**Available online at http://www.ifgdg.org**

Int. J. Biol. Chem. Sci. 10(4): 1602-1616, August 2016

ISSN 1997-342X (Online), ISSN 1991-8631 (Print)

International Journal of Biological and Chemical Sciences

***Original Paper*** http://ajol.info/index.php/ijbcs http://indexmedicus.afro.who.int

# Floristic and structural changes in secondary forests following agricultural disturbances: the case of Lama forest reserve in Southern Benin

Alain Jaures GBETOHO[1*], Augustin Kossi Nounagnon AOUDJI[1], Kourouma KOURA [1], Sylvie GOURLET-FLEURY[2], David KENFACK[3], Charles De CANNIERE[4] and Jean Cossi GANGLO[1]

[1] *Laboratoire des sciences forestières, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, 03BP 2819, Cotonou, Bénin.*
[2] *UR BSEF, Centre International de Recherche Agronomique pour le Développement (CIRAD), 34398 Montpellier, France.*
[3] *Missouri Botanical Garden, 4500 Shaw Blvd., St, Louis, MO 63110, USA.*
[4] *Service d'Ecologie du paysage et Systèmes de production végétale, Ecole interfacultaire de bioingénieurs, Université Libre de Bruxelles, Avenue F.D. Roosevelt 50 CP 169, B-1050, Bruxelles, Belgique.*
[*] *Corresponding author; E-mail: gljaures@gmail.com*

***ACKNOWLEDGMENTS***

*Data from the first inventory in secondary and old-growth forests were collected thanks to a funding of the AIRES-Sud project. The inventory done in 2012 was funded by the French Embassy in Benin. This manuscript was elaborated while the first author was under IFS individual research grant. The authors are very grateful to these funding institutions.*

---

## ABSTRACT

Structural changes in secondary forests are less known in West Africa, and this precludes their management. This study aims at providing quantitative information on floristic composition and structure of the Lama secondary forests (Benin), so as to contribute to their restoration, and fill part of knowledge gaps on West African secondary forests. Data of 77 permanent plots each of 0.5 ha were used to analyze the floristic composition, the trajectory of the recovery and the recovery of stocking in these forests, compared to nearby old-growth forests. The results showed that the forests were less diversified with few species very common in the forest stands; the most dominant were *Lonchocarpus sericeus* and *Anogeissus leiocarpa* in the secondary forests, and *Dialium guineense*, *Diospyros mespiliformis* and *Afzelia africana* in the old-growth forests. The secondary forests hold more species than the mature ones. Their compositions will recover that of the original forest because species of the original forest were actively regenerating in the secondary forests. About 28 years after recovery, large trees were insufficient and basal area was about 60% of those of the mature forests. Further studies are needed to elucidate barriers to tree regeneration and dynamics of tree population.

**Keywords:** Secondary forest, recovery, diversity, species composition, timber stock, Benin.

---

*2648-IJBCS*
DOI : http://dx.doi.org/10.4314/ijbcs.v10i4.13

## INTRODUCTION

Secondary forests are increasingly a major part of forest ecosystems because of forest degradation which have exceeded 5 millions of hectares per year in the world and about 3.5 millions of hectare per year in Africa (FAO, 2011). Their management is essential to enhance recovery and sustain their utilization, but the critical information that will guide that management is lacking. In particular in West Africa, few studies have predicted the successionnal processes of secondary forests.

African secondary forests came generally from long term conversion of large areas by human activities. Traditional shifting cultivations, pastures, and other land uses that completely and repeatedly remove vegetations, are the main threats to the biodiversity and the structure of the forests (Guariguata and Osterstag, 2001; Ganglo, 2004; Ganglo and de Foucault, 2006). Secondary forests could recover richness in few decades after abandonment, but the recovery of species composition may be slow due to the slow turnover rate of canopy species (Finegan, 1996). The differences in species composition and structure of the secondary forests are linked to several factors: the type of forest disturbed, the type and intensity of disturbances, local site factors, existence of propagules sources, species life-history and age since abandonment (Guariguata and Osterstag, 2001; Ayingweu, 2004).

It was suggested that secondary successions may follow a predictable pathway to the same end point (Adler and Lauenroth, 2003). However, floristic changes in secondary successions are not always directional or predictable, but many pathways could lead to a range of mature forest types than a single stable end point (Gleason, 1926; Chazdon et al., 2007). For shifting agriculture in particular, characterized by abandonment of depleted land and clearing of nearby site, a mosaic of secondary forest with different composition and ages could be observed (Ayingweu, 2004); whether they will follow a unique pathway towards the original forest or not need to be tested through long term studies (Chazdon et al., 2007). “Space-for-time” analyses have been used to reconstitute temporal succession from one time spatial sequence of forest regrowth but are constrained by the assumption of the unique pathway (Kassi and Decoq, 2008). However, multivariate analyses on floristic tables, used by that method, have shown separation between secondary and primary forests plots according to their floristic composition (Makana and Thomas, 2006; Kassi and Decoq, 2008). Each particular floristic composition of secondary forests represents a pathway of secondary succession, and each particular floristic composition of mature stand represents a probable endpoint of such succession (Mesquita et al., 2001). Therefore, the trajectory of recovery could be foreseen with one time inventory data by analyzing data on regeneration of species, saplings density in particular, that will determine future composition of forests (Vayreda et al., 2013) and data on current composition in adult trees (Mesquita et al., 2001).

Besides species compositions, considerations about secondary forests concerned their stocking. Scholars have considered tree density, basal area and diameter structures, as simple parameters to account for the reconstitution of forest biomass (Bonino and Araujo, 2005; Makana and Thomas, 2006). It is expected that the changes in tree size and density must be linked to competition at the cost of small trees while forest is growing (Coomes and Alen, 2007). The recovery of aboveground biomass depends mainly on the appearance of large trees (Brown and Lugo, 1992; Clark and Clark, 2000) and expresses recovery of forest functions because several progressive phenomena, such as nutrient cycle, root dynamics, recovery of mycorrhyzal communities, etc. are operating until complete recovery (Guariguata and Osterstag, 2001). Then, the quantitative assessment of secondary forest biomass compared to old-growth stands provides the maximum values to be reached thanks to management actions, and so the gaps to be filled (Bonino and Araujo, 2005). Knowledge about floristic changes and stocking of secondary forests in Benin is actually lacking and this precludes sound recommendations on their sustainable management. To contribute to fill that knowledge gap, our study aimed at assessing changes in the structure and composition of the secondary forests of Lama, so as to contribute to the restoration and sustainable management of forests in Benin where forest resource is limited and degraded (Sokpon, 1995). The following questions were explored during our investigation: (i) Do the secondary forests of Lama recover the diversity of near old-growth forests? (ii) Will these secondary forests recover the same composition of the old-growth forest? (iii) What is the current state of stocking of these secondary forests?

