Journal of Applied Biosciences 180: 18851– 18866
ISSN 1997-5902

Influence of toposequence and Marantaceae cover on the spatial distribution of *Guarea cedrata* (A. Chev.) Pellegr. and *Guarea thompsonii* Sprague & Hutch. in the central basin forests around Kisangani (Tshopo, DR Congo)

Roger KATUSI LOMALISA[1], Marie FUNDIKO CAKUPEWA[2,3], Hyppolyte NSHIMBA SEYA WA MALALE[1] , Jean De Dieu MANGAMBU MOKOSO[3]*

[1] Laboratoire d'Écologie et Gestion de la Biodiversité Végétale (LEGEBIV), Département d'Écologie et Gestion des Ressources Végétales, Faculté des Sciences, Université de Kisangani, R.D. Congo

[2] Department of Environmental Sciences, Faculty of Sciences, University of Cinquantenaire of Lwiro, South-Kivu, the Democratic Republic of the Congo.

[3] Laboratory of Plant Systematics, Biodiversity and Ecosystem Management (LSVBME), Department of Biology, Faculty of Science, Official University, Bukavu/ RD Congo.

*Corresponding author: mangambujd@gmail.com , mangambu2000@yahoo.fr

Submitted on 24th October 2022. Published online at www.m.elewa.org/journals/ on 31st December 2022
https://doi.org/10.35759/JABs.180.6

ABSTRACT

A study on the influence of toposequence and Marantaceae on the distribution of two species of the genus *Guarea* was carried out in the forest massif around Kisangani, in the Tshopo province, in DR Congo.

Objective: The general objective of this study is to characterize the spatial distribution of individuals of two *Guarea* species in relation to toposequence and Marantaceae.

Methodology and results: For this study, two sites of 200 ha each were installed, one in the Yangambi Biosphere Reserve between 0° 38' and 1° 10' N, 24° 16' and 25° 08' E, and the other in the Yoko Forest Reserve between 0° 15' and 0° 20' N, 25° 14' and 25° 20' E. Within two devices, all individuals of two *Guarea* species were measured at 1.30 m above the ground and positioned by x, and y coordinates. After the inventory and data analysis, the population density of the two species was higher in Yangambi than in Yoko and the same was true for basal area values. The spatial distribution of individuals of two species is aggregated in Yoko. While the distribution is significantly random for *G. cedrata, it is* weakly aggregated for *G. thompsonii* in Yangambi.

Conclusion and applications of results: This heterogeneous distribution of two species can be related to the topography of the land as well as to the presence and/or absence of Marantaceae. As for the soil texture, both reserves have sandy-clay soils, characteristic of the soils of the forest massifs of the Kisangani region and its surroundings.

Keywords: Spatial distribution, Yangambi, Yoko, DR Congo

INTRODUCTION

In tropical rainforests, soil succession resulting from topography influences the spatial distribution of plant species. The clustering of plant species in a habitat, especially due to soil types and topography, is relatively well studied (Boyemba, 2011; Katembo, 2020; Katusi, 2015). These studies have shown that plant species establish themselves according to their preference which sometimes relates to soil texture (sandy or clay soils) (Anderson, 1981; Fine *et al*., 2010; De Assis and Wittmann, 2011; Wittmann *et al.*, 2013; Fortunel *et al*., 2014; Katusi, 2015), affinity to soil nutrients (Condit *et al.*, 2013) as well as to the particularity of the habitat (Harms *et al*., 2001; Valencia *et al*., 2004; Chuyong *et al*., 2011). Hence, it has been hypothesised that in tropical rainforests, soil variables differentiate plant groups such as monodominant forests (Hart *et al*., 1989; Sabongo, 2015) that prefer low-nutrient soils in contrast to mixed forests that prefer high-nutrient soils (Richards, 1996). There are contrasting results for this hypothesis (Katembo, 2020); however, the dynamics of organic matter being significant between these two forest types (Lokonda *et al*., 2018) can even occupy more particular environmental conditions such as plateaus, slopes, flooded or non-flooded lowlands (Letouzey, 1983; Hart, 1990; Barbier *et al.*, 2017). Whatever the edaphic conditions, structural parameters (Prader, 2008; Pappoe *et al.*, 2010, Pereira Junior *et al.*, 2016; i.e., tree density, basal area and/or above-ground biomass) of the stand may differ according to the topo-sequence and vary locally according to fine environmental conditions (Makana *et al*., 2004; Djuikouo *et al*., 2010) as well as the grouping of individuals of a given species in aggregates or not (Katusi, 2015). The same applies to Marantaceae forests, which constitute a regressive system leading in the long term to the almost total disappearance of the tree cover due to the absence of woody regeneration (Lejoly, 1996; Kukupula, 2009; Mbayu, 2017).

MATERIALS AND METHODS

Study area: The study was conducted in two sites: Yangambi site located in Isangi territory, 100 km west of the city, between 0° 38' and 1° 10' N, 24° 16' and 25° 08' E. The Yoko site located in Ubundu territory, 32 km south-east of Kisangani city, between 0° 15' and 0° 20' N, 25° 14' and 25° 20' E (Boyemba, 2011; Katusi, 2015; Adeito *et al.* ., 2018; Katusi *et al.* ., 2021) (Figure 1).

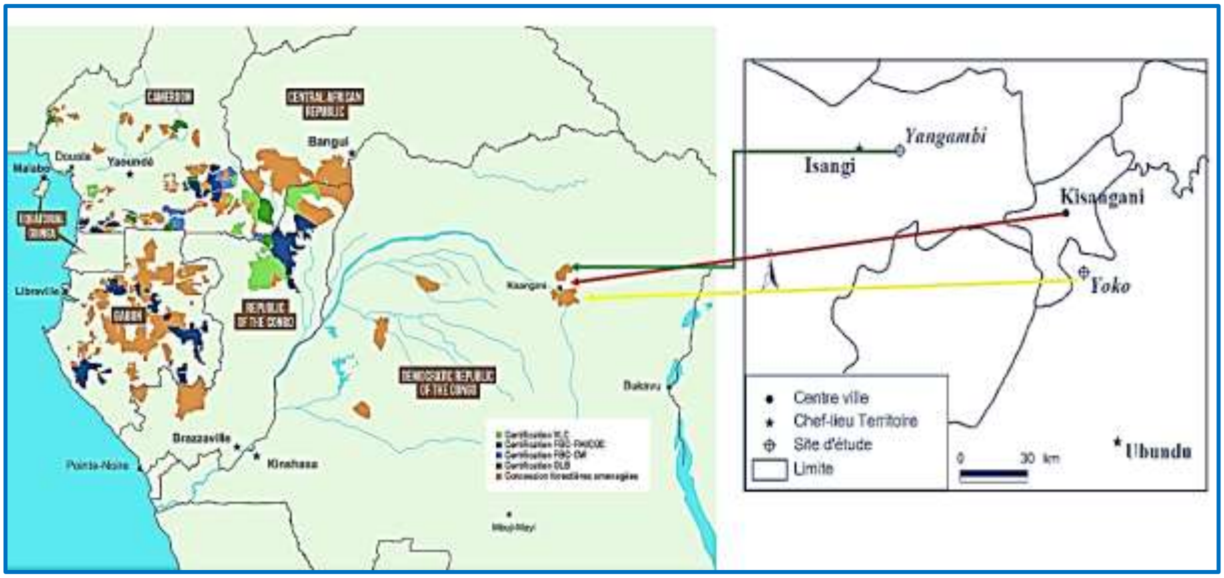

Fig. 1. Location of two sites in relation to the city of Kisangani. The tropical forest of the Congo Basin, the "second green lung" of the planet, after the Amazon.

