the assumption that seedlings survived best near to parent trees, where they would have increased access to a common EcM network. Over time, this positive distance-dependence will maintain a low diversity, monodominant forest by promoting conspecific aggregation of EcM trees (McGuire 2007). However, it was reported that survival rates of EcM seedlings were better (up to 100 %) when seedlings were located further away (2.5 to 5 m) from the adult trees (Teste et al. 2008). On the contrary, Diédhiou et al. (2010) suggested a net positive impact for seedling established close to adult trees. Seedlings can be favoured by adult trees through the presence of the mycelial network, regardless of the distance between them (Mcguire 2007). The results of these past studies explained the distance relation between adult EcM trees and seedlings whereby without disturbance of the habitats, we could observe the same distribution between adult trees.

In the present study, it is premature to conclude how different individuals of the same or different tree species can benefit from the mycorrhizal network in such a way as to lead to a repulsive distribution. Our results could be from the recurrent debate whether EcM trees share the same or different EcM fungi. At the same time, the putative impact of mycorrhizal network on the present distribution of forest trees remains open. Long-term (4–5 years) monitoring of fungal communities, as well as the combined molecular typing methods and application of stable isotopes seems necessary to unravel the complexity of EcM community and its potential impact on spatial structure of EcM trees in CRE and GSZ ecozones.

CONCLUSIONS

This study has shown that spatial distribution of ectomycorrhizal trees in adulthood is essentially aggregative within the same species but repulsive between species. These results seemed odd especially since the transfer of nutrients through the mycelial network annihilated the cause of repulsion observed between different species in the Sudanian zone. In order to take into account the repulsive behaviour in enrichment processes based on valuable species studied in the Sudanese region, we suggest the adoption of minimum spacing of 1 to 2 m between trees of the same species (except *U. togoensis*) and 1 to 4.5 m between different species in the wooded areas of the Sudanese zone. However, early mortality rates and poor growth of the species concerned suggest that these spacings may not be optimal.

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