## MATERIALS AND METHODS

### Study area

Our study was conducted in the natural forest of Lama (Benin) located between 6°55'-7°00' N and 2°04'-2°12' E. During the 1970s, Lama forest, in the Center and South Benin, underwent disturbance processes, mainly due to clearance for shifting cultivation. In 1987, the farmers where pushed out of the forest so that forest recovery and rehabilitation were enabled and resulted in secondary forests (ONAB, 2011). Currently, the natural forest covers 4,785 ha composed of 1,900 ha of dense semi-deciduous fragments, 296 ha of *Tectona grandis* L.f. and *Gmelina arborea* Roxb. plantations, and the remaining surface include secondary forests and fallows (ONAB, 2011). Some areas were enriched with *Khaya senegalensis* (Desr.) A.Juss., *Khaya grandifolia* C.DC., *Holoptelea grandis* (Hutch.) Mildbr., *Terminalia superba* Engl. & Diels, *Triplochiton scleroxylon* K.Schum., etc., and natural regenerations of some pioneer species were assisted to enhance recovery.

The original vegetation of Lama is floristically composed of *Dialium guineense* Willd. and *Diospyros mespiliformis* Hochst. ex A.DC. old-growth forest (OGF), referred to as OG1 in this study, and of *D. guineense* and *Afzelia africana* Sm. OGF, referred to as OG2 (Hounkpèvi et al., 2011). The secondary forests (SF) were characterized by a mosaic of *Lonchocarpus sericeus* (Poir.) Kunth and *Ceiba pentandra* (L.) Gaertn. forests referred to as SF1; *L. sericeus* and *A. leiocarpa* forests referred to as SF2; and *L. sericeus* and *Albizia zygia* (DC.) J.F.Macbr. forests referred to as SF3 (Assouma, 2009). Fallows were dominated by pioneer species such as *Chromolaena odorata* (L.) R.M.King (Assouma, 2009; Hounkpèvi et al., 2011).

The climate of the study area is subequatorial with a mean annual rainfall of 1,124 mm. The long rainy season extends from March to June, and the short rainy season lasts from September to November (ONAB, 2011). The mean annual temperature is 27.5 °C and the annual relative humidity is higher than 60%.The topography is almost flat and the vertisols, “black cotton soils”, are dominant.

### Sampling design and data collection

Seventy seven 0.5 ha plots (50 m × 100 m each) were randomly set in 2010 in representative parts of the SF as follows: 27 plots in SF1, 20 plots in SF2, and 30 plots in SF3. The plots were separated by a minimum distance of 50 m. Each tree with dbh $\geq$ 10 cm was numbered and marked at breast height with red painting. The plots were inventoried in 2010 and 2012. The data of 2012 were used in this paper. The dbh and the total height of each marked tree were measured. Tree regenerations (individuals with dbh < 10 cm) were counted or measured according to their growing stage (seedlings or saplings) in 4 quadrats of 0.01 ha within each plot. The data of OGF came from census in two 1 ha plots set in each OGF (Hounkpèvi et al., 2011). These plots were divided in 0.5 ha subplots for data analysis purposes.

## Data analysis

### *Comparison of the diversity of secondary and of old-growth forests*

Some basic diversity indices were computed to compare the diversity of the forest:

- the mean number of species (*s*) per hectare and per forest;
- the species richness (*S*) of each forest;
- the number of taxonomic family ($N_F$) in each forest;
- the mean Shannon's index (*H'* in bit) of each forest; the Shannon's index was computed per plot by: $H' = -\sum(\frac{ni}{n})\log_2(\frac{ni}{n})$ with ni the number of trees of the species i in a plot, n the number of trees of all species in the plot;
- the mean Pielou's eveness (*Eq*) of each forest; *Eq* was computed per plot by: $Eq = H'/log_2Sp$ where *Sp* is the number of species in the plot; and
- the Fisher's α per hectare for each forest: $Sp=\alpha ln(1 + n/\alpha)$.

## Analyzing secondary forests' composition

The Importance Value Index (IVI) was used to analyze the floristic composition of each forest in terms of dominant and rare species. For a species *x* in a given forest, the IVI was computed as follows (Curtis and Macintosh, 1951):

$IVIx = RDx + RFx + RCx$

$RD_x = n_x/\sum n_x$ is the relative density of the species *x* where $n_x$ is the number of trees of the species in the whole forest. $RFx = (\frac{jx}{k})/\sum(\frac{jx}{k})$ is the frequency of the species *x* as a proportion of the sum of the frequencies for all species; $j_x$ is the number of plots in which the species *x* was present and k is the total number of plots. $RC = C_x/\sum C_x$ is called the relative coverage for the species with $C_x = a_xN_x/n_x$; $a_x$ is the sum of the cross-sectional area at 1.3 m above the ground level, expressed in m², of all trees of the species *x* ; $N_x$ is the tree-density of the species *x* and $n_x$ is the total number of trees sampled for that species. The IVI is comparable to a percentage of a given species among all species that composed a forest, but its value ranges from 0 to 3 (not from 0 to 100 as for percentage); the IVI is very relevant to account for forest composition (Curtis and Macintosh, 1951; Assogbadjo et al., 2009).

A Principal Component Analysis (PCA) was performed in R software on a matrix that contained, in the cells, the IVI of each species in each forest to analyze commonness and species rarity in Lama forests.

## Predicting trajectory of the recovery

Following Steininger (2000) and Mesquita et al. (2001), the forests of Lama with their different floristic composition represented the current pathways of forest succession in the Lama forest reserve. However, these floristic compositions were analyzed only on the basis of adult trees. Therefore, the saplings (1≤dbh<10 cm) of pioneer and non-pioneer canopy species regenerating in the SF were first evaluated. Then, saplings and adult trees were combined to determine the trajectories that the secondary forests may follow. The density of saplings was determined per species and per plot by $Nr = \frac{1}{4sq}\sum_{i=1}^{4} n_{si}$, where $n_{si}$ is the number of saplings of a species *i*, and *sq*, the unit area of the regeneration plot. The means were computed per forest and compared using ANOVA or Kruskall-Wallis test when the data were not normally distributed. Furthermore, a multi-dimensional scaling with the ALSCAL procedure was performed in SPSS on a matrix of number of trees (adult trees and saplings) of each species per plot, to cluster the plots according to their similarity. The result of this ordination, based on the combination of actual forest composition (adult trees) and forest regeneration (saplings) suggests the floristic composition (of OGF) that Lama SF may recover.

### *Evaluation of stocking in the forests*

To evaluate stocking, the following parameters were computed:

- the density of tree (*N*) of each plot, $N = ni/n$ with *ni* and *n* as described above;
- the diameter (*Dg*) of each plot, $D_g = \sqrt{\frac{1}{n}\sum_{i=1}^{n} d_i^2}$ with $d_i$ the
- diameter (in cm) of a tree *i*; and
- the basal area (*G*) for each plot, $G = \frac{\pi}{40000}\sum_{i=1}^{n} di^2$.

The mean of each parameter was computed and the forests were compared using ANOVA test followed by the Student-Newman-Keuls test. Then, the diameter structure was established for each forest by grouping the trees in 5 cm size-classes. A regression of the density by the diameter was performed followed by the establishment of diameter structure for the most dominant species of each SF. The skewness of the last diameter structures were computed in R software.