Located in the equatorial zone, the two study areas benefit from an equatorial climate with an average monthly temperature varying between 22.4 and 29.3 °C, with an annual average close to 25 °C, and annual rainfall varying between 1500 and 2000 mm, with an average of 1750 mm (Vandenput, 1981).

Methodological approach

Survey strategy: Two inventory systems were used for the study: the plot at the Yoko site (200 ha) (Picard, 2008) and the plot at the Yangambi site (200 ha). In both sites, the plots were delimited by transverse layons with 100 m spacing, oriented towards the North (y), and by longitudinal layons with 50 m spacing, oriented towards the East (x), using a decameter (Picard, 2008). The inventory of two Guarea species, namely *G. cedrata* and *G. thompsonii* at dhp ≥ 10 cm (at 1.30 m from the ground or above the footings) was carried out in both sites. Tree mapping (coordinates (x, y)) required, in addition to the compass, the use of two decameters positioned on the ground, in x and y along the layon and the intermediate breakthrough. Three operators conducted the survey: one operator, A, moved within the one-hectare square and passed from tree to tree, while the other two operators, B, and C, moved along the layon y and the breakthrough x, each holding a decameter and a compass. Each operator, B, and C, aim at the tree designated by operator A at the point perpendicular to the direction of the path or breakthrough. The reading of the decameter gives the value of the distance x or y from the origin of the square (distance 0 of origin, i.e., the north-western corner of the square or hectare), the Cartesian coordinates of the trees (x, y) are then provided (Boyemba, 2011) (Figure 2).

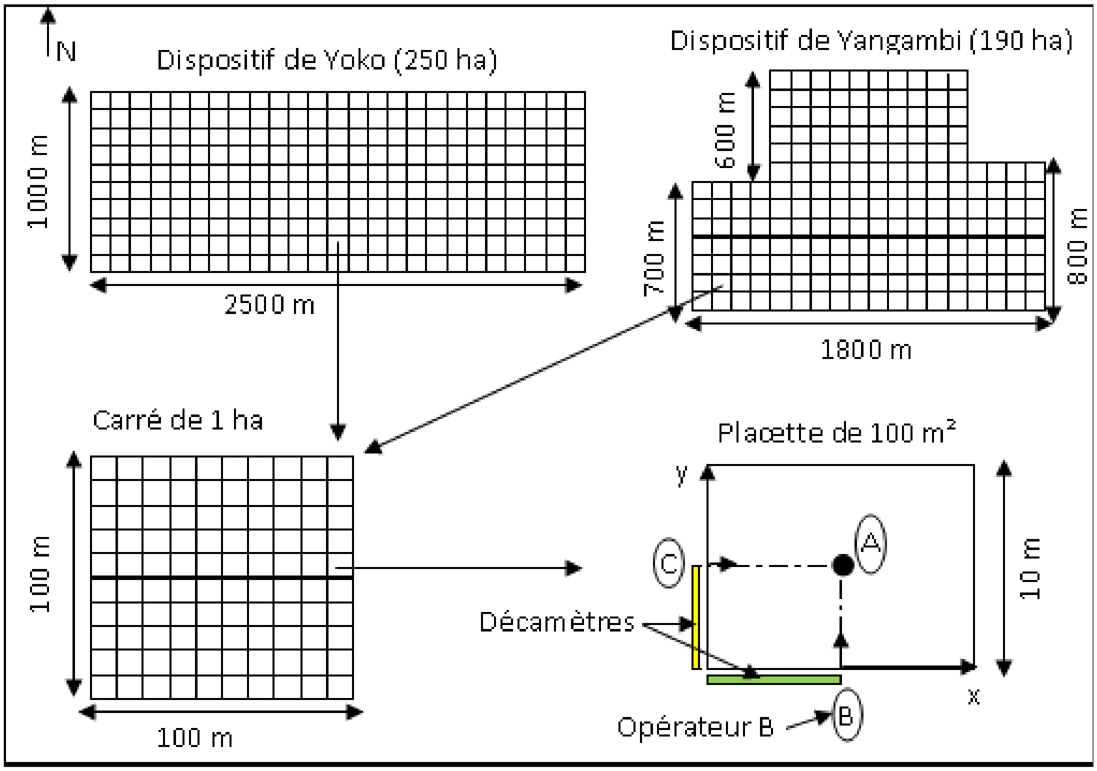

Fig. 2. Dispositif d'inventaire pour les sites de Yangambi et Yoko (Boyemba, 2011; Katusi, 2015)

Characterization of edaphic conditions (soil analysis) and degree of Marantaceae cover. One hundred hectares (100 ha) were sampled, of which 50 ha were in Yangambi and 50 in Yoko. In each ha, soil sampling was done in the four corners of the hectare including the center, i.e., 5 samplings per ha using the auger (Katusi, 2015). It should be highlighted that for each ha, the different soil samples were extracted at 50 cm depth and mixed in soil bags, air dried, and analysed at the Laboratory of Pedology of the Faculty of Management of Renewable Natural Resources at the University of Kisangani. The granulometric analysis was done by gravimetry, followed by chain hydrometry as described by Hanotiaux *et al.* (1975) and Pauwels *et al.* (1992). The topographic study of the soil was done with a Suunto clinometer and the different topographic categories were selected according to the percentage of slope: plateau: 0-10%; gentle slope: 10-25%, and steep slope >25%. As for the evaluation of the degree of the cover of Marantaceae in the understory, it was estimated according to the presence (1) and absence (0) (Menga, 2011; Katusi, 2015).

Statistical analysis: The t-student test was used to compare the mean values of basal area of individuals of two Guarea species and the mean values of the proportions of sand, clay, and silt within two reserves, respectively. At the plot scale, the analysis of the spatial distribution of *Guarea* individuals was performed using Ripley's (1977) K(r) function implemented in the R software (version 2.5, Kfun function of the ads package) whose graphical interpretation is facilitated by Besag's transformed K(r) function or L(r) (Besag, 1977; Goreaud, 2000; Walter, 2006), according to the equation :

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

With Besag's L(r); K(r): Ripley function, r: radius of the aggregates, and π: 3.14. For the aggregated (L(r) > 0) and regular (L(r) < 0) processes, the curves lie above and below the confidence envelope, respectively. For a random process (following a Poisson distribution), L(r) = 0 at all distances from r, and the L(r) curve remains within the confidence interval. The confidence interval is calculated at a 5% risk, from 100 simulations, using the Monte Carlo method (Pelissier et Goreaud, 2001). The analysis is made possible from mapped data of different Guarea stands (diameter ≥ 10 cm) using Cartesian coordinates x,y.