## RESULTS

### Floristic diversity and composition of secondary and old-growth forests

A total of 32 to 37 species, mainly pioneer light-demanding, from 23 families, were recorded in the SF (Table 1). All species used in enrichment were found in SF1 and SF3. In the OGF, 15 to 19 species, mainly shade-bearers, from 13 families, were recorded. The mean number of species per hectare ranged between 11 and 16. All species recorded in OGF, except *Cynometra megalophylla* Harms (Leguminosae-Caesalpinioideae), were also recorded in the SF. There was no clear trend for the Fisher's alpha (2.30-3.50) from SF to OGF; the highest values were recorded in SF3 followed by OG1. In SF3, there was an abundance of enrichment species, and in OG1, it was recorded many trees of pioneer species. *H'* and *E* were respectively lower than 2 bits and 0.5 for SF1 and SF3, but higher than 2 bits and 0.5 for SF2 and the OGF (Table 1).

The analysis of Figure 1 showed that the axis 1 was linked to the importance value of the species in the forests while axis 2 was linked to the type of forest. This Figure 1 showed that the floristic compositions of SF were different from those of OGF. For SF, the most characteristics species were *L. sericeus* (Leguminosae-Papilionoideae), *A. leiocarpa* (Combretaceae), *C. pentandra* (Bombacaceae), *A. zygia* (Leguminosae-Mimosoideae), *Ficus exasperata* Vahl (Moraceae) and *Ficus sur* Forssk. (Moraceae). The most characteristics species of OGF were *D. guineense* (Leguminosae-Caesalpinioideae), *D. mespiliformis* (Ebenaceae), *A. africana* (Leguminosae-Caesalpinioideae), *Drypetes floribunda* (Müll.Arg.) Hutch. (Euphorbiaceae), *Celtis brownii* Rendle (Celtidaceae), *Mimusops andongensis* Hiern. (Sapotaceae), and *Lecaniodiscus cupanioides* Planch. Ex Benth. (Sapindaceae) (Figure 1). The other species were rare.

In SF1 and SF3, *L. sericeus* (IVI = 1.15-1.56) was the most dominant species, associated to *C. pentandra, A. zygia* and *Ficus spp.*, very common in these forests (Table 2). In SF2, *A. leiocarpa* (IVI = 1.12) was the most abundant, associated to *L. sericeus, C. pentandra, A. zygia* and *Ficus spp*. The whole

IVI of species used in enrichment was the highest in SF3. In OGF, *D. guineense* was the most important (IVI = 0.82-0.87) but the IVI of *D. mespiliformis*, *A. africana*, *D. floribunda*, *C. brownii* and *M. andongensis* were relatively high. In OG1, *A. leiocarpa*, *L. sericeus* and *A. zygia* were relatively abundant (overall IVI = 0.42). Overall, the forests were dominated by the Leguminosae family (> 50%) along with the Bombacaceae and Moraceae families in SF and the Ebenaceae, Celtidaceae, Euphorbiaceae, and Sapotaceae families in OGF.

## Trajectory of forest recovery

The densities of saplings in the forests are presented in the Table 3. In this table, only saplings of the most regenerating canopy species and species used in enrichment were presented. The densities of the pioneer species did not vary significantly in the forests ($p > 0.05$). There were 18 and 32 saplings.$ha^{-1}$ for *L. sericeus* while saplings of *C. pentandra*, *A. zygia,* and *A. leiocarpa* occurred at low density (< 5 saplings.$ha^{-1}$) in SF (Table 3). The saplings of *A. leiocarpa* and *L. sericeus* were relatively abundant in OG1 and rare in OG2. There was a lack of saplings for *A. africana* in SF and also in OG2. The density of saplings of *D. guineense* was very low in SF (3-22 saplings.$ha^{-1}$) compared to OGF (>113 saplings.$ha^{-1}$). The same observation applied for *D. mespiliformis* but the gap was not as high as for *D. guineense*. The densities of these two species are increasing through the SF (SF2 > SF1 > SF3). Saplings of *Khaya* spp and *Holoptelea grandis* (introduced species in Lama) were mostly abundant in SF3 and OG1. Saplings of *K. senegalensis* in SF1 and SF3 (15-39 saplings.$ha^{-1}$) were more abundant than those of *D. guineense* and *D. mespiliformis* (3-14 saplings.$ha^{-1}$) in the same forests.

The result of the multidimensional scaling on the number of trees and saplings of each species in the forests is presented on Figure 2. The two axes were more linked to the composition of the forests. The first axis discriminated *L. sericeus* dominated forests, characterized by SF1 and SF3 plots mixed at the right part of this axis, from SF2 and OGF plots at the left part of the same axis where *L. sericeus* trees were not dominant. The plots of SF2 were divided in two groups. The SF2-1 group was constituted by plots only dominated by *A. leiocarpa*. In these plots, *L. sericeus*' individuals were scarce. Some plots of SF2 were closed to SF1-SF3 group as these plots were characterized by a codominance of *A. leiocarpa* and *L. sericeus*. The axis 2 opposed SF2 plots where *A. leiocarpa* was dominant to those of OGF where old-growth species were dominant. All OGF plots were grouped at the left part of the factor map, upward axis 2. Only *D. guineense* and *D. mespiliformis* had relatively good regeneration in the SF. Then, the composition of the SF is likely to evolve to the composition of OGF. However, the next stage of SF1 and SF3 may be modified by the presence of enrichment species, in particular *K. senegalensis*.

## Comparison of structural attributes according to forest stage of development

The mean density decreased while the mean diameter increased from SF to OGF (Table 3). The mean density was highest in SF1 and SF2 (>298 trees.$ha^{-1}$), intermediate in the OGF and lowest in SF3 (244 trees/$ha^{-1}$). The diameter was highest in OG2, intermediate in OG1 and SF2, and lowest in SF1 and SF3. The relationship between diameter and density in the SF was significant but the prediction value was weak ($p < 0.000$, r-sq = 48%) (Figure 2). There was no significant difference between basal area of OG1 and the SF, but the basal area of the OG2 was the highest; the SF accounted for less than 62% of the basal area of OG2.

The comparison of diameter structures (Figures 4a-e) revealed that SF1 (Figure 4a) and SF3 (Figure 4c) had the same structure

($\chi^2$ = 3.156, p = 0.676), while the other forests were characterized by different shapes. Trees with dbh ≤ 35 cm were abundant in the SF while those with dbh ≥ 35 cm were abundant in the OGF, especially in OG2 ($\chi^2$ = 121.003, p = 0.000). The density of trees in the first classes of diameter was decreasing in the populations of the dominant species in secondary forests; therefore their diameter distributions were left skewed (Figures 4f, 4g, 4h). The diameter structure of *A. leiocarpa* was bell-shaped, while those of *L. sericeus* showed some deficits of trees in the first class.

**Table 1:** Floristic diversity of trees with dbh ≥ 10 cm in Lama forests.

| Parameters | SF1 | SF2 | SF3 | OG1 | OG2 |
|---|---|---|---|---|---|
| $s$ (ha$^{-1}$) | 12 | 13 | **16** | 14 | 11 |
| $S$ | 37 | 32 | **36** | 19 | 15 |
| $N_F$ | 22 | 20 | **23** | 13 | 9 |
| *H'(bits)* | 1.22 | 2.01 | **1.89** | 2.61 | 2.42 |
| *Eq* | 0.341 | 0.538 | **0.473** | 0.697 | 0.710 |
| *Fisher's α* | 2.36 | 2.98 | **3.50** | 3.20 | 2.30 |

$s$ = number of species sampled per hectare; $S$ = species richness of the whole forest; $N_F$ = the number of taxonomic families, $H'$= Shannon index, $Eq$ = Pielou's eveness; SF1: Secondary Forest of *L. sericeus* and *C.* pentandra; SF2: Secondary Forest of *L. sericeus* and *A. leiocarpa*; SF3: Secondary Forest of *L. sericeus* and *A. zygia*; OG1: Old-growth forest of *D. guineense* and *D. mespiliformis*; OG2: Old-growth forest of *D. guineense* and *A. africana.*

**Table 2:** Importance value index of species in secondary and old-growth forests of Lama**.**

| Parameters | SF1 | SF2 | SF3 | OG1 | OG2 |
|---|---|---|---|---|---|
| *L. sericeus* | **1.56** | **0.32** | **1.15** | **0.18** | 0.03 |
| *C. pentandra* | **0.37** | **0.36** | **0.29** | 0.06 | **0.14** |
| *A. zygia* | **0.18** | **0.16** | **0.38** | **0.10** | 0.00 |
| *Ficus spp* | **0.13** | 0.03 | **0.22** | 0.00 | 0.00 |
| *D. mespiliformis* | 0.08 | 0.09 | **0.10** | **0.51** | **0.56** |
| *D. guineense* | 0.05 | **0.12** | 0.07 | **0.89** | **0.87** |
| *A. africana* | 0.03 | 0.02 | 0.03 | **0.24** | **0.45** |
| *A. leiocarpa* | 0.03 | **1.12** | 0.01 | **0.14** | 0.00 |
| *C. brownii* | 0.02 | 0.00 | 0.00 | **0.16** | **0.21** |
| *D. rotundifolia* | 0.02 | **0.11** | 0.05 | 0.06 | 0.00 |
| *M. andongensis* | 0.02 | 0.00 | 0.02 | **0.19** | **0.20** |
| *D. floribunda* | 0.00 | 0.07 | 0.01 | **0.11** | **0.28** |
| *K. senegalensis* | 0.05 | 0.01 | **0.12** | 0.00 | 0.00 |
| *Others enrichment species* | 0.02 | 0.00 | **0.13** | 0.00 | 0.00 |

Only species with IVI ≥ 0.01were presented in this table. SF2: Secondary Forest of *L. sericeus* and *A. leiocarpa*; SF3: Secondary Forest of *L. sericeus* and *A. zygia*; OG1: Old-growth forest of *D. guineense* and *D. mespiliformis*; OG2: Old-growth forest of *D. guineense* and *A. africana.*

**Table 3:** Regeneration densities of main pioneer, non-pioneer and enrichment species in SF and OGF

| Species | SF1 | SF2 | SF3 | OG1 | OG2 | Prob. |
|---|---|---|---|---|---|---|
| *A. zygia* | 0 | 5 | 1 | 0 | 0 | 0.051 |
| *A. leiocarpa* | 0 | 5 | 2 | 13 | 0 | 0.094 |
| *C. pentandra* | 3 | 3 | 1 | 0 | 0 | 0.689 |
| *L. sericeus* | 32 | 18 | 25 | 25 | 6 | 0.303 |
| *A. Africana* | 0 | 0 | 0 | 31b | 6a | 0.000 |
| *D. guineense* | 14ab | 22b | 3a | 188c | 113c | 0.000 |
| *D. mespiliformis* | 8a | 26ab | 6a | 38b | 31b | 0.005 |
| *H. grandis* | 9 | 0 | 17 | 0 | 0 | 0.051 |
| *K. grandifolia* | 1 | 0 | 8 | 25 | 0 | 0.243 |
| *K. senegalensis* | 15a | 3a | 39ab | 31ab | 0 | 0.011 |

SF1: Secondary Forest of *L. sericeus* and *C.* pentandra; SF2: Secondary Forest of *L. sericeus* and *A. leiocarpa*; SF3: Secondary Forest of *L. sericeus* and *A. zygia*; OG1: Old-growth forest of *D. guineense* and *D. mespiliformis*; OG2: Old-growth forest of *D. guineense* and *A. africana.* For a species, values followed by the same letter are not significantly different at p = 0.05 ; a < b < c

**Table 4:** Structural characteristics of Lama forests.

| | N (trees.ha$^{-1}$) | | Dg (cm) | | G(m².ha$^{-1}$) | |
|---|---|---|---|---|---|---|
| | **Mean** | **CV%** | **Mean** | **CV%** | **Mean** | **CV%** |
| SF1 | 312b | 18.7 | 22.9a | 12.54 | 12.56a | 17.30 |
| SF2 | 244a | 29.3 | 26.0ab | 9.93 | 12.63a | 25.81 |
| SF3 | 298b | 18.8 | 23.6a | 9.27 | 13.28a | 20.67 |
| OG1 | 229ab | 47.7 | 28.2ab | 12.35 | 13.79a | 36.56 |
| OG2 | 270ab | 17.54 | 31.9c | 8.42 | 21.20b | 8.79 |
| Prob. | 0.002 | - | 0.000 | | 0.000 | |

N = density; G = basal area; Dg = mean diameter; CV = coefficient of variation; Values followed by the same letters in the same column are not significantly different at p = 0.05; a < b < c