RESULTS

Density and basal area*:* Across the two sites, the numbers of individuals are 105 individuals, or a density of 0.525 ft/ha in Yangambi and 72 individuals, or 0.36 ft/ha in Yoko for *G. cedrata* while for *G. thompsonii*, they are 2086 individuals, or a density of 10.43 ft/ha in Yangambi and 1104 individuals, or a density of 5.5 ft/ha in Yoko. As for basal area values, they are 0.1712 m²/ha (0.0016 ± 0.0018 m²/ha) in Yangambi and 0.0695 m²/ha (0.0010 ± 0.0013 m²/ha) in Yoko site for *G. cedrata* while for *G. thompsonii*, they are 0.6646 m²/ha (0.0003 ± 0.0005 m²/ha) for Yangambi site and 0.3937 m²/ha (0.0004 ± 0.0008 m²/ha) in Yoko. Mean basal area values were different at the 5% threshold at both sites for *G. cedrata* (t = 2.4; p = 0.009), but not for *G. thompsonii* (t = 3.9; dl= 1; p = 0.16)

Distribution of individuals within study sites: Individuals of *G. cedrata* are distributed throughout most of the study area in Yangambi while in Yoko, they are less distributed in the sections from 600 to 1000 m in the y-direction and from 1600 to 2000 in the x-direction (Figure 3).

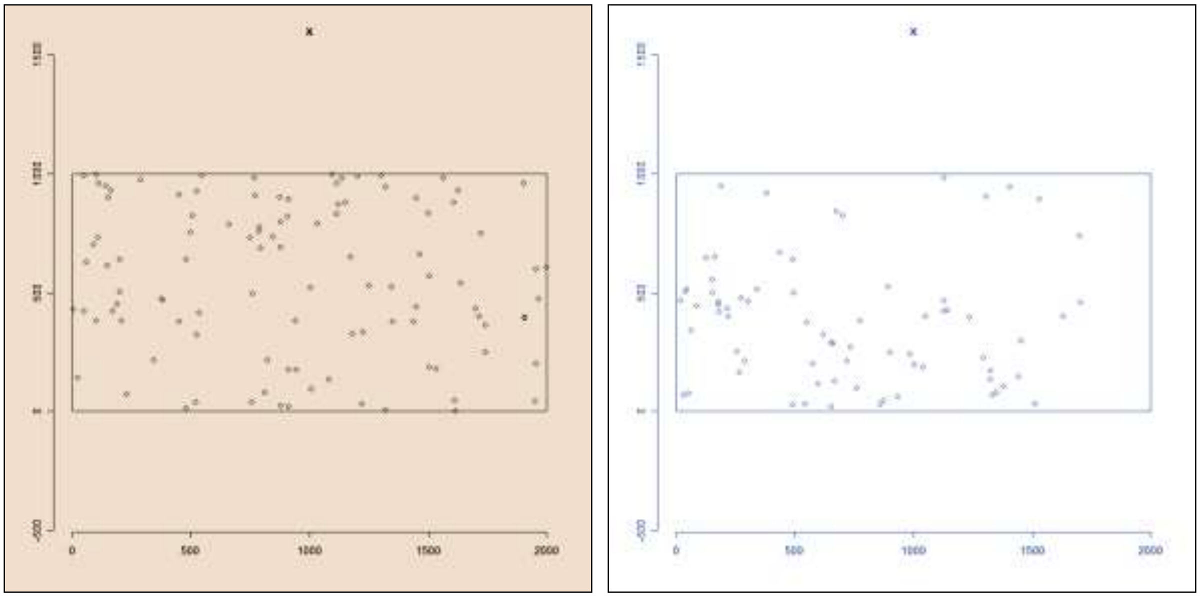

Fig. 3. Distribution of *G. cedrata* individuals in the 200 ha (a: Site_Yangambi and b: Site_Yoko).

Spatial structure of *G. cedrata* individuals*:* The spatial distribution of all *Guarea cedrata* individuals at dhp ≥ 10 cm shows a random distribution in the Yangambi site (Figure 4a) while in the Yoko site, it is random from 0 to 50 m from the analysis distance and then, aggregated beyond 50 m from the analysis distance (L (r) > 25 m; Figure 4b).

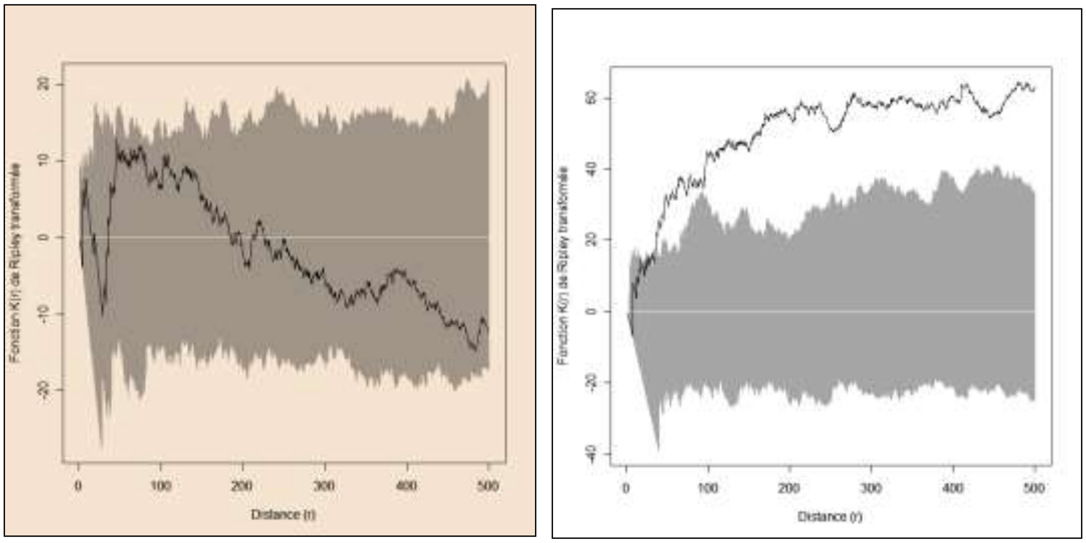

Fig. 4. Spatial structure of *G. cedrata* individuals in the 200 ha (a: Yangambi and b: Yoko).

Distribution of individuals within the study sites *:* As observed for the species *G. cedrata*, individuals of *G. thompsonii* are distributed in almost the entire study area in Yangambi while in Yoko they are less distributed in the sections from 800 to 1000 m in the y-direction and from 1600 to 2000 in the x-direction (Figure 5)