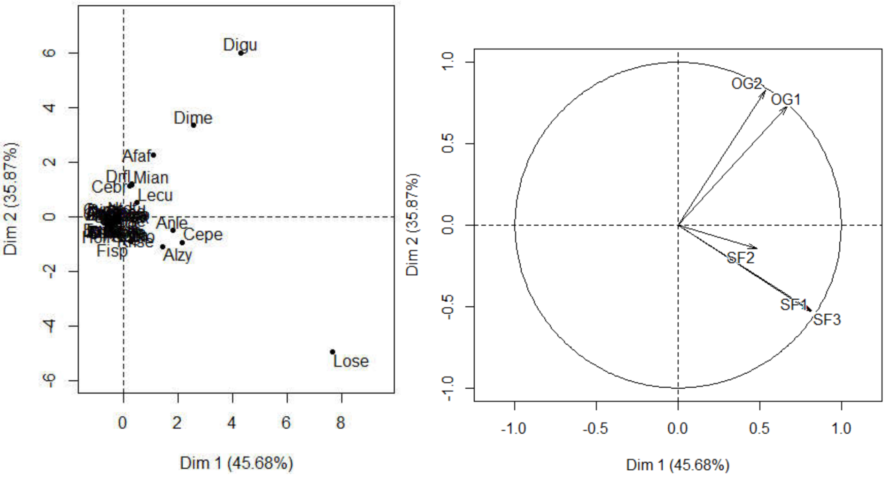

**Figure 1:** Floristic composition of Lama secondary and old-growth forests.

Afaf = *A. africana*, Alzy = *A. zygia*, Anle = *A. leiocarpa*, Cebr = *C. brownii*, *Cepe=C. pentandra,* Digu = *D. guineense*, Dime = *D. mespiliformis*, Drfl = *D. floribunda*, Fisp = *Ficus spp,* Lecu = *Lecaniodiscus cupanioides*; Losu=*L. sericeus,* Mian = *M. andongensis*. SF1: Secondary Forest of *L. sericeus* and *C. pentandra*; SF2: Secondary Forest of *L. sericeus* and *A. leiocarpa;* SF3: Secondary Forest of *L. sericeus* and *A. zygia;* OG1: Old-growth forest of *D. guineense* and *D. mespiliformis;* OG2: Old-growth forest of *D. guineense* and *A. africana.*

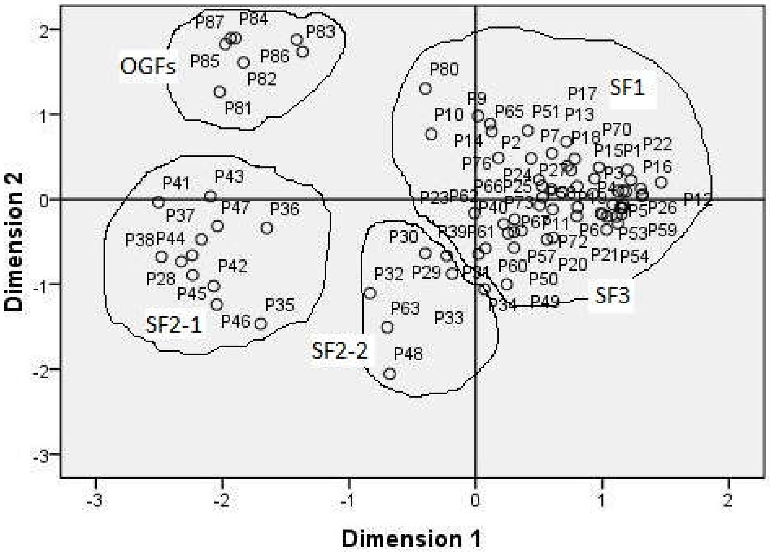

**Figure 2:** Analysis of the trajectory of recovery in SF.

SF1: Secondary Forest of *L. sericeus* and *C. pentandra*; SF2: Secondary Forest of *L. sericeus* and *A. leiocarpa;* SF3: Secondary Forest of *L. sericeus* and *A. zygia;* OG1: Old-growth forest of *D. guineense* and *D. mespiliformis;* OG2: Old-growth forest of *D. guineense* and *A. africana*

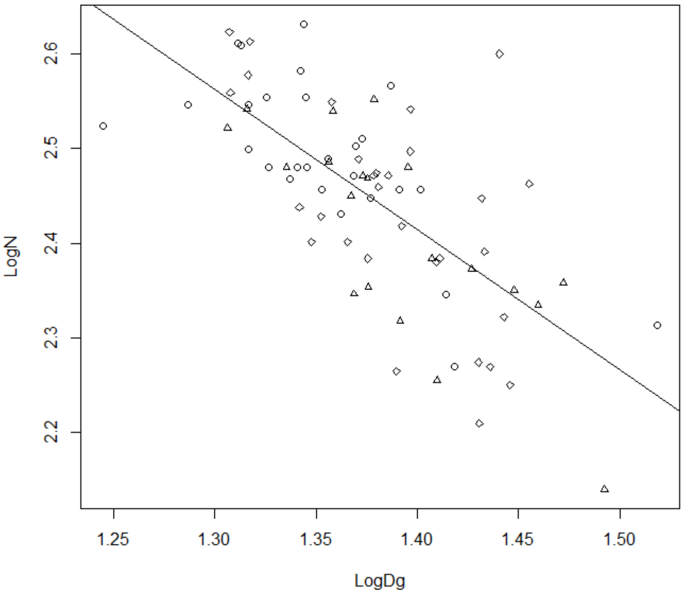

**Figure 3:** Evolution of density according to tree-growth.

N= density, Dg = mean diameter but LogN=4.49 – 1.48LogDg

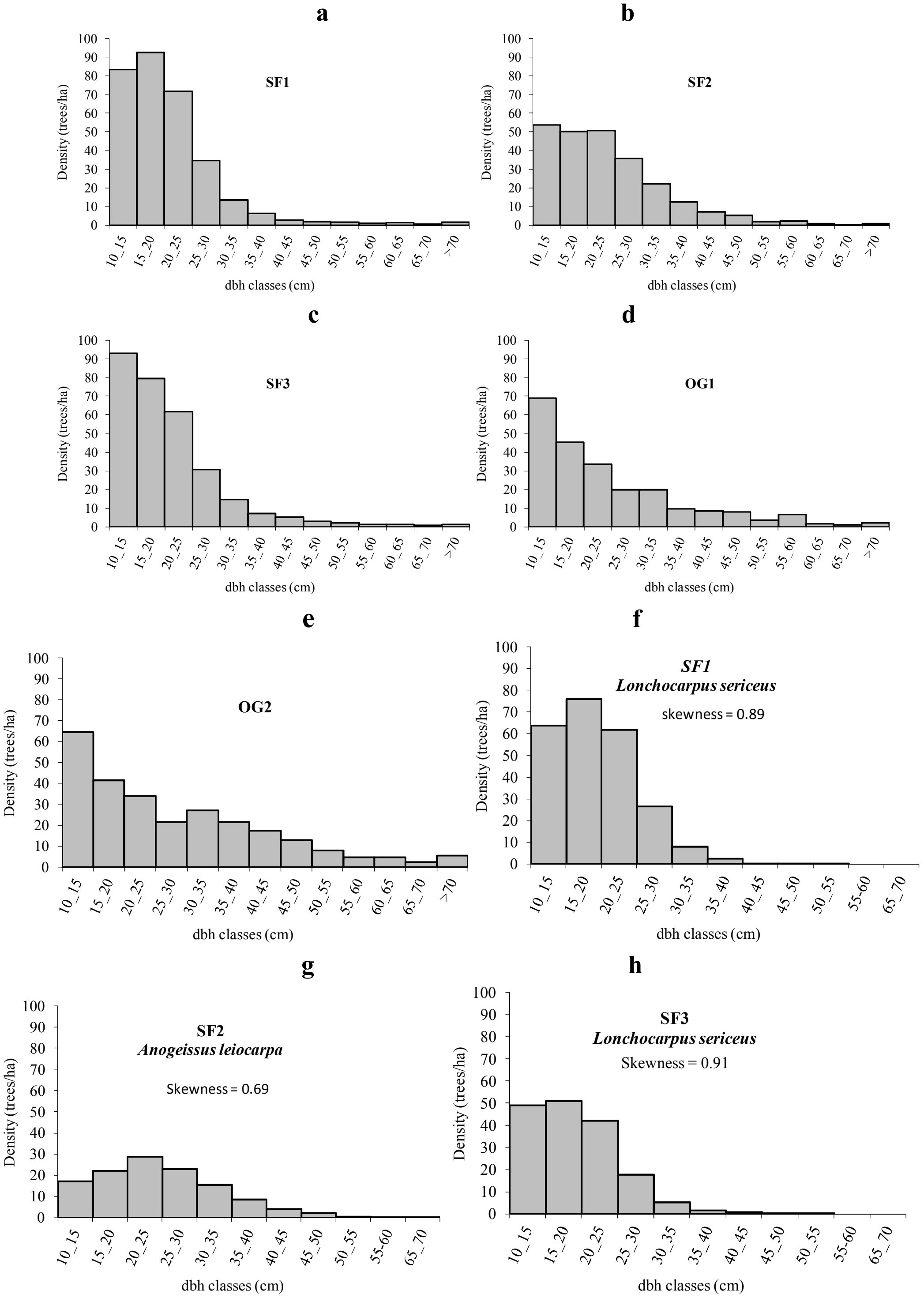

**Figure 4:** Diameter structures of SF, OGF and the pioneer species with the highest IVI in SF.
SF1: Secondary Forest of *L. sericeus* and *C. pentandra;* SF2: Secondary Forest of *L. sericeus* and *A. leiocarpa;* SF3: Secondary Forest of *L. sericeus* and *A. zygia;* OG1: Old-growth forest of *D. guineense* and *D. mespiliformis;* OG2: Old-growth forest of *D. guineense* and *A. africana;* s = Skewness.

## DISCUSSION

### Secondary forests of Lama recover species richness, not species composition

The forests of Lama share almost the same species: few species were common at all stages of vegetation and the others were rare. All species found in SF were also recorded in the OGF except *Cynometra megalophylla* which occurs near ponds in the Lama forest reserve (ONAB, 2011), and *Cedrella odorata* an exotic species introduced in the forests. However, the Fisher's α values were too low to state that there were many rare species. Indeed, the Fisher's α gave importance to rare species (Magurran, 2004). The value was highest in SF3 due to enrichment species. The number of species recorded in the SF is higher than those of OGF. They are composed of a mix of pioneer light-demanding species of the early successionnal stages of vegetation, and shade-tolerant species of the late developmental stages. Therefore, the Lama SF recovers the diversity of the OGF. In well diversified forests of Central Africa, Kenfack et al. (2007) and Gourlet-Fleury et al. (2012) found Fisher's α > 30 and this corresponded to richness of more than 87 species ha$^{-1}$ against 12 to 16 species ha$^{-1}$ in Lama forest. Moreover, in the highlands of Lebialem (Bangang forest, Western Cameroun), a 48 to 72 species per ha and a maximal diversity ($2.97 < H' < 5.80$ bits and $0.52 < Eq < 0.96$) was observed by Tiokeng et al. (2015). Therefore Lama forests are less diversified than those of Central Africa. Higher diversity, in less-disturbed vegetation, is determined by niche variability and therefore the variability of biotic and abiotic factors favorable to the development of several species (Tiokeng et al., 2015). Among the abiotic factors, soil properties affected the establishment of tree species (Olatunji et al., 2015), and it may be the case due to the vertisols (black-cotton ill drained soil) in Lama forest. In SF, our results support those of Makana and Thomas (2006) who also observed good recovery of the diversity of SF in Ituri (Democratic Republic of Congo) because of edge effects, relatively low diversity of the primary forests, and the age since abandonment.

Two main types of SF were identified: the *L. sericeus* dominated forests (SF1 and SF3), and the *A. leiocarpa* dominated forests (SF2). SF1 and SF3 were found in very flooded areas during rainy seasons while SF2, were mostly located at upslope in less hydromorphic areas. Indeed, *A. leiocarpa* is a sudano-guinean species, found in dry forests, savannahs and forest galleries (Couteron and Kokou, 1997; Müller and Wittig, 2002). Therefore, the confinement of *A. leiocarpa* to SF2, though its great dispersal abilities (Anemochorous species), may stem from ecology. Indeed, the settlement of a species in a forest area, depends on its dispersal abilities and ecology (Comita et al., 2007).

Though the presence of OGF species (*D. guineense*, *D. mespiliformis* and *A. africana*), the composition of SF were very different from that of OGF. In Ituri forests, the OGF's vegetation showed different features dominated by several species (Makana and Thomas, 2006). That is not the case for Lama forests with its particular floristic composition dominated by *D. guineense*, *D. mespiliformis* and *A. africana*.

All species of OGF, and therefore all functional groups of OGF species, were found in SF. Pena-Claros (2003) and Breugel et al. (2008) also found, respectively in Bolivia and Mexico, that all functional groups (including shade-tolerant) were present in secondary forests. These authors assume that species assemblages in these secondary forests were consistent with the 'initial floristic composition model'. According to the 'initial floristic composition model', all species arrived in the stand at the beginning of forest recovery, but have different abundances according to the stage of succession, in terms of age of the forest (Egler, 1954; Sheil, 1999). The opposite is the relay floristic model where species arrived in the forest by waves during forests succession (Egler, 1954; Sheil, 1999). In the initial floristic composition model, after canopy closure, shade-tolerant species are favored and therefore the evolution of forests to old-growth stages is enhanced (Pena-Claros, 2003; Breugel et al., 2008). Species assemblages in Lama secondary forests corresponded more to that model.

### Species compositions may evolve towards those of old-growth forests

The ordination of SF plots highlighted two main pathways: a pathway represented by

*L. sericeus* dominated forests (SF1 and SF3), and the second pathway represented by *A. leiocarpa* dominated forests (SF2-1, Figure 1b). However, the SF2-1 group (Figure 1b) could be considered as a third pathway where there was a codominance of *A. leiocarpa* and *L. sericeus*. This third pathway may be related to edge effects for plots located in SF2 at frontier with SF1 or SF3. Steininger (2000) and Mesquita et al. (2001), also identified in Amazon secondary forests, different pathways, each characterized by a dominance of a particular pioneer species, due to past disturbances or ecological characteristics. The OGF represented a unique pathway characterized by a dominance of *D. guineense*.