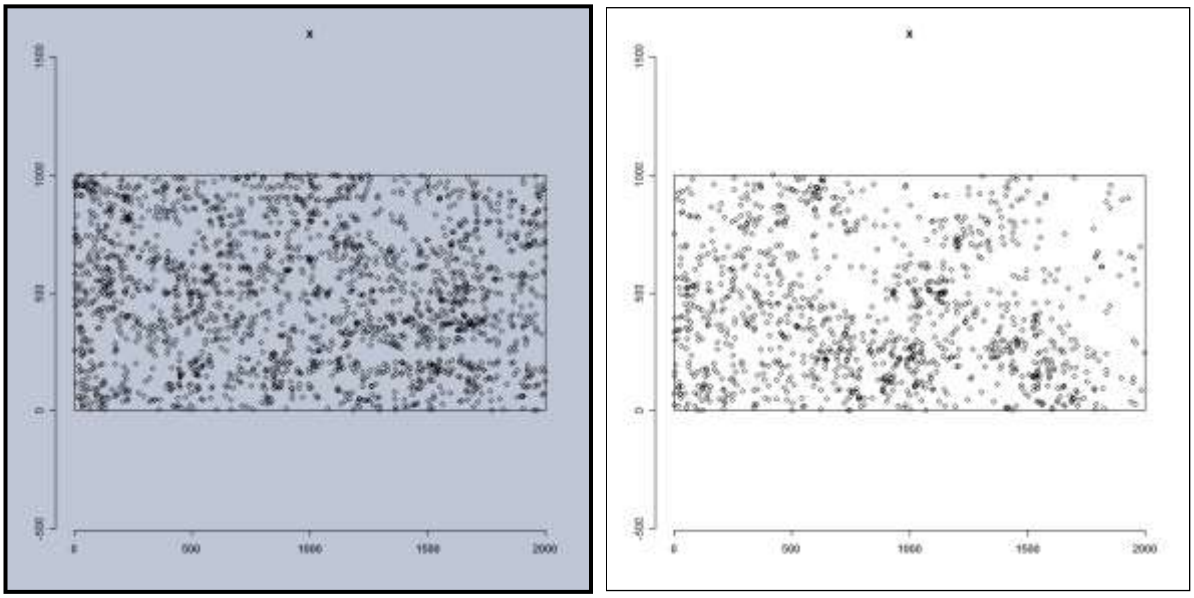

Fig.5. Distribution of *G. thompsonii* individuals in the 200 ha (a: Yangambi and b: Yoko)

Spatial structure of individuals within the study sites: The spatial distribution of *G. thompsonii* individuals with dhp ≥ 10 cm shows a weak aggregation in the Yangambi site between 10 to 250 m of the analysis distance with a peak at the 50 m level and L(r) > 5m (Figure 6a) while in Yoko, it shows strong aggregation over the entire analysis distance with a peak at the 300 m level and L (r) > 25 m (Figure 6b).

Soil particle size analysis*:* In general, at both the Yoko and Yangambi reserves, the soil is sandy-clay. Table 1 shows that at the Yangambi site, the proportion of sand is 69.7 ± 0.47%; silt is 8.6 ± 3.3% and clay is 32.5 ± 6.6% while at Yoko, the proportion of sand is 66.9 ± 14.2%; silt is 7.3 ± 3.9% and clay is 25.9 ± 12.8%. Comparing the proportions of sand (t = 1.2; p-value > 0.05), clay (t = -1.9; p > 0.05) and silt (t = 1.6; p > 0.05) within the two sites, there are no significant differences.

Table 1. Mean values of soil textural parameters

Site	Sand(%)				Silt (%)				Clay (%)			
	Mean	Sd	Max	Min	Mean	Sd	Max	Min	Mean	Sd	Max	Min
Ybi	69,7	0,47	81,3	61,1	8,6	3,3	17,3	2,8	32,5	6,6	32,5	4,6
Yk	66,9	14,2	83,9	24,0	7,3	3,9	19,9	2,0	25,9	12,8	63,5	11,6

Legend: Avg: mean; Sd: standard deviation; Max: maximum and Min: minimum) in Yangambi (Ybi) and Yoko (Yk) sites

Influence of slope, soil texture and Marantaceae on the spatial distribution of Guarea species. At the Yangambi site, the first two axes of the PCA account for 36% of the total inertia of soil survey points × soil texture variables and the presence of Marantaceae (Figure 6a). Axis 1 separates the soil textural elements; it appears, a negative correlation between sand and clay (R = -0.88) on one hand and, silt and clay (R = -0.74) on the other hand while there is a positive correlation between sand and silt (R = 0.34). It should be noted that slope and Marantaceae do not influence Guarea density in the Yangambi plot since the topography is almost flat (plateau) with an almost total absence of Marantaceae. At the Yoko site, the first two axes of the PCA account for 43% of the total inertia of soil survey points × soil textural variables and Marantaceae presence (Figure 7b).

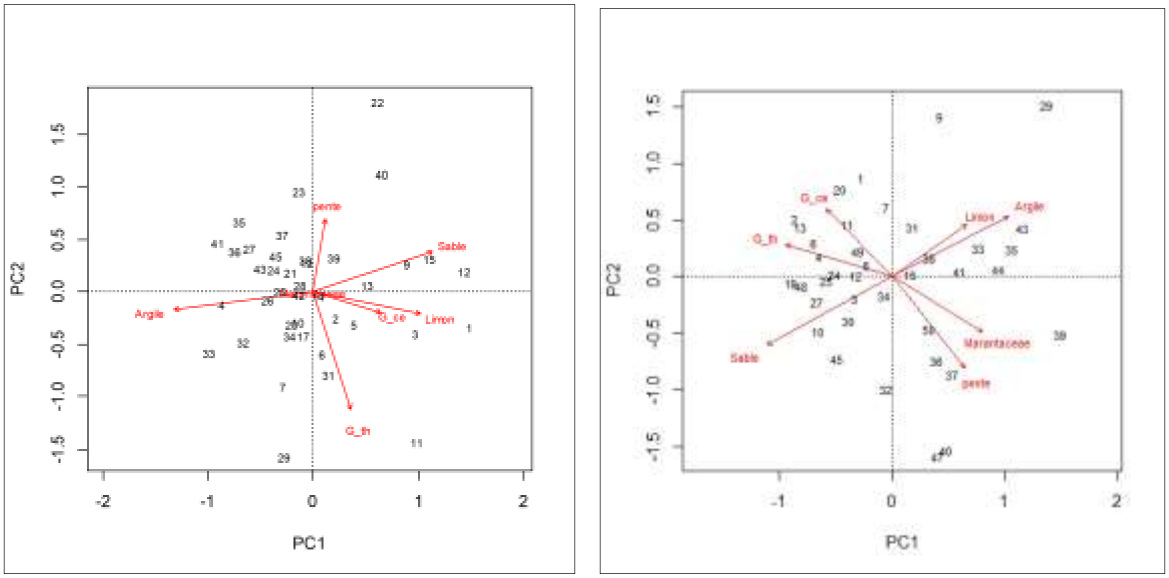

Fig. 6. Ordination of soil survey points × textural variables; topography (slope) and presence of Marantaceae at Yangambi and Yoko by PCA. G_ce: *Guarea cedrata* and G_th: *Guarea thompsonii*. 1; 2; 50: soil profiles. (a): Yangambi site (PC1/PC2: 25/11%) and (b): Yoko site (PC1/PC2: 30/13%).

Axis 1 separates soil textural elements; there is a negative correlation between sand and clay (R = -0.96) on the one hand and, sand and silt (R = -0.49) on the other hand while there is a positive correlation between silt and clay (R = 0.24). This axis also separates the density of Guarea and the slope as well as the presence of Marantaceae; it appears, a negative correlation between the slope and the density of Guarea species on the other hand (R = -0.26 for G. cedrata and R = -0.43 for *G. thompsonii*) and on the other hand, between the presence of Marantaceae and the density of Guarea (R = -0.27 for G. cedrata and R = -0.43 for *G. thompsonii*). In other words, Guarea individuals are more clustered on the plateau where there are no Marantaceae than on the slope or the lowland and/or where there is the presence of Marantaceae.