The pioneer species had weak regenerations in the forests; *A. leiocarpa* in particular failed to regenerate and to recruit with a bell-shaped diameter distribution in SF2. The regeneration of the light demanding species in the secondary forests is constrained by the availability of light. Indeed, pioneer species failed to recruit under their own shade (Bonino and Araujo, 2005). The notion of 'own shade' means both effects of reduction of light and intraspecific competition between trees that leads to density-dependent regeneration, recruitment and mortality (Comita et al., 2010). *D. guineense* and *D. mespiliformis* were the main OGF species regenerating in the SF while *A. africana* had a problem of regeneration in the SF. The importance of light demanding species in OG1 is due to logging history of targeted trees of the forests in the past. Gourlet-Fleury et al. (2012) reported that the importance of pioneer species in M'Baïki primary forest increases with the degree of disturbance (logging and thinning > logging > no disturbance). During the past logging in Lama forest, trees of *A. africana, D. mespiliformis and C. pentandra*… were exploited selectively for commercial purposes. Therefore, the regeneration of OGF species in OG1 was more important, even not significantly higher than that of OG2, because it increases with the availability of light. Makana and Thomas (2006) reported good timber regeneration of both OGF and SF species in Ituri secondary forests (Democratic Republic of Congo) after clearance in contrary to the low regeneration in Lama forest. The combined effect of light availability, invasion by *C. odorata* and flooding could explain the low regeneration noted in Lama forest.

In the initial floristic composition model, after canopy closure, pioneer species failed to recruit, so that shade-tolerant species become more abundant and the evolution of forests to old-growth stages is enhanced (Pena-Claros, 2003; Breugel et al., 2008). Therefore, the composition of SF is likely to evolve to a *D. guineense* and *D. mespiliformis* dominated forest. Regeneration, recruitment, mortality, and longevity of pioneer species determined the rate of conversion of SF to OGF, as demonstrated by Steininger (2000) and Mesquita et al. (2001). Also, the introduction of *K. senegalensis*, very abundant in SF3, may alter the future composition of SF3. Ongoing long-term studies conducted in the Lama secondary forests will provide more information about the future composition of these forests.

### Stocking was far from the OGF's values due to dominance of small pioneer species

Correlation between the SF's structural attributes and their age are not always linear (Chazdon et al., 2007; Kassi N'Dja and Decocq, 2008). The basal areas of Lama SF represented less than 62% of that of OGF. Similar values were found by Pena-Claros (2003) in Bolivia, and Pascarella et al. (2000) for 25 to 30 years of regrowth in Puerto Rico. The basal area and the diameter of OG1 were low maybe because of past-logging. The basal areas and densities of Lama OGF were less than those of the semi deciduous forest of Central Africa (Kenfack et al., 2007; Gourlet-Fleury et al., 2012) and suggested a low stocking of that forest.

The SF of Lama were characterized by abundance of young trees of 10-30 cm dbh, while trees with dbh ≥ 35 cm were abundant in OGF. The difference in basal area between the forests may be supported by the accumulation of trees with dbh ≥ 35 cm in OGF. Therefore, silvicultural actions must be carried out in order to enhance the accumulation of these trees in SF. Deficit in the first classes of dominant light-demanding species, *L. sericeus* and *A. leiocarpa*, suggested that their structure will evolve to bell-shaped curve. Yêhouénou-Tessi et al. (2012) and Agbangla et al. (2015) reported similar structures for light-demanding species, respectively in Itchèdè, Bonou and Niaouli forests in South Benin. However, Assogbadjo et al. (2009) and Sanon et al. (2015) have reported J-reversed shape and good regeneration for *A. leiocarpa* in open forests. Intraspecific competition for light and nutrients at the expenses of small trees (Coomes and Alen, 2008), recruitment of trees in the upper diameter classes, and dispersal barriers of seeds could explain the observed structures. We can also assume that tree growth, expressed by diameter increase, lead to mortality of young trees and decrease in density. Conspecific density-dependent mortality could also explain the low stocking of Lama forest (Uriarte et al., 2004). The relationship between diameter and tree density did not have great predictive power because all SF plots were mixed, but were constituted by species with their own dynamic. The analysis must be done using long term data for each secondary forest. The long term analysis is also the most suitable to determine the developmental phases of the forest (Coome and Alen, 2008). However, competition to the detriment of young trees suggests accumulation of large trees which is consistent with progressive evolution.

## COMPETING INTERESTS

The authors declare that they have no competing interests.

## AUTHORS' CONTRIBUTIONS

The first author set the permanent plot in the Lama secondary forests, collected the data and drafted the present manuscript. The others authors had carefully read and contributed to the present version of the manuscript.

## ACKNOWLEDGMENTS

The authors are also grateful to all people who contributed to data collection.

## REFERENCES

Adler PB, Lauenroth WK. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecological Letters,* **6**: 749-756.

Agbangla MM, Aoudji AKN, Akouehou GS, Gbetoho JA, Sanon K, Ayina O, De Cannière Ch, Ganglo JC. 2015. Caractéristiques structurales et écologiques des populations d'espèces commerciales : une base pour une sylviculture dans les peuplements forestiers de Niaouli (Sud-Bénin). *Tropicultura,* **33**(3): 238-252.

Akoègninou A, Van der Burg WJ, Van der Maesen LJ. 2006. *Flore Analytique du Bénin*. Backhuys Publishers.

Assouma H. 2009. Contribution à la gestion durable des forêts: Caractéristiques écologiques et structurales de la forêt naturelle d'Akpè (Lama) au Sud du Bénin. Thèse d'Ingénieur agronome, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, p. 119.

Assogbadjo AE, Glèlè Kakaï RL, Sinsin B, Pelz D. 2009. Structure of *Anogeissus leiocarpa* Guill. Perr. natural stands in relation to anthropogenic pressure within Wari-Maro Forest Reserve in Benin. *African Journal of Ecology,* **48**: 644-653.

Ayingweu CL. 2003. Sur les aspects écologiques des forêts secondaires en Afrique centrale et occidentale francophone. In Actes : *FAO/UICN Atelier Regional sur la Gestion des Forets Tropicales Secondaires en Afrique Francophone: Realites et Perspectives*, Douala (Cameroun), 17-21 Nov 2003 / FAO, Rome (Italy). Dept. des Forêts, 2004, 43-60.

Bertault JG. 1986. Etude de l'effet d'interventions sylvicoles sur la régénération naturelle au sein d'un périmètre expérimental d'aménagement en forêt dense humide de Côte d'Ivoire. Diplôme d'études doctorales, Université de Nancy, France.

Bonino EE, Araujo P. 2005. Structural differences between a primary and a secondary forest in the Argentine Dry Chaco and management implications. *Forest Ecology and Management,* **206**: 407–412.

Bonou W, Glèlè Kakaï R, Assogbadjo AE, Fonton HN, Sinsin B. 2009. Characterisation of *Afzelia africana* Sm. habitat in the Lama forest reserve of

Benin. *Forest Ecology and Management*, **258**: 1084–1092.

Brown S, Lugo AE. 1990. Tropical secondary forests. *Journal of Tropical Ecology,* **l6**: 1-32.

Gleason HA. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club*, **53**: 7–26.

Chazdon RL, Letcher SG, van Breugel M, Martinez-Ramos M, Bongers F, Finegan B. 2007. Rates of change in tree communities of secondary neotropical forests following major disturbances. *Philosophical Transactions Royal Society B,* **362**: 273-289.