DISCUSSION

Spatial characterization : The spatial distribution of individuals of a species is largely related to the mode of dissemination of diaspores (Howe et Smallwood, 1982; Sabatier, 1983; Foresta (De) *et al.,* 1984; Gautier-Hion *et al.,* 1985; Howe, 1989; Cabrara & Gignoux, 1990; Koukou, 1992; Loubry, 1993 & 1994; Collinet, 1997; Walter, 2006), to their natural regeneration (Forget, 1988; Puig *et al.,* 1989; Bariteua, 1993; Ribbens *et al.,* 1994, Pascal, J.P. et Pelissier, R., 1995), and to microenvironmental conditions (Puig *et al.,* 1989; Sabatien *et al.,* 1997; Clark *et al.,* 1998; Condit *et al.,* 2000) as well as to soil conditions (Forget, 1988; Puig *et al.,*1989 ; Barthes, 1991 ; Boyemba, 2011 ; Katusi, 2015) because the latter (soil conditions) are likely, at short distances, to vary significantly in aggregation or not (Darrieu de Madron, 1989 ; Koukou, 1994). It should be highlighted that the spatial distribution of the two Guarea species within two sites is heterogeneous, as it is significantly aggregated for both Guarea species at Yoko (see figures 4b and 6b), while it is random for *G. cedrata* and weakly aggregated for *G. thompsonii* at Yangambi (see figures 4a and 6a).

Spatial heterogeneity is related to soil structure and toposequence as well as to the presence of Marantaceae : In the framework of this study, the observations made on both study sites, Yangambi and Yoko, showed that the soil of the two sites is sandy-clay (Cf table 1), but the averages of the percentage of sand (Yangambi: 69.7% and Yoko: 66.88%), silt (Yangambi: 8.62% and Yoko: 7.26%) and clay (Yangambi: 32.49% and Yoko: 25.87%) are relatively higher at Yangambi than at Yoko. In addition, within the two sites; there appears a negative correlation between sand and clay (R = -0.94) and the surface of the study area is more uneven in Yoko than in Yangambi. In Yoko, there is a negative correlation between the density of two species of *Guarea* and the slope on the one hand, and between the density and the presence of Marantaceae on the other hand, while in Yangambi this does not appear, since the topography of the study area is almost homogeneous and Marantaceae are almost non-existent (Figure 7). In the same figure, we also note that in Yangambi, the soil texture is relatively homogeneous and the almost total absence of Marantaceae means that the different soil profiles are almost confined to the intersection of the PCA axes. In Yoko however, the heterogeneity of the soil texture combined with the presence of Marantaceae shows the demarcation of the soil profiles between the PCA axes. On the one hand, one can distinguish soil profiles related to the presence of the slope (≥ 25%) and Marantaceae where the percentage of clay is higher than that of sand, and on the other hand, those profiles related to the absence of slope and Marantaceae and where the percentage of sand is relatively higher than that of clay. In other words, individuals of these two species are more clustered on the plateau with sandy-clay soil and absence of Marantaceae than on the slope or hillside with relatively high clay content and/or abundance of Marantaceae . Based on these observations, it was concluded that the aggregate structure of two *Guarea* species in Yoko may be topographically related (Katusi, 2015) although the majority of semi-deciduous forest species are habitat generalists with respect to topography (Hubbell & Foster, 1986); this seems to reinforce the observation that, for particular edaphic and topographic conditions, many tree species may be habitat-specific (Ashton, 1964; Gartlan *et al.*, 1986; Newbery *et al.*, 1986; Baillie *et al.*, 1987; Ashton & Hall, 1992; Ashton *et al.*, 1995; Richards, 1996; Chen *et al.*, 1997; Collinet 1997; He *et al.*, 1997; Clark *et al.*, 1998; Clark *et al.*, 1999; Hubbell *et al.*, 1999; Svenning, 2000; Harms *et al.*,2001; Hall *et al.*, 2004; Yamada *et al.*,2005; Jones *et al.*,2006; Boyemba, 2011). The often-poor relationship between topographic position and species distribution (Hubbell & Foster, 1986; Niiyima *et al.*, 1999; Webb & Peart, 2000). Traissac (2003), emphasises that edaphic factors and topography are always determinant for at least some species. Condit *et al.* (2000), comparing several devices, relate the degrees of aggregation for a given density with the topography and conclude that the greatest degrees of aggregation are observed for devices with the most irregular topography. This seems to confirm the observations made for the two species of Guarea in the Yoko site.

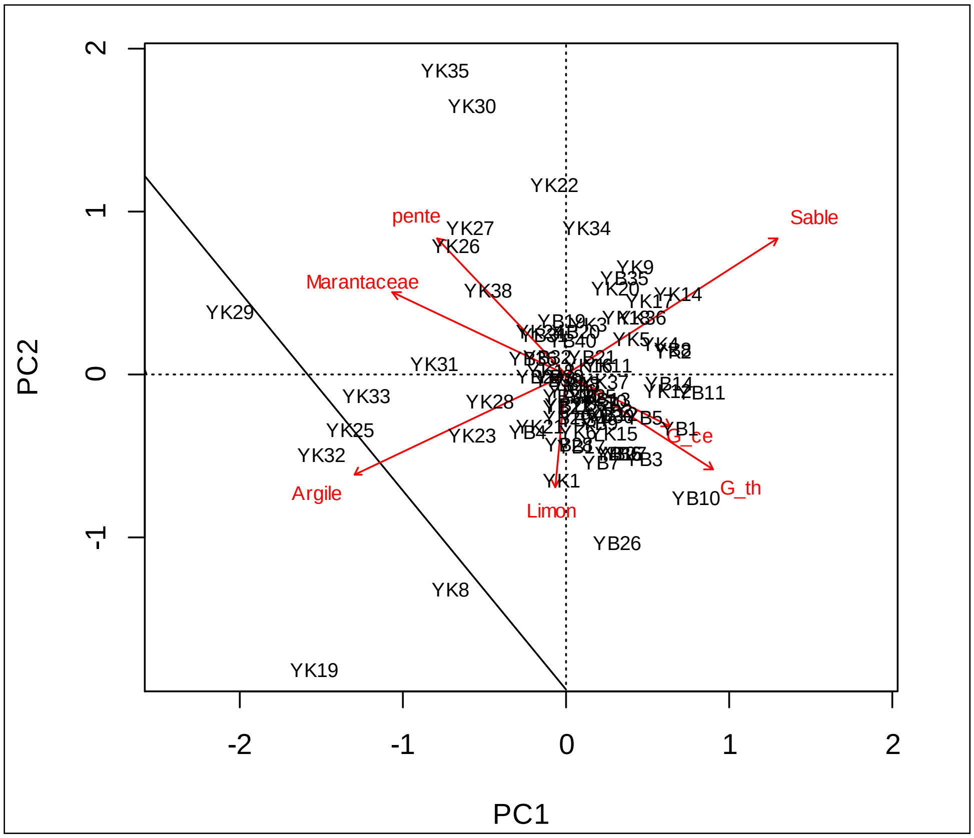

Fig. 7: Ordination of soil survey points × textural variables; topography (slope) and presence of Marantaceae at Yangambi and Yoko by PCA (PC1/PC2: 27/12%). G_ce: *Guarea cedrata* and G_th: *Guarea thompsonii*. Ybi1; Ybi2; Ybi50: soil profiles in Yangambi site and YK1; YK2; YK50: soil profiles in Yoko site.

However, Plokin *et al.* (2002) and Harms *et al.* (2001), assessing the relationships between the spatial distribution of species according to soil (water and fertility) and topographic position (plateau, slope, lowland), observed that the relative importance of edaphic habitat in the structuration of species was relatively low and that this preference for habitat could explain the spatial distribution of 25% of the species (Debski *et al*., 2002). Boyemba (2011), assessing the position of *P. elata* according to the slope in the Yoko Forest, concluded that the spatial distribution of individuals depends on the slope where individuals are denser in areas with low slopes: 73.1% are present in areas with slope ≤ 10%, corresponding to plateaus, while only 0.9% are present on land with 25% slope and 0% on land with 30% slope; this confirms previous observations made on the two species of *Guarea* within the same forest. But Collinet (1997) was able to detect that the edaphic preferences of *Discoryna guianensis* do not seem to constrain its spatial distribution. In addition, besides the topography, it was observed that the presence of Marantaceae, characteristic of a forest disturbance (Ashton *et al*., 1995; Molino & Sabatier, 2001; Schnitzer & Carson, 2001; Mbayu, 2017) in Yoko, cannot facilitate a good regeneration and establishment of the two woody species as they are semi-heliophilous requiring more shade than light in the juvenile stages. One of the causes of the low densities observed in the Yoko reserve is the fact that the forest undergrowth is sometimes overcrowded with large, difficult-to-penetrate herbaceous plants belonging to the Marantaceae families (*Megaphrynium macrostachyum, Sarcocephallum schweinfurtianum,* and *Haumannia liebrechtsiana*) and Commelinaceae (*Palisota hirsuta* and *P. ambigua*). Similar results were observed by Menga (2011) in Maindombe Forest. These Marantaceae have powerful branched rhizomes that allow them to occupy large areas (De Foresta, 1990) and the cover of the upper strata is very light and the density of individuals is low (Doucet, 2003), and many of them tend to cluster. The presence of Marantaceae could be linked to the paleo-incendies and in addition to edaphic and paleo-climatic arguments, which resulted in phases of aridity that may have considerably reduced the floristic richness of African tropical forests (Shnell, 1976; Morley, 2000; White & Edwards, 2001; Maley, 1996a, b), this is probably the case of the Yoko Forest. While in Yangambi the homogeneity of the topography and the absence of Marantaceae would allow the dissemination of diaspores during the settlement of juveniles until the senescence phase in interaction with abiotic and biotic factors of the environment, individuals did not tend to group together to form aggregates. Therefore, we would assume the random distribution of *G. cedrata* and weak aggregate of *G. thompsonii* as a result of these two factors.

CONCLUSION AND APPLICATION OF RESULTS

The density of *Guarea* populations is much higher in Yangambi (0.525 feet/ha for *G. cedrata* and 10.43 feet/ha for *G. thompsonii*) than in Yoko (0.36 feet/ha for *G. cedrata* and 5.5 feet/ha for *G. thompsonii*) and it is more important to have a good density of Guarea in Yangambi than in Yoko thompsonii) and the same is true for the basal area value (0.1712 m^2/ha for G. cedrata and 0.6646 m^2/ha for *G. thompsonii* in Yangambi and, 0.0695 m^2/ha for G. cedrata and 0.3937 m^2/ha for *G. thompsonii* in Yoko). For both species of *Guarea*, the spatial distribution is aggregated in the Yoko site while in the Yangambi site it is random for *G. cedrata* and very weakly aggregated for *G. thompsonii*. As for soil texture, both sites have sandy-clay soils, characteristic of the forest soils of the Kisangani region and its surroundings. Like the other forest synusia, the herbaceous forest layer is made up of plant species whose importance in the maintenance of the whole forest equilibrium is not negligible. Herbaceous communities can somewhat be regarded as the "forest cradle" since other the other species that contribute to the general forest architecture once sojourned there. The herb layer can therefore impact the dynamics of the entire forest. Its importance in the carbon storage process has also been evidenced and more importantly its impact of animal communities. We believe it could be interesting to thoroughly investigate the case of this species partitioning to account for potential edaphic ecotypes of these two species which develop in this plant grouping.

BIBLIOGRAPHIE

Adeito, M S ; Katusi, L R ; Konunga, M G Et Nshimba, S H, 2018. Caractérisation des structures diamétrique et spatiale de peuplement à Guarea thompsonii Hutch. & Sprague, dans les réserves de Yoko et Yangambi, Province de la Tshopo, RD Congo. Afrique Science 14 (5): 136-146

Anderson A.B., 1981. White-Sand Vegetation of Brazilian Amazonia. Biotropica 13, 199-209

Ashton, P.S., 1964. Ecological studies in the mixed Dipterocarp forests of Brunei state. Oxford Forestry Memoirs 25: 1-75.

Ashton, P.S., Hall P., 1992. Comparisons of structure among mixed Dipterocarp forests of north-western Borneo. Journal of Ecology 80: 459-481.

Ashton, P.S., Gunatilleke, C.V.S., Gunatilleke, I.A.U.N, 1995. Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. Journal of Tropical Ecology 11: 263-179.

Baillie, I.C., Ashton, P.S., Court, M.N., Anderson, J.A.R., Fitzpatrick, E.A., Tinsley, J., 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. Journal of Ecology 3: 201-220.

Barbier N., Libalah M.B., Katembo J., Ploton P., Droissart V., Texier N., Kamdem N.G., Viennois G., Pelissier R., Couteron P., F, B.B. et Sonke, B., 2017. Pistes pour l'étude de la distribution des peuplements de *Gilbertiodendron dewevrei* comme signature des impacts climatiques ou anthropiques anciens. Pour une écologie Hist. en Afrique Cent. 157–170.

Bariteau, M., 1993. La régénération naturelle avant et après exploitation sur le dispositif d'expérimentation sylvicole de Paracou en Guyane française. Thèse de doctorat, ULP VI, 264 p.

Barthes, B., 1991. Influence des caractères pédologiques sur la répartition spatiale de deux espèces du genre *Eperua* (Caesalpiniaceae) en forêt guyanaise. Revue d'Écologie (Terre et Vie), 46 : 303-320.

Besag J., 1977. Contribution to the discussion of Dr Ripley's paper. Journal of the royal statistical society, B 39: 193-195.

Boyemba, B., 2011. Ecologie de *Pericopsis elata* (Harms) Van Meeuwen (*Fabaceae*), arbre de forêt tropicale africaine à répartition agrégée. Thèse de doctorat, ULB, Bruxelles, 181 p.

Cabrera-Gaillard, C, Gignoux, J., 1990. Répartitions spatiales et sylviculture en forêt guyanaise. CTFT, Kourou, 19 p.

Chen, Z-S., Hsieh, C-F., Jiang, F-Y., Hsieh, T-H., Sun, I-F., 1997. Relations of soil properties to topography and végétation in a subtropical rain forest in southern Taiwan. Plant Ecology 132(2): 229-241.

Clark, D. B., Clark, D. A, Read, J. M., 1998. Edaphic variation and mesoscale distribution of tree species in a neotropical rain forest. Journal of Ecology 86:101-102

Collinet, F., 1997. Essai de regroupements des principales espèces structurantes d'une forêt dense humide d'après l'analyse de leur répartition spatiale (Forêt de Paracou-Guyane). Thèse de doctorat, Université Claude Bernard, Lyon I, 203 p

Condit, R., Ashton, P.S, Baker, P., Bunyavejchewin, S., Gunatilleke, N., Gunatilleke,S., Hubbel, S.P., Foster, R.B., Itoh , A., Lafrankie, J.V., Lee, H.S., Losos, E., Manokatan, N., Sukumar, R., Yamakuta, T., 2000. Spatial patterns in the distribution of tropical tree species. Sciences 288: 1414-1418.