Clark DB, Clark DA. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management,* **137**: 185–198.

Comita LS, Condit R, Hubbell SP. 2007. Developmental changes in habitat associations of tropical trees. *Journal of Ecology,* **95**: 482-492.

Coomes DA, Alen RB. 2007. Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology,* **95**: 27-40.

Corlett RT, Primack RB. 2006. Tropical rainforests and the need for cross-continental comparisons. *Trends in Ecology and Evolution,* **21**: 104-110.

Couteron P, Kokou K. 1997. Woody vegetation spatial patterns in semi-arid savanna of Burkina-Faso. *West African Plant Ecology,* **132**: 211–227.

Dupuy B. 1998. Bases pour une sylviculture en forêt dense tropicale humide africaine. Série FORAFRI, CIRAD-Forêt.

FAO. 2011. Evaluation des Ressources Forestières Mondiales. Rome, Italie.

Finegan B. 1996. Pattern and process in neotropical secondary rain forest: the fist 100 years of succession. *Trends in Ecology and Evolution,* **11** : 119-124.

Ganglo JC. 2004. Phytosociologie appliquée à l'aménagement des forêts : cas du périmètre forestier de Toffo (sud-bénin, département de l'atlantique). Rapport technique. Faculté des Sciences Agronomiques de l'Université d'Abomey-Calavi, Bénin.

Ganglo JC, de Foucault BD. 2006. Plant communities, forest site identfication and classification in Toffo reserve, South-Benin. *Bois et Forêts des Tropiques,* **288**(2) : 25 – 38.

Gourlet-Fleury S, Beina D, Fayolle A, Ouédraogo D-Y, Mortier F, Bénédet F, Closset-Kopp D, Decocq G. 2012. Silvicultural disturbance has little impact on tree species diversity in a Central African moist forest. *Forest Ecology and Management,* **304**: 322–332.

Guariguata MR, Ostertag R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management,* **148**: 185-206.

Hitimana J, Kiyiapa JL, Njunge JT. 2004. Forest structure characteristics in disturbed and undisturbed sites of Mt. Elgon Moist Lower Montane Forest, western Kenya. *Forest Ecology and Management,* **194**: 269-291.

Hounkpèvi A, Yèvidé AS, Ganglo JC, Devineau J-L, Azontondé AH, Adjakidjè V, Agbossou EK, de Foucault B. 2011. Structure et écologie de la forêt à *Diospyros mespiliformis* Hochst. ex A.DC. et à *Dialium guineense* Willd. de la réserve de Massi (la Lama), Bénin. *Bois et Forêts des Tropiques,* **308**(2): 33-46.

Kassi N'Dja J, Decocq G. 2008. Successionnal patterns of plant species and community diversity in a semideciduous tropical forest under shifting cultivation. *BioOne,* **19**(6): 809-820.

Kenfack D, Thomas DW, Chuyong G, Condit R. 2007. Rarity and abundance in a diverse African forest. *Biodiversity and Conservation,* **16**: 2045–2074.

Magurran AE. 2004. Measuring Biological Diversity. Blackwell, Oxford.

Makana JR, Thomas SC. 2006. Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. *Biodiversity and Conservation,* **15**: 1375–1397.

Mesquita RCG, Ickes K, Ganade G, Williamson GB. 2001. Alternative successionnal pathways in the Amazon Basin. *J. Ecol.,* **89**: 528–537.

Müller J, Wittig R. 2002. L'état actuel du peuplement ligneux et la perception de sa dynamique par la population dans le Sahel burkinabé – présente à l'exemple de Tintaboora et de Kollangal Alyaakum. Etudes sur la Flore et la végétation du Burkina Faso et des Pays Avoisinants, 6 : 19–30.

Nishimura S, Yoneda T, Fujii S, Mukhtar E, Kanzaki M. 2008. Spatial patterns and habitat associations of Fagaceae in a hill dipterocarp forest in Ulu Gadut, West Sumatra. *Journal of Tropical Ecology*, **24**: 535-550.

Olatunji OA, Oke SO, Isola EF, Akinyemi DS, Omodara AA. 2015. Relationship between the standing vegetation, soil properties and soil seed bank of an industrially degraded vegetation of Iron Smelting Factory. *Int. J. Biol. Chem. Sci.,* **9**(2): 614-632.

ONAB. 2011. Plan Directeur d'Aménagement et de Gestion du Noyau Central de la Forêt Classée de la Lama 2011-2020.

Pascarella JB, Aide TM, Serrano MI, Zimmerman JK. 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. *Ecosystems,* **3**: 217–228.

Peet RK, Christensen NL. 1987. Competition and tree death. Bioscience, 37: 586–595.

Peña-Claros M. 2003. Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica,* **35**: 450–461.

Peña‐Claros M, Poorter L, Alarcòn A, Blate G, Choque U, Fredericksen TS, Justiniano MJ, Leaño C, Licona JC, Pariona W, Putz FE, Quevedo L, Toledo M. 2012. Soil effects on forest structure and diversity in a moist and a dry tropical forest. *Biotropica,* **44**(3): 276–283.

Sanon Z, Hien M, Yameogo JT, Bachmann Y, Somda I. 2015. Dynamique structurale des îlots de forêt claire à *Anogeissus leiocarpa* (DC.) Guill. et Perr. dans le Sud-Ouest du Burkina Faso. *Int. J. Biol. Chem. Sci.,* **9**(2): 847-860.

Sheil D. 1999. Developing tests of successionnal hypotheses with size-structured populations and an assessment using long-term data from a Ugandan rain forest. *Plant Ecol.,* **140**:117-127.

Sokpon N. 1995. Recherche écologique sur la forêt dense semi-décidue de Pobè au Sud-Est du Bénin : Groupements végétaux, structure, régénération naturelle et chute de litière. Thèse de Doctorat, Université Libre de Bruxelles, 365p.

Steininger M K. 2000. Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *J. Trop. Ecol.,* **16**: 689–708.

Tiokeng B, Mapongmetsem P-M, Nguetsop VF, Tacham WN. 2015. Biodiversité floristique et régénération naturelle sur les hautes terres de Lebialem (Ouest Cameroun). *Int. J. Biol. Chem. Sci.,* **9**(1): 56-68.

Uriarte M, Canham CD, Thompson J, Zimmerman JK, Brokaw N. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density dependence and the spatial distribution of parent trees. *Journal of Ecology,* **93**: 291–304.

Vayreda J, Gracia M, Martinez-Vilalta J, Retana J. 2013. Patterns and drivers of regeneration of tree species in forests of peninsular Spain. *Journal of Biogeography,* **40** : 1252–1265.

Yêhouenoutessi DR, Akouèhou GS, Ganglo JC. 2012. Caractéristiques structurales et écologiques des populations de *Antiaristoxicaria*(Pers.) Lesch et de *Ceibapentandra*(L.) Gaertn dans les forêts reliques du Sud-Benin. *Int. J. Biol. Chem. Sci.,* **6**(6) : 5056-5067.