Chuyong G.B., Kenfack D., Condit R., Comita L.S., 2011. Habitat specificity and diversity of tree species in an African wet tropical forest 1363–1374.

Debski, I., Burslem, D.F.R.P., Palmiotto, P.A., Lafrankie, J.V., Lee, H.S., Manokaran, N., 2002. Habitat preferences of Aporosa in two Malaysian forests: implications for abundance and coexistence. Ecology 83(7): 2005-2018.

De Foresta, H., Charles-Dominique, C., Arard, C., Prevost, M-F., 1984. Zoochorie et premiers stades de la régénération naturelle après coupe en forêt guyanaise. Revue d'Ecologie (Terre et Vie) 39 : 369-400.

De Foresta, H. 1990. Origine et évolution des savanes intramayombiennes (R.P. du Congo).II. Apports de la botanique forestière. In : Lafranchi R. & Schwartz D. (eds). ORSTOM. Paris 326-355.

De Assis R.L., Wittmann F., 2011. Forest structure and tree species composition of the understory of two central Amazonian várzea forests of contrasting flood heights. Flora Morphol. Distrib. Funct. Ecol. Plants 206, 251–260.

Djuikouo M.N.K., Doucet J.L., Nguembou C.K., Lewis S.L., Sonke B., 2010. Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere Reserve, Cameroon. Afr. J. Ecol. 48, 1053–1063.

Doucet, J-L. 2003. L'Alliance délicate de la gestion et de la biodiversité dans les forêts du Gabon. Thèse de doctorat, Faculté Universitaire des Sciences Agronomiques Gembloux, 323 p + Annexes.

Fine, P.V.A., Garcia-Villacorta R., Pitman N.C.A., Mesones I., Kembel S.W., 2010. A Floristic Study of the White-Sand Forests of Peru. Ann. Missouri Bot. Gard. 97, 283–305.

Forget, P-M., 1988. Dissémination et régénération naturelle de huit espèces d'arbres en forêt guyanaise. Thèse de doctorat, Université de Paris VI, 245 p.

Fortunel C., Paine C.E.T., Fine P.V., Kraft N.J.B., Baraloto C., 2014. Environmental factors predict community functional composition in Amazonian forests. J. Ecol. 102, 145–155.

Gartlan, S., Newbery, D.M., Thomas, D.W., Waterman P.G., 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest reserve, Cameroon. Vegetation 65: 131-148.

Gautier-Hion, A. D., Quris, J. M., Feer, R., Sourd, F., Decoux, C., Dubost, J.M., Emmons, G., Erard, L., Hecketsweiler, C., Moungazi, P. H., Roussilhon, A., Thiollay, C.J.M.,1985. Fruits characters as a basis of fruit choice, and seed dispersal by a tropical forest vertebrate community. Oecologia 65:324-337.

Goreaud, F., 2000. Apports de l'analyse de la structure spatiale en forêt tempérée à l'étude et la modélisation des peuplements complexes. Thèse de doctorat en Sciences forestières, ENGREF, 362 p.

Hall, J.S., Mckenna, J.J., Ashton, P.M.S., Gregoire, T.G., 2004. Habitat characterizations underestimate the role of edaphic factors controlling the distribution of *Entandrophragma*. Ecological Society of America, Ecology 85(8): 2171-2183.

Hanotiaux, G., Delecour, F., Legros, A., Mathieu, L. Geets M., 1975. Techniques d'analyses pédologiques. Gembloux, Belgique, Faculté Universitaire des Sciences Agronomiques (Laboratoire de la science du sol), 105 p

Harms, K.E., Condit R., Hubbell, S.P., Foster, R., 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. Journal of Ecology 89: 947-959.

Hart T., Hart, J. & Murphy P., 1989. Monodominant and Species-Rich Forests of the Humid Tropics: Causes for Their Co-Occurrence. Am. Nat. 133, 613–633.

HART, T.B. 1990. Monospecific dominance in Tropical rain forest. Trends in Ecology and Evolution 5: 6 – 11.

He, F., Legende, P. & Lafrankie, J.V., 1997. Distribution patterns of tree species in Malaysian tropical rain forest. Journal of Vegetation Science 8: 105-114.

Howe, H. F. , Smallwood, J.H., 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematic 13: 201-228.

Howe, H. F., 1989. Scatter-and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: pp 417-426.

Hubbell, S.P., Foster, R.B., 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. In: Cody M.L., Diamond L. (Eds). Community ecology. New York: Harper & Row: 314-329.

Hubbell S.P., Foster, R.B., O'brian, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. , De Loo Lao, S., 1999. Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283: 554-557

Jones, M.M., Tuomisto, H., Clark, D.B., Olivas, P., 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. Journal of Ecology 94 (1): 181-195.

Katembo M J, 2020. Déterminants de la composition floristique et estimations des stocks de carbone des peuplements forestiers matures de Uma (Tshopo, RDC). Thèse, FS/Unikis, 133 p

Katusi, K, 2015. Ecologie de *Guarea cedrata* (A. Chev.) Pellegr. et *Guarea thompsonii* Sprague & Hutch. dans les forêts des environs de Kisangani : Cas des Réserves forestières de Yoko et Biosphère de Yangambi (Province Orientale, RDC). Thèse, FS/Unikis, 136 p

Katusi, L.R, Mangambu, M. J-D, Aruna, S J, Nshimba, S. M. H, 2021. Etudes phénologiques et dispersions des fruits de *Guarea cedrata* et *Guarea thompsonii* (Meliaceae) dans les forêts semi-caducifoliées du massif forestier de Kisangani (République Démocratique du Congo). Geo-Eco-Trop., (45): 145-159

Koukou, K., 1992**.** Contribution du déterminisme écologique de la répartition spatiale de l'Angélique (*Dicorynia guianensis*) en forêt dense guyanaise. Mémoire de DEA de Géographie des espaces Tropicaux de L'Université de Bordeaux III/ENGREF, 88 p

Koukou, K., 1994**.** Evolution spatiale des agrégats d'Angélique de Guyane (*Dicorynia guianensis*, Caesalpiniaceae) sur le dispositif d'étude « Forêt naturelle » de Paracou en Guyane française. Acta botanica Gallica, 141(3), 351-359.

Kukupula D P, 2009. Etude de la dynamique spatio-temporelle de Megaphrynium macrostachyum (Benth.) Milne-Redhead (Marantaceae) dans la réserve forestière de Yoko (Kisangani, RDC). DEA, FS/Unikis, 67 p.

Lejoly, J. 1995. Utilisation de la méthode des transects en vue de l'étude de la biodiversité dans la zone de conservation de la forêt de Ngotto (RCA). Rapport technique: Projet ECOFAC, Agreco-CTFT. 114 p

Letouzey R., 1983. Quelques exemples camerounais de liaison possible entre phénomènes géologiques et végétation. Bothalia 14, 739–744.

Lokonda M., Freycon V., Gourlet-Fleury S., Kombele, F., 2018. Are soils under monodominant Gilbertiodendron dewevrei and under adjacent mixed forests similar? A case study in the Democratic Republic of Congo. J. Trop. Ecol. 34, 176–185.

Loubry, D., 1993. Les paradoxes de l'Angélique (*Dicorynia guianensis* Amshoff) : dissémination et parasitisme des graines avant dispersion chez un arbre anémochore de la forêt guyanaise. Rev. Ecol. (Terre Vie), 48 : 353-363.

Loubry, D., 1994. Déterminisme du comportement phénologique des arbres en forêt tropicale humide de Guyane française (5°lat, N). Thèse de Doctorat., Université Pierre et Marie Curie. Paris VI: 566.

Makana, J.-R., Hart, T.B., Hibbs, D.E. & Condit, R. 2004. Forest structure and diversity in the Ituri Forest Dynamics Plots. In: E. Losos and E. Leigh, Jr. (eds.) Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Network, University of Chicago Press, Chicago, pp.159-174

Mbayu, M L F, 2017. Forêt à Marantaceae et son impact sur la régénération des ligneux dans la réserve forestière de Yoko (Ubundu, Province de la Tshopo, RD Congo) ; Thèse, FGRNR/Unikis, 207 p.

Menga, M, P., 2011. Ecologie des peuplements naturels de *Millettia laurentii* De Wild. (Wenge) dans la région du lac Maï-Ndombe, en RD Congo. Thèse de doctorat, FS/ UNIKIN, 190 p + annexes

Maley, J. 1996a. The African rain forest-main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. Proceedings of the Royal Society of Edinburgh 104B, 31-73.

Maley, J. 1996b. Le cadre paléoenvironnemental des refuges forestiers africains : quelques données et hypothèses. In : van der Maesen L.J.G., van der Burgt X.M., van Medenbach de Rooy J.M. (eds). The Biodiversity of African Plants. Kluwer Academic Publishers, Netherlands, 519-535.

Molino, J.F., Sabatier, D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. Science 294: 1702-1704.

Morley, R.J. (2000). Origin and Evolution of Tropical Rain Forests. John Wiley & Sons Ltd, Chichester, 362 p.

Newbery, D.M., Gartlan, J.S., Mckey, D.B. Waterman, P.G., 1986. The influence of drainage and soil phosphorus on the vegetation of Douala-Edea Forest Reserve, Cameroon. Vegetation 65: 149-162

Niiyama, K., Rahman, K.A., Lida, S., Kimura, K., Azizi, R. & Appanah, S., 1999. Spatial patterns of common tree species relating to topography, canopy gaps and understorey vegetation in hill

Dipterocarp fores tat Semangkok Forest Reserve, Peninsular Malaysia. Journal of Tropical Forest Science 11 (4): 731-745.

Pappoe, A.N.M., Armah, F.A., Quaye, E.C., Kwakye, P.K. & Buxton, G.N.T. 2010. Composition and stand structure of a tropical moist semi-deciduous forest in Ghana. International Research Journal of Plant Science 1 (4): 95-106.

Pereira Junior, L.R., De Andrade, E.M., De Queiroz Palacio, H.A., Lemos Raymer, P.C., Ribeiro Flho, J.C. & Soares Pereira, F.J. 2016. Carbon stocks in a tropical dry forest in Brazil. Revista Ciência Agronômica 47 (1): 32 – 40.

Prader, W. 2008. Tree diversity and vegetation dynamics of a one hectare forest plot census in the lowland rain forests of the Piedras Blancas National Park ("Regenwald der Österreicher"), Costa Rica. Universität Wien.

Pascal, J.P., Pelissier, R., 1995. Structure and floristic composition of tropical evergreen forest in south-west India. Journal of Tropical Ecology 12: 191-214.

Pauwels, J.M., Van Ranst, E., Verloo, M., Mvondo, Z. A., 1992. Manuel de laboratoire de pédologie: méthodes d'analyses de sols et de plantes, équipement, gestion de stocks de verrerie et de produits chimiques. Bruxelles: AGCD, Publ. Agricoles, 28, 265p.

Pelissier, R., Goreaud, F. 2001. A practical approach to the study of spatial structure in simple cases of heterogeneous vegetation. Journal of Vegetation Science **12**(1): 99-108.

Picard, N., 2008. Manuel de référence pour l'installation de dispositifs permanents en forêt de production dans le Bassin du Congo. CIRAD, Département Environnements et Sociétés, UPR Dynamique des forêts naturelles, Montpellier, France, 265 p

Plotkin, J.B., Chave, J. & Ashton, P.S., 2002. Cluster Analysis of Spatial Patterns in Malaysian Tree Species. American Naturalist 160: 629-644.

Puig, H., Forget, P-M., Sist, P., 1989. Dissémination et régénération de quelques arbres en forêt tropicale guyanaise. Bulletin de la Société Française, 136. Actualité Botanique (3/4), 119-131.

Ribbens, E., Silander, J. A., Paul, .S.W., 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology 75 (6): 1794-1806

Richards, P.W., 1996. The tropical rain forest. 2nd Edition, Cambridge University Press, Cambridge, 575 p.

Sabatier, D., Grimaldi, M., Prevost, M. F., Guillaume, J., Godron, M., Dosso, M. , Curmi, P., 1997. The influence of soil cover organisation on the floristic and structural heterogeneity of a Guiana rain forest. Plant Ecology 131: 81-108.

Sabongo Y P, 2015. Etude comparative de la structure et de la diversité des forêts à *Gilbertiodendron dewevrei* (De Wild.) J. Léonard des régions de Kisangani et de l'Ituri (R.D. CONGO). Thèse, FS/Unikis, 158 p

Schnitzer, S.A., Carson, W.P., 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82: 913-919.

Svenning, J., 2000. Small canopy gaps influence plant distribution in the rain forest understory. Biotropica 32 (2): 252-261

Traissac, M. S, 2003. Dynamique spatiale de Vouacapoua americana (Aublet), arbre de la forêt tropicale humide à répartition agrégée. Thèse de doctorat, Université Claude Bernard-Lyon I, 217 p

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J.C., Hernandez, C., Romoleroux, K., Losos, E., Magard, E., Balsley, H. 2004: Tree species distributions and local habitat variation in the Amazon: a large forest plot in eastern Ecuador. *Journal of Ecology* 92: 214 – 229

Vandenput, R., 1981. Les principales cultures en Afrique centrale. Tournaï: édit. Lesaffre, 458 p.

Walter, J-M. N., 2006. La méthode de Riplay pour l'analyse des structures spatiales elles en écologie, Notice, université Louis Pasteur (ULP), Strasbourg, 10 p

Webb, C.O., Peart, D.R., 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88: 464-478.

White, L., Edward, A. 2001. Conservation en forêt pluviale africaine - Méthodes de recherché. Ed, WCS, New York, 456 p.

Wittmann F., Householder E., Piedade M.T.F., De Assis R.L., Schöngart, J., Parolin P., Junk W.J., 2013. Habitat specifity, endemism and the Neotropical distribution of Amazonian white-water floodplain trees. *Ecography (Cop.)*. 36, 690–707.

Yamada, T., Suzuki, E., Yamakura, T., Tan, S., 2005. Tap-root depth of tropical seedlings in relation to species-specific edaphic preferences. *Journal of Tropical Ecology* 21: 155